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# INTERNATIONAL SOCIETY OF HYMENOPTERISTS

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

**This issue was mailed 22 August 1996**

# NOTICE

Beginning in 1997, the Journal of Hymenoptera Research will be published twice per year, the issues appearing in April and October.

The deadline for receipt of manuscripts is **1 October** for the April issue and **1 April** for the October issue.

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**Results of Recent Elections for Officers, 1997–2000
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# ADVANCED NOTICE

## International Society of Hymenopterists

## Fourth International Conference

### Canberra, Australia
### January 6–11, 1999

Following the highly successful Third International Conference held in 1995 at the University of California, Davis, the Fourth International Conference will be held at the Australian National University, Canberra. It will follow shortly after the 13th International Congress of the International Union for the Study of Social Insects (IUSSI) which will be held in Adelaide, December 29, 1998 to January 4, 1999.

Complete information will be available by the end of this year from the organising committee chaired jointly by I. D. Nauman and A. D. Austin. The conference address for further contacts is:

4th Conference, International Society of Hymenopterists
c/o CSIRO, Division of Entomology
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Canberra, ACT 2601, Australia
Fax: 61-6-246-4264     E-mail: iann@ento.csiro.au

# Biodiversity of Wasp Species (Insecta: Hymenoptera) in Burned and Unburned Habitats of Yellowstone National Park, Wyoming, USA

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*Abstract.*—Four months of Malaise trapping in two burned and unburned habitats, 2 yr after the 1988 fires in Yellowstone National Park (YNP), resulted in a total of 603 species from 36 families of Hymenoptera. The majority of the species were Ichneumonoidea (60%). The unburned habitats peaked at 107 and 113 species during a 2-week sampling period, while the corresponding burned habitats had maxima of 88 and 90 species. Hymenopteran species diversity (Shannon-Wiener) was primarily a function of richness, with evenness differing only slightly between habitats (range 78–98%). Diversity and richness in burned sites were generally 75–85% of the values in unburned sites. The two burned habitats had greater community similarity (23.5 ± 4.6%) than that found between adjacent burned and unburned habitats at either site (13.8 ± 1.9%). The unburned habitats had relatively low community similarity (12.4 ± 5.4%), indicating a surprisingly high degree of between-patch endemism in mature lodgepole pine forests. This endemism also suggests the possibility that species may have been extirpated from some burned habitats in YNP. Comparison of trophic associations, including inference of relative (ordinal) host abundance from parasitoid abundance, indicate that burned habitats were dominated by herbivores of nonwoody plants and unburned habitats are characterized by fungivores and detritivores. These findings are consistent with observations that burned sites were typified by the establishment of grasses and forbs and the loss of litter, which would have been concomitant with a deceleration of arthropod- and fungal-mediated organic decomposition. There was no evidence of dead wood having provided a major source of nutrients for insects in burned habitats, and there was no evidence of insect outbreaks in the region of our trap sites.

## INTRODUCTION

The 1988 fires in Yellowstone National Park (YNP), Wyoming, USA, burned 400,000 ha or 45% of the park (Christensen *et al.* 1989). Knight and Wallace (1989) predicted that overall species richness would gradually increase over a period of 25 yr, eventually surpassing that of the old growth forest prior to the fires. They also noted that some species (e.g., bark beetles) would likely outbreak shortly after the fire. The reliability of these forecasted dynamics is contingent upon the similarity of fires investigated in previous research (Taylor 1969, 1973, 1974; Taylor and Barmore 1980; Knight 1987) to those that occurred in 1988. Although some evidence

suggests that extremely large-scale fires have been part of the history of YNP (Christensen *et al.* 1989), catastrophic fires of the magnitude seen in 1988 have never been studied. In this context it is important to consider that striking qualitative changes in ecological conditions and processes may result from increasing (or decreasing) the scale of reference (Allen and Hoekstra 1992).

Before the 1988 fires, managers anticipated the development of a new biotic community immediately following a burn, with insects quickly utilizing the new food sources provided by the freshly killed trees (Despain 1978). Based on experience with smaller fires, it was posited that few vertebrates and no species, were lost in

the 1988 fires (Christensen *et al.* 1989, Schullery 1989, Skinner 1990). While some insect populations were undoubtedly reduced by the fires, there were several observations that suggested that insects were recovering within a year (McEneaney [YNP Ornithologist] *in* Carr 1990, Skinner 1990, Varley [YNP Chief of Research] *in* Jeffery 1990), and anecdotal evidence indicated possible outbreaks of species capable of exploiting fire-damaged trees (Romme and Despain 1989, Skinner 1990). Qualitative observations indicated that the rate of recolonization for some taxa was extraordinarily rapid. Skinner (1990) reported finding black bears feeding on abundant, large wood wasps while they oviposited in the smoldering stumps, and Lewin (1988) forecasted a resurgence of insects exploiting the new growth of grasses and herbs. Such evidence was extended into a more general prediction that biodiversity was or would be enhanced by the fires (Knight and Wallace 1989, Romme and Despain 1989, Varley *in* Jeffery 1989, 1990). Conversely, Elfring (1989) and Conniff (1989) warned that reported recovery rates were overestimated (Elfring 1989, Conniff 1989).

The observations and predictions regarding the recovery of fire-adapted and other insect species form an important and compelling basis for developing and testing ecological hypotheses. However, the controversy surrounding competing claims of ecological recovery persists largely due to a lack of quantitative ecological data. Despite the intriguing observations of insect fauna, there are no published data related to the post-fire terrestrial insect fauna of YNP. There have only been about a dozen published studies of entomological research within the Park in the last 20 yr, and the only relevant, quantitative data were restricted to the litter habitat (Lavigne *et al.* 1990). Indeed, the insect fauna of YNP has been estimated to range from 12,000 to "tens of thousands" of species (Clark *et al.* 1989), the vast majority

(>95%) of which were not documented prior to the fires. As Minshall *et al.* (1989) noted, a more complete faunal database and systematic sampling are essential in assessing the impacts of the fires to the biodiversity of YNP (Christensen *et al.* 1989, Schullery 1989, Roemhild 1994). Simply put, without empirical data it is not possible to assess predictions of the rate and form of ecological recovery.

The central questions related to the short-term effects of the YNP fires on biodiversity are: 1) has species diversity, richness, or evenness increased in the time since the fires, 2) are any species found only in burned areas (suggesting the potential for enhanced richness or diversity) or unburned areas (suggesting the possibility of extirpation from YNP), and 3) have there been any insect outbreaks of fire-adapted species? Initial studies demonstrated that in the 2 yr following the fires insect species diversity in the litter habitat were almost invariably reduced in burned locations relative to unburned sites, although diversity consistently increased in burned sites from 1989 to 1990 (Lavigne *et al.* 1990). Because extrapolating from this habitat to the forest ecosystem is problematical, we undertook an intensive study of the Hymenoptera as an indicator taxon (*sensu* Cook 1976, Sheehan 1984, Munn 1988, Hawksworth and Ritchie 1993) in 1990.

The Hymenoptera were chosen as the indicator of biodiversity because: 1) they are easy and cost-effective to collect, 2) the parasitic species rely on a wide spectrum of herbivorous hosts, 3) the parasitoids of herbivorous insects provide an indirect but effective measure of biodiversity of this lower trophic level and the condition of the vegetative community, and 4) one of us (SRS) is a hymenopteran systematist, facilitating identification work [see Noss (1990), Spellerberg (1991), and Hawksworth and Ritchie (1993) for more complete descriptions of the desired qualities of a biodiversity indicator taxon]. Logisti-

cal, financial, and regulatory limitations restricted our study to a single year of intensive data collection, 2 yr after fires, so we adopted the strategy of comparing adjacent burned and unburned areas to address the effects of the fires and the nature of the recovery.

## MATERIALS AND METHODS

Two sites in Yellowstone National Park were chosen for setting pairs of Townes-style Malaise traps (approximately 2 × 2 × 2 m; Golden Owl Publishers, Lexington Park, MD). The number of sites and traps was limited by logistical and resource constraints and YNP policies regarding the frequency and intensity of trap monitoring. These sites represented different fires within YNP (which merged into the Snake River fire complex) and therefore functioned as true replicates. The northern sites included a burned habitat and an unburned (control) habitat, 5.4 and 5.8 km, respectively, from the South Entrance to the Park. The southern sites included a severely burned habitat and an unburned (control) habitat, 4.0 and 2.3 km from the South Entrance. Control habitats were selected to represent topographic and presumed vegetative characteristics of the burned areas prior to the fires. Malaise trapping is highly efficient but may be influenced by the local conditions, so trap positioning and microhabitat conditions were replicated as precisely as possible between sites. As such, physical proximity was secondary to the ecological characteristics.

The traps were in adjacent burned and unburned areas, about 500 m from the edge of the burn. Traps were first set during the last week of May, 1990. Owing to YNP regulations that traps be constantly "attended", they could only be left in place for 2-wk intervals. Insects were collected from the traps on June 10 and 14, July 7 and 14, August 11 and 19, and September 7. Traps were damaged by weather, wildlife, or vandals on five occasions,

resulting in missing data (northern burned site on July 7; southern unburned site on July 14; northern burned, northern unburned, and southern burned sites on September 7). The collections were stored in 70% ethanol and returned to the laboratory where the Hymenoptera were separated. The Hymenoptera were prepared, identified to subfamily (in some cases genus, and occasionally species), and sorted to morphospecies. Voucher specimens of all morphospecies are deposited in the Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie.

We examined the hymenopteran community structure from the perspectives of diversity, evenness, and richness (Kotila 1986). As with all sampling methods, Malaise traps are biased in the groups that they collect (e.g., primarily small insects flying <2 m above ground level (Matthews and Matthews 1971, Darling and Packer 1988)). However, the application of diversity indices to selected portions of a biotic community (e.g., Kappelle et al. 1995) is appropriate as long as the results are interpreted in the context of the constraints of the sampling methodology (Southwood 1978).

Diversity (a measure of both the abundance and equitability of species) was expressed using the Shannon-Wiener index (H) (Southwood 1978). This measure was chosen because: 1) it is normally distributed (Taylor 1978), 2) it is more appropriate than the Simpson-Yule index, which is strongly influenced by the underlying distribution for samples with more than 10 species (May 1975), 3) it was more appropriate than the Berger-Parker index because there were several cases of co-dominant species, 4) it is dependent on both evenness and richness (Magurran 1988), and 5) it is perhaps the most commonly encountered index in the literature (Magurran 1988, Spellberg 1992) and was used in the analysis of litter arthropod communities after the YNP fires (Lavigne

*et al.* 1990). The disadvantages of using **H** are that the index is a purely relative measure, without absolute meaning [as opposed to the Simpson-Yule index (Southwood 1978)], but we were particularly interested in comparisons between communities from burned and unburned habitats, so the relativity of this index was not problematical. In addition, **H** is not sensitive to the character of the ratio of species to individuals and it is dominated by the abundant species (May 1975), but these qualities did not constitute disadvantages in the context of our application.

Having chosen **H** as the measure of diversity, we used the Shannon-Wiener index of evenness (Kotila 1986). This measure is the ratio of the maximum value of **H** (assuming that the individuals were evenly distributed among the species) to the realized value of **H**. As such, this measure of evenness ranges from 0.0 to 1.0.

We expressed the species richness as the number of species. Although this measure has the clear advantage of simplicity, it has the disadvantage of oversensitivity to numerically rare species. Findley (1973) and Hendrickson and Ehrlich (1971) have criticized restricting expressions of diversity to the number of species present while failing to consider the forms and functions of the species. However, our assessment of species richness avoids this pitfall in that we employed concomitant analyses of diversity and we have a good understanding of the ecological functions of the species in the taxon of interest. Given the sampling constraints, the use of numerical species richness is appropriate (Magurran 1988).

We used analysis of variance (MSU-STAT software, version 3.2) to assess differences in the ecological measures (diversity, evenness, richness) between burned and unburned habitats; an arc sine transformation was applied to evenness (Snedecor and Cochran 1980). Measures from the sites representing each habitat type (burned and unburned) were pooled into

three time blocks: spring (before 21 June, $N = 4$), early summer (between 21 June and 1 August, $N = 3$) and late summer (after 1 August, $N = 4$), so as to allow an equal number of data points in each block and eliminate the confounding effects of phenology.

To assess the taxonomic overlap between habitats and sites (i.e., community similarity), we used a direct calculation of percent similarity (Kotila 1986). This measure of similarity provides results consistent with other common expressions [e.g., Jaccard's coefficient (Christiansen *et al.* 1990)], which give equal weight to all species and therefore tend to place excessive significance on rare species (Southwood 1978). In our study, rare species are conceptually very important, so overemphasizing their contribution to the community was not considered a serious shortcoming. Some coefficients of similarity take relative abundance into consideration (e.g., Bray and Curtis 1957), but these approaches have other shortcomings (Austin and Orloci 1966).

To understand how the entire community structure of the burned and unburned habitats differed, where possible, we classified the Hymenoptera into trophic categories based on the lowest taxonomic level of identification (Borror et al. 1989). Clearly, there are exceptions to these general categories, but this approach was consistently applied across all samples and allowed us to make reasonable inferences about trophic structure in the community, including those elements that were not directly sampled (e.g., plants, non-hymenopteran herbivores, fungivores, etc.). Because the missing samples were balanced between burned and unburned samples and represented similar times of year, we were able to validly pool the available data across dates and sites to avoid the problem of low sample sizes in generating an overall expression of community structure in burned and unburned habitats. Analysis of trophic associations in burned

and unburned habitats was performed using chi-square tests (Siegel 1956).

## RESULTS

The Malaise trap samples yielded a total of 2,331 hymenopteran specimens, representing 603 species (morphospecies) from 36 families (Table 1). The majority of the species were Ichneumonoidea (60%); Chalcidoidea comprised 16% of the species, and Proctotrupoidea made up 9% of the species. The aculeate Hymenoptera comprised only 10% of the species.

Species diversity increased sharply from early June through July and then gradually increased until September in all sites (Fig. 1). The sharp drop in diversity across all sites on the second sampling date was associated with an unusual cold front that caused snow at both sampling sites. The values and dynamics of species diversity in burned and unburned habitats were remarkably similar between sites. At both sites, the species diversity in burned habitats was generally lower than in unburned habitats throughout the summer, although the indices converged in late August or September. Diversity did not differ significantly ($F \leq 1.02$, $P > 0.30$) between burned and unburned sites in spring or late summer, but diversity was significantly ($F = 5.68$, $P = 0.07$) greater in unburned habitats in early summer.

The changes in species diversity appear to have been largely a function of species richness (Figs. 2). As with the trends in diversity, the number of hymenopteran species was significantly ($F = 7.74$, $P = 0.05$) greater in unburned habitats in early summer, with no significant ($F \leq 0.52$, $P \geq 0.50$) differences in other time periods. Richness generally increased throughout the summer. At site 1, the number of species in the unburned habitat increased rapidly in the first 6 wk of the survey, while the species richness in the burned habitat increased most rapidly later in the summer. At site 2, species richness increased at a relatively constant rate in both

Table 1. Species richness of Hymenoptera from Yellowstone National Park, 2 yr after the 1988 fires (taxa are arranged in descending order of species richness)

| Taxon | Number of species | | |
|---|---|---|---|
| Apocrita | 596 | | |
| Ichneumonoidea | | 362 | |
| Ichneumonidae | | | 253 |
| Braconidae | | | 109 |
| Chalcidoidea | | 96 | |
| Pteromalidae | | | 40 |
| Torymidae | | | 14 |
| Eulophidae | | | 11 |
| Encyrtidae | | | 8 |
| Mymaridae | | | 7 |
| Eupelmidae | | | 6 |
| Eurytomidae | | | 3 |
| Eucharitidae | | | 1 |
| Perilampidae | | | 1 |
| Trichogrammatidae | | | 1 |
| unidentified | | | 5 |
| Proctotrupoidea | | 55 | |
| Diapriidae | | | 46 |
| Proctotrupidae | | | 5 |
| Platygastridae | | | 2 |
| Scelionidae | | | 2 |
| Sphecoidea | | 19 | |
| Sphecidae | | | 19 |
| Apoidea | | 18 | |
| Halictidae | | | 9 |
| Anthophoridae | | | 3 |
| Megachilidae | | | 3 |
| Apidae | | | 2 |
| Andrenidae | | | 1 |
| Formicoidea | | 16 | |
| Formicidae | | | 16 |
| Cynipoidea | | 14 | |
| Cynipidae | | | 1 |
| unidentified | | | 13 |
| Chrysidoidea | | 6 | |
| Chrysididae | | | 3 |
| Dryinidae | | | 2 |
| Bethylidae | | | 1 |
| Ceraphronoidea | | 5 | |
| Megaspilidae | | | 3 |
| Ceraphronidae | | | 2 |
| Pompiloidea | | 2 | |
| Pompilidae | | | 2 |
| Vespoidea | | 2 | |
| Vespidae | | | 2 |
| Tiphioidea | | 1 | |
| Tiphiidae | | | 1 |
| Symphyta | 7 | | |
| Tenthredinoidea | | 4 | |
| Tenthredinidae | | | 3 |
| Argidae | | | 1 |
| Siricoidea | | 2 | |
| Siricidae | | | 2 |
| Megalodontoidea | | 1 | |
| Xyelidae | | | 1 |
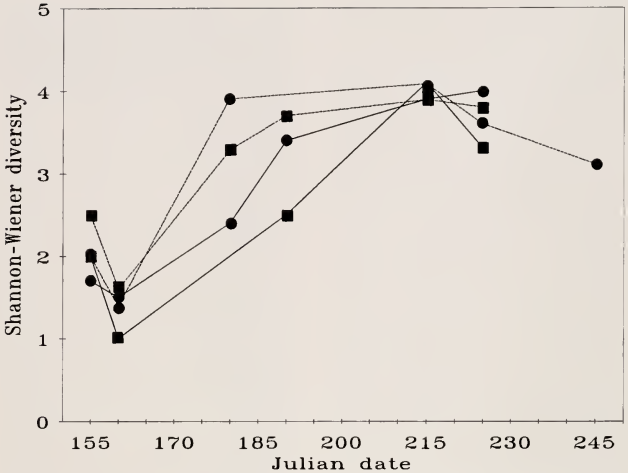
Fig. 1. Shannon-Wiener diversity in unburned (dashed line) and burned (solid line) habitats, at the southern (circles) and northern (squares) sample sites, 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August; 245 = 2 September).

unburned and burned habitats after June. At the end of the summer, the number of species declined in all locations except the burned habitat at site 1. At both sites, more species were found in unburned habitats than in burned habitats throughout July and August. The unburned habitats peaked in 107 and 113 species, while the corresponding burned habitats had maxima of 88 and 90 species.

Species evenness was generally higher in unburned habitat than in burned habitats (Figs. 3). Indeed, unburned habitats had significantly greater ($F = 7.71$, $P = 0.03$) evenness than did burned sites during the spring, but no significant differences were found during the summer ($F \leq 0.25$, $P \geq 0.72$). Except for one sample from the burned habitat at site 1, species

evenness was greater than 80% in all samples. There was a general trend of decreasing species evenness in unburned habitats across the summer, but there was no discernible trend of evenness in burned habitats.

The hymenopteran communities from burned and unburned habitats at both sites were 0 to 20% similar across the summer (Fig. 4). Community similarity of burned and unburned habitats ranged from 0 to 14% at site 1, with a general trend towards increasing similarity with time. At site 2, community similarity ranged from 16 to 20%, with no discernible trend during the summer. The hymenopteran community similarities from the two burned habitats ranged from 5 to 30% throughout the summer. At only one
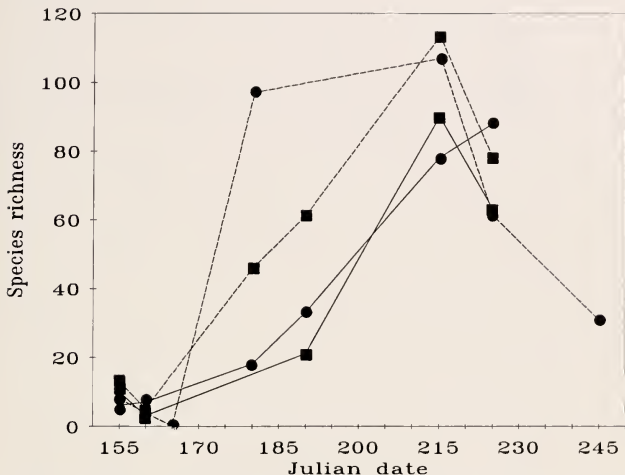
Fig. 2. Species richness in unburned (dashed line) and burned (solid line) habitats, at the southern (circles) and northern (squares) sample sites, 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August; 245 = 2 September).

time was community similarity of the two burned habitats less than that found between the burned and unburned habitats within a site.

The community similarity between the two unburned habitats was consistently lower than between the burned habitats. The unburned habitats had community similarities ranging from 0 to 30%, with higher similarities later in the season. Thus, the similarity between hymenopteran communities in widely separated, burned habitats was greater than that found either between burned and unburned habitats at a single site or between widely separated, unburned habitats.

Analysis of trophic associations in burned and unburned habitats revealed significant differences in community structure ($X^2 = 298.4$, 8 df, $P < 0.0001$; Table 2). In burned habitats parasitoid groups associated with herbivores on or in foliage but not in wood (e.g., Dryinidae, Microgastrinae, Hormiinae, and platygastrids) were significantly more frequent than in unburned habitats ($X^2 = 118.4$, 1 df, $P < 0.0001$). The domination of this trophic group in burned habitats (71% of the hymenopteran fauna) indicated that various grasses and forbs were providing the primary food source. This hypothesis is further substantiated by the significantly higher frequency ($X^2 = 24.8$, 1 df, $P < 0.0001$) of nectar-feeding Hymenoptera in these habitats as well. The herbivores of nonwoody plants and nectar-feeding species comprised only 52% of the hymenopteran community in unburned habitats. In
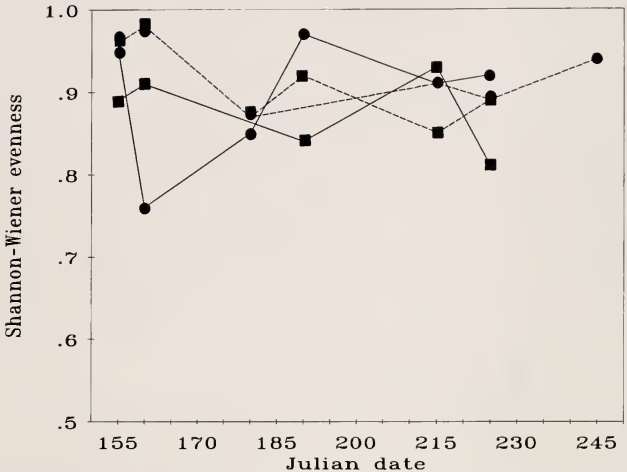
Fig. 3.  Shannon-Wiener evenness in unburned (dashed line) and burned (solid line) habitats, at the southern (circles) and northern (squares) sample sites, 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August; 245 = 2 September).

burned habitats, woody herbivores (i.e., Siricidae) and parasitoids of woody herbivores (e.g., *Dolichomitus imperator* (Kriechbaumer), *Rhyssa alaskensis* (Ashmead), *Triaspsis pissodis* Viereck, *Allodorus crassigaster* (Provancher), and *Odontocolon* sp.) were significantly more frequent ($X^2$ = 43.6, 1 df, $P < 0.0001$) than in unburned habitats, where these trophic associations comprised only 1% of the Hymenoptera. In unburned habitats, parasitoids of fungivores and detritivores (e.g., Diapriidae, Proctotrupidae, Megaspilidae, and Ceraphronidae) were significantly more frequent than in burned habitats ($X^2$ = 200.0, 1 df, $P < 0.0001$). Being the most common trophic association (32%), these parasitoids indicated the importance of forest litter as a food source. These organisms

were infrequently found in burned habitats (9%), suggesting that the litter community and decompositional processes may have been adversely affected by fire.

DISCUSSION

The results of our surveys of hymenopteran species diversity in YNP 2 yr after the fires allow us the first opportunity to address empirically the central issues related to the effects of the fires on terrestrial biodiversity. Our findings 2 yr after the fires are particularly relevant to ecological and management discussions of short-term recovery in YNP (Lewin 1988, Romme and Despain 1989, McEneaney *in* Carr 1990, Skinner 1990, Varley *in* Jeffery 1990). In this context, we believe that the consistency of the data between these sites, the
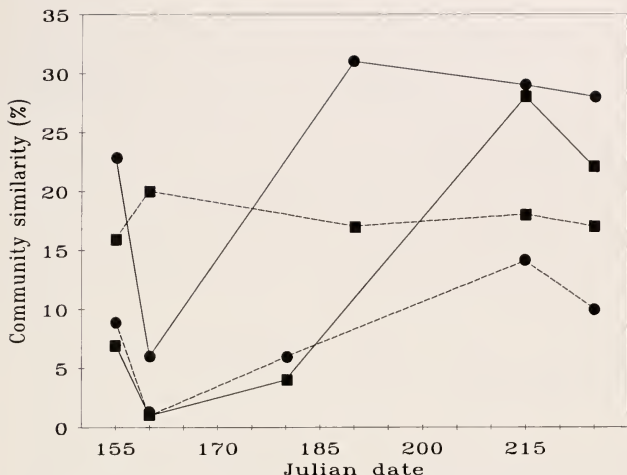
Fig. 4. Community similarity of burned habitats (solid line with circles), unburned habitats (solid line with squares), and burned and unburned habitats within sites (dashed line, southern site = circles, northern site = squares), 2 yr after the fires in YNP (Julian date 155 = 4 June; 185 = 4 July; 215 = 3 August).

quality of the taxonomic data, and the ecological qualities of the indicator taxon allow us to draw some reasonable inferences with respect to the effects of the fire on biodiversity. As previously noted, although Malaise traps, and all other collecting devices, are biased in the groups that they collect, the application of diversity indices to the data is appropriate as long as the interpretation of the analyses is developed in the context of the constraints of the sampling methodology (Southwood 1978). In this light, we can begin to address the three central questions raised previously.

*Has biodiversity increased since the fires?*— Although we do not know what the status of biodiversity was immediately following the fires, we can reasonably infer that few

exposed insect populations survived the severe burns. As such, it would appear that a great number of species have recolonized burned habitats. Indeed, the species diversity and species richness in these habitats reached about 80% of presumed pre-fire levels within 2 yr. Thus, it is evident that substantial recovery of biodiversity has occurred since the fires.

The rapid recovery of biodiversity is not a function of an impoverished insect fauna prior to the fires. The notion that mature lodgepole pine forests are biological deserts (Romme and Despain 1989) is clearly erroneous. The diversity and richness of Hymenoptera in the unburned habitats was 5- to 10-fold greater than that reported for sagebrush habitats in Wyoming (Christiansen *et al.* 1990). If we assume

Table 2.   Trophic associations of Hymenoptera collected from burned and unburned habitats of Yellowstone National Park, 2 yr after the 1988 fires

| Trophic association (representatives) | Percent of sample from habitat (n, individuals) | |
|---|---|---|
| | unburned | burned |
| parasitoid of herbivores on or in foliage (most ichneumonids and braconids) | 51 (750) | 71 (844) |
| parasitoid of herbivores in wood (doryctine and helconine braconids) | 1 (21) | 6 (73) |
| parasitoid of detritivores, fungivores, and other litter associates (diapriids, proctotrupids, orthocentrine ichneumonids, alysiine and opiine braconids) | 32 (464) | 9 (104) |
| nest provisioning predator (sphecids, pompilids, vespids, chrysidids) | 3 (41) | 3 (38) |
| herbivore on or in foliage (tenthredinids, argids, xyelids, eurytomids, cynipids) | 1 (15) | 1 (9) |
| herbivore in wood (siricids) | 0 (1) | 0 (2) |
| nectar-pollen feeder (apoids) | 1 (12) | 4 (42) |
| scavenger (formicids) | 11 (157) | 5 (60) |
| hyperparasitoid (mesochorine ichneumonids) | 0 (5) | 1 (9) |

that Hymenoptera account for 20% of insect species richness based on North American estimates (Schaefer and Kosztarab 1991), then an old-growth lodgepole pine habitat is likely to include 500 to 1,000 insect species. Although the vegetation may appear to approach a monoculture in these habitats, it is evident that the insect communities are diverse and differ markedly between stands. Even if the 20% insect community similarity between old-growth habitats is somewhat underestimated (for a discussion of this issue, see *Are there species unique to burned or unburned habitats?*), the total insect diversity supported in YNP's mature lodgepole pine forests is almost certainly of the order of several thousands of species. In this context it is important to note that the early successional insect communities in spatially disjunct burned habitats were more similar to one another than the communities in unburned habitats. This finding suggests that early successional communities tend to be relatively homogeneous,

and insect communities diverge with forest recovery.

Earlier work has suggested that the greatest diversity of selected plant (herbs, shrubs, and trees) and selected vertebrate (birds and mammals) species is found in young (1 to 25 yr-old) lodgepole pine forests (Taylor 1969, 1973, 1974; Taylor and Barmore 1980). Unfortunately, the species diversity of vertebrates in the 5 yr following a fire was not measured by Taylor (1969, 1973, 1974). However, plant species richness 1 to 3 yr after a burn was 9 to 23% of the maximum, which occurred 25 years after a burn. Bird and mammal species richness 7 to 13 yr after a burn was 65 to 81% of the maximum richness, which also occurred 25 yr after a burn. Species diversity dropped to 46% of the maximum in forests 57 to 111 yr after a burn.

Our data demonstrate that insect (Hymenoptera) biodiversity may recover at a rate similar to that of the plant community. If we assume that the biodiversity of

Hymenoptera tracks that of plants which harbor insects, we would expect the species richness 3 yr after a burn to be 79% of the richness found in a 60- to 100-yr old forest habitat, and our data indicate an 80% recovery. This rate of recovery is also similar to that found for aquatic macroinvertebrates (Minshall *et al.* 1990). The unburned habitats in our study were in forests that were at least 60-yr old and probably more than 100-yr old given that less than 3% of YNP had burned since 1930 (Taylor 1974). Cores from trees 4.2 km north of the South Entrance to YNP were determined to be 161 years old (Taylor 1969).

It should be noted that the 80% recovery does not take into account spatial patterns of diversity. In particular, the communities within the two burned habitats were much more similar to one another than were the communities from the two unburned habitats. As such, there appeared to have been a net loss of biodiversity across sites that was not reflected between habitats within sites.

The general similarities in the rate and pattern of biodiversity following the 1988 fires in the context of Taylor's (1969) research are somewhat surprising given that earlier conclusions were drawn from relatively species-poor groups and small-scale fires. There have been no previous attempts to measure biodiversity with insects, and the greatest recorded species richness of a forest habitat (using herbs, shrubs, trees, birds, and mammals combined over a 2 yr period) was 112 (Taylor 1973), which is one less than the number of hymenopteran species caught in a single trap over a 2-wk period (site 2, unburned habitat, July 14 to August 11). Given this finding and the relative rate of catch per unit effort for various taxa, there is little question that insects are superior indicators of biodiversity with respect to both information value and sampling efficiency (Hawksworth and Ritchie 1993).

We also might have expected differences between our biodiversity measures and those of Taylor (1969, 1973) due to the intensity of the 1988 fires relative to those studied in previous research. Indeed the total area burned by all fires in the YNP from 1930 to 1970 (24,030 ha) is just 6% of the area burned in 1988. However, it should be noted that our samples were taken within 500 m of the edge of the burned sites; sampling closer to the center of the major burns may well have revealed fewer species and slower recovery rates.

*Are there species unique to burned or unburned habitats?*—To address this question, we must first provide an interpretive context for the community measures derived from our study. It is clear that our sampling did not constitute a complete census of the hymenopteran community, so some species were undoubtedly missed in the course of our study. Although measures of endemism are sensitive to sampling intensity (i.e., incomplete sampling may artificially increase the apparent frequency of rare species, thereby reducing community similarity), in our study community similarity did not closely track sample size, suggesting that the frequencies of rare species across time and space were not an artifact of sampling intensity. Moreover, even if a habitat has a high frequency of apparently rare species by virtue of a sampling regime, this bias should be constant across sites so relative differences within our study are informative. Nonetheless, most measures of community similarity overemphasize the importance of rare species (Southwood 1978). Placing relatively greater weight on rare species is only problematical where emphasizing these taxa is undesirable, as may be the case in some ecological studies but not particularly in the context of biodiversity management and conservation in YNP. In light of these issues we can consider whether some species were unique to particular habitats and what this might mean in the context of conservation and management.

The fires evidently reduced hymenopteran diversity primarily through the loss of species (as opposed to decreasing species evenness). The low community similarities between burned and unburned habitats indicated that some species had not recolonized impacted areas in the 2 yr following the fires. In addition, some extraordinarily rare species were found in unburned habitats, including *Loxocephalus boops* (Wesmael), a euphorine braconid, presumed to be a parasitoid of adult ants and one of the rarest (or least often collected) braconids in North America. Given the occurrence of rare species and the low community similarities between unburned habitats at different sites, it appears that there is considerable habitat-level endemism among insect communities in lodgepole pine forests. Considering these factors in light of the scale of the 1988 fires, it is likely that species were locally extirpated, and it is possible that some species were extirpated from the Park. However, true extinctions are unlikely (Schullery 1989, Christensen *et al.* 1989, Skinner 1990), as there is no direct evidence that any hymenopteran species were endemic to our trap sites or YNP. Thus, without pre-fire surveys and more complete surveys of the insect fauna the actual loss of species from YNP can not be ascertained (Minshall *et al.* 1989).

Our measures of community similarity also provide some insight with regard to the dynamics which underlie the apparent habitat-level endemism in YNP. The low similarity between burned and unburned habitats at each site suggests that the postfire hymenopteran fauna included species that were rarely or never collected in mature forests. These species were presumably exploiting hosts that were also rare in unburned habitats. In particular, the wasp fauna of burned sites was dominated by parasitoid species attacking larvae of Lepidoptera and Diptera. This provides a sharp contrast from the 1989 data (Lavigne *et al.* 1991), in which about 90% of the

hymenopterans sampled were aculeates (bees and predatory wasps). These results may indicate that large, strong-flying, flower-foraging hymenopterans were the first to migrate into the burned areas during 1989, and the insect host populations in burned areas may not have initially been sufficient to support many parasitoids. Thus, it appears that the new growth of grasses and forbs following the fires supported a herbivore community that differed markedly from that found in a mature forest. These unique, early-successional insect faunae were relatively homogeneous between burned habitats, but the communities reached a rather high level of biodiversity (80% of the species diversity and 70% of the species richness found in unburned sites) within 2 yr of the fire. It should be noted that the dramatic change in parasitoid populations may also be due, in part, to differences in the sampling methods from 1989 to 1990. Sweep sampling, although done periodically in 1989, favors collection from low vegetation (especially flowers) and consequently tends to selectively sample greater numbers of aculeates. Malaise traps, used in 1990, continuously sample flight activity and consequently capture many more minute forms, widely dispersing individuals, and crepuscular or nocturnal species.

In light of our findings and the challenges of interpretation, a thorough survey, perhaps even an All Taxon Biological Inventory (Yoon 1993, Janzen 1994), must be conducted in YNP if sound conservation policies are to be developed. Although this recommendation was first made 25 yr ago (Taylor 1969) it has not been heeded, and the management and conservation of biodiversity YNP and other ecological preserves continues to be handicapped as a consequence (Janzen 1994). The imminent need for such a survey is clearly demonstrated by our work, which included the collection of 46 species of Diapriidae, a family that was previously known to include only three species in

Wyoming, with no records from YNP (Lavigne and Tepidino 1976).

*Have there been outbreaks of fire-adapted species?*—Although we can not assert a direct, proportionate relationship (i.e., interval or ratio level of measurement) between host and parasitoid abundance, it is obvious that these variables are related at the nominal level of measurement and interpretations at the ordinal level are certainly valid (Siegel 1956). That is, to the extent that density-dependent relationships occur commonly (Hassell *et al.* 1989), but not invariably (Stiling 1987), in the Hymenoptera, more frequent occurrences of parasitoids can be interpreted as an indication of relatively greater host abundance. In this regard, the high levels of species evenness throughout this study suggest that there was not a numerically dominant hymenopteran species. If any life history could be considered dominant, it would appear that the majority of the parasitic Hymenoptera were probably attacking leaf-feeding, lepidopteran hosts in newly regenerating meadows. Anecdotal reports of tremendous ant biomass (McEneaney *in* Carr 1990) and wood wasp outbreaks (Skinner 1990) in burned areas were not substantiated, although Malaise traps are not the most effective method for sampling either of these insect taxa. Ant abundance was substantially reduced in burned habitats. Only three wood wasps were found in our samples, and aggregations of wood wasps, when they occur, are probably very localized phenomena. Contrary to the assertions of Skinner (1990) it is not likely that these insects are a very regular, or significant, contribution to the diet of bears. In fact, our results indicate that wood wasp populations, along with other insects associated with decaying wood, are not dramatically enhanced by the fires.

Relatively few hymenopteran species in our samples were associated with wood or arbivorous hosts. Furthermore, it appears that there were no ongoing outbreaks of host species of hymenopteran parasitoids at the burned sites. We found relatively few parasitoids of wood-boring beetles or arboreal Lepidoptera. Given that the major forest outbreak coleopterans and lepidopterans have associated hymenopteran parasitoids, it would seem that the forecasted outbreaks of bark beetle and other pests have not materialized (Knight and Wallace 1989). Knight and Wallace (1989) also noted the possibility that insectivorous birds had the potential to keep an impending outbreak in check (Taylor and Barmore 1980, Knight and Wallace 1989). Although slightly higher frequencies of arbivores and their parasitoids were found in burned sites, the dead wood did not provide the basis for a dramatic expansion of these trophic groups. Rather, the burned communities were typified by a marked increase in parasitoids of non-woody herbivores and nectar-feeders (indicating a flush of grass and forb growth) and a significant loss of parasitoids of fungivores and detritivores (indicating a loss of litter). It is likely that in the burned areas, much of the dead wood suitable for insect feeding was burned in the fires, and the severely charred trees were of little use to Hymenoptera or their hosts, except as nesting sites for some aculeates (ants, sphecid wasps, and bees). Thus, leaf cutter bees, which were found only in the burned habitats, may serve as a good indicator of the ecological conditions, as these insects depend on available nectar sources, broad-leaved plants, and nesting cavities.

## ACKNOWLEDGMENTS

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# *Pison antiquum*, a New Species from Dominican Amber (Hymenoptera: Sphecidae)

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*Abstract.*—*Pison antiquum*, a new species from Dominican amber presumably of the Oligocene or Upper Eocene age, is characterized by a broad face, prominent middle clypeal lobe, and propodeum with no longitudinal or oblique carinae on dorsum but with a carina between the gastral articulation and spiracle. The species resembles members of the *euryops* group of Menke, 1988, in most characters, but differs in having a tooth on the inner mandibular margin, the occipital carina interrupted mesoventrally, a large, transverse pronotal pit, and recurrent vein I ending on submarginal cell I.

We previously described *Pison electrum* from Baltic amber (Antropov and Pulawski, 1989), and this paper deals with a new species from Dominican amber. The only other fossil *Pison* are *cockerellae* Rohwer, 1908, from shale beds of Florissant, Colorado, now believed to be Lower Oligocene (Wilson, 1978), and *oligocenum* Cockerell, 1908 (= *oligocaenum* Cockerell, 1909), from Baltic amber. The morphological terminology used here is based on Bohart and Menke (1976), but we mainly follow Michener and Fraser (1978) in their use of mandibular terms. The upper and lower interocular distances, abbreviated UID and LID, respectively, are as defined by Menke (1988).

The specimen was examined under a stereomicroscope in a thick sugar solution rather than immersion oil in order to minimize the possibility of damage.

## Pison antiquum
Antropov and Pulawski, new species

*Name Derivation.*—Antiquum, a Latin neuter adjective meaning old, antique.

*Material Examined.*—Holotype: a nearly complete specimen in Dominican amber (personal collection of George O. Poinar,

Jr, Type H-10-15, currently at Oregon State University, Corvallis, Oregon). Missing are: apical half of right foretibia, right foretarsus, left midtarsomeres III–V, and small apical portion of forewings.

*Collecting Site and Geological Age.*—The specimen came from one of the mines in Cordillera Septentrional between Santiago and Puerto Plata, Dominican Republic. The age of amber in that region varies from approximately 25 to 40 million years, i.e., from Oligocene to upper Eocene (Lambert, Frye, and Poinar, 1985; Poinar, 1992).

*Generic Characters.*—The specimen is easily recognized as a *Pison* because of the overall body shape; inner orbits emarginate; mandible not carinate between adductor swelling and apex of condylar ridge; sterna without visible or exposed graduli; forewing with three submarginal cells (second petiolate); and apex of marginal cell acutely angulate.

*Comparison with Fossil Species.*—We previously studied types of *electrum* and *cockerellae* (Antropov and Pulawski, 1989), but the unique specimen of *oligocenum* (probably lost with most of the Königsberg col-

Figs. 1 and 2. Photographs of *Pison antiquum*. 1, dorsal view. 2, ventrolateral view.

lection at the end of World War II) is known solely from Cockerell's descriptions (1908, 1909). We have found the following differences from these species. In *antiquum*, the flagellomeres are markedly longer than in *oligocenum* and *electrum* (length 2.7–3.2 × width rather than 2.0 or less). Unlike *cockerellae*, the propodeal dorsum of *antiquum* has no median carina or oblique ridges and unlike *electrum*, the clypeal lobe is roundly trapezoidal, the posterior mandibular margin is not emarginate, the head and thorax are densely punctate, and the propodeum has a carina that extends from the spiracle to gastral articulation.

The following details of forewing venation in *antiquum* may also be specific rather than individual:

—height of submarginal cell II less than its petiole (equal to petiole in *cockerellae*, more than petiole in *electrum* and *oligocenum*);

—petiole as long as anterior margin of submarginal cell III (shorter in *electrum* and *oligocenum*, longer in *cockerellae*).

—distance between recurrent vein I and submarginal cell II more than distance between the cell and recurrent vein II (equal in *cockerellae*, recurrent vein I interstitial in *electrum* and *oligocenum*).

—discoidal cell I elongate: maximum length 4.0 × maximum height (2.0 in *cockerellae* and 2.5 in *electrum*, unknown in *oligocenum*);

—M diverging distad of crossvein cu-a (similar in *cockerellae* and *electrum*, slightly proximal of cu-a in *oligocenum*);

—an imaginary line between apex of marginal cell and distal hindcorner of discoidal cell II not crossing submarginal cell III (crossing in *cockerellae* and *electrum*, unknown in *oligocenum*).

*Comparison with Extant Species.*—*Pison antiquum* is not identical to any of the Neotropical species revised by Menke (1988). It resembles members of Menke's *euryops* group in having a broad face (eye length

14% less than distance between eye notches), a roundly truncate middle clypeal lobe, a complete episternal sulcus (reaching mesopleural foremargin), a carina present between the propodeal spiracle and gastral articulation, in lacking median and oblique ridges on the propodeal dorsum, and in having a hindcoxa with a well defined inner and a rudimentary outer carina. Unlike species of the *euryops* group, however, *antiquum* has a tooth near the midlength of the inner mandibular margin; a large, transverse pronotal pit; an impunctate tegula; and recurrent vein I ending on submarginal cell I.

*Description.*—Female (Figs. 1–10). Head transverse in frontal view (Fig. 7), width 1.27 × height. Labrum hidden under clypeus. Mandibular apex acute, inner margin with well defined tooth at midlength (Fig. 9), posterior margin neither notched nor stepped, but condylar ridge meeting adductor ridge at a slightly obtuse angle (Fig. 8); basal (broad) portion with longitudinal sulcus parallel to condylar ridge. Occipital carina interrupted midventrally, almost reaching hypostomal carina. Clypeus moderately convex, median lobe protruding, its free margin arcuate mesally and evenly concave laterally (Figs 7, 9). Frons markedly convex in upper half, with median sulcus below midocellus. Eyes asetose, UID = 0.57 × LID, eye length 14% less than distance between eye notches. Vertex in frontal view convex behind hindocelli (Fig. 7). Ratio of ocellocular distance, hindocellar diameter, and interocellar distance = 0.3:1.0:0.6. Distance between hindocelli = 0.55 × distance between mid- and hindocellus. Length of flagellomere I 3.2 × width, of flagellomere × 2.7 × width. Punctures uniform, one diameter apart on frons and on scutum anteriorly (puncture diameter about 0.1 hindocellar diameter); finer than that on eye notch, vertex, scutum posteriorly, and scutellum. Eyes glabrous; head, scutum, and scutellum with erect setae (setal length about 0.1–0.2 hindocellar diameter); me-
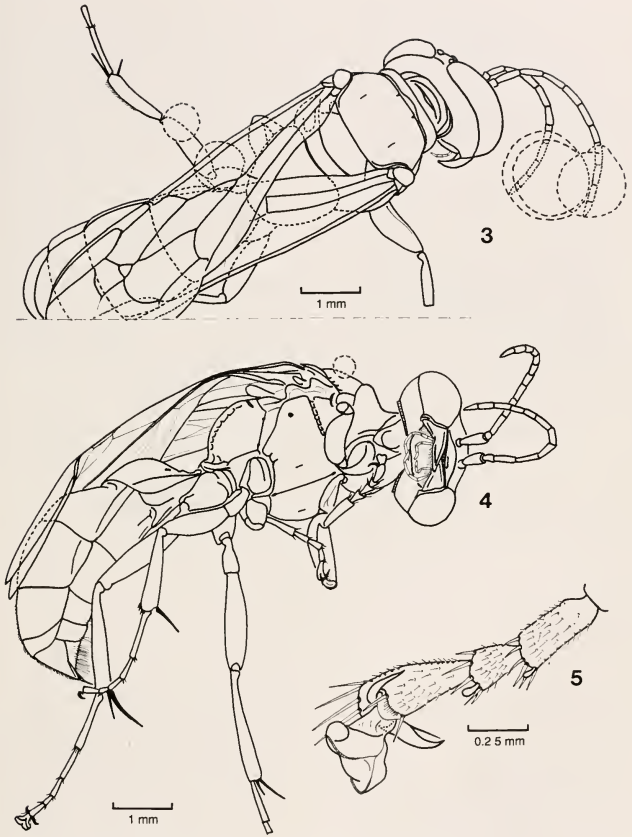
Figs. 3–5. *Pison antiquum.* 3, dorsal view. 4, ventrolateral view. 5, hindtarsal apex.
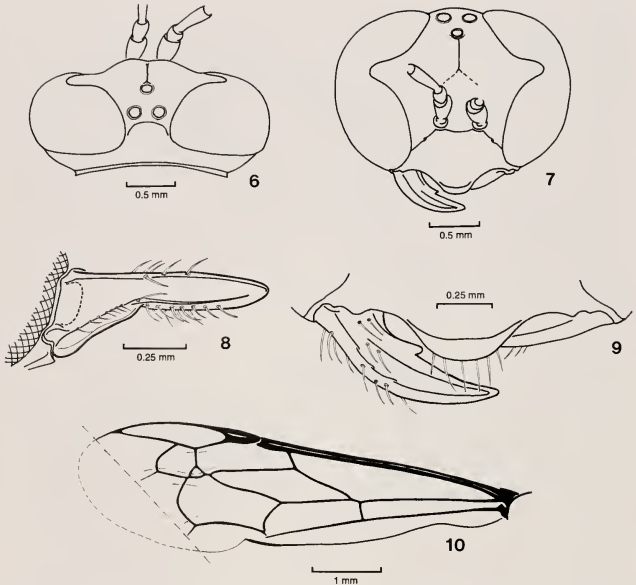
Figs. 6–10. *Pison antiquum.* 6, head dorsally. 7, head frontally. 8, mandible, outer side. 9, ventral portion of clyeus and mandible. 10, forewing.

sopleural setae semi-erect, up to 0.25 hind-ocellar diameter long, curving posterad. Pronotum anteriorly with transverse, elliptical pit whose hindmargin is lamelliform, inclined posterad; pronotal hindmargin straight, collar rounded laterally, transversely raised mesally. Metanotal sculpture evanescent. Tegula impunctate. Episternal sulcus extending to mesopleural foremargin. Metapleural flange narrower than ocellar diameter. Propodeum with longitudinal carina between spiracle and gastral base (carina poorly visible from most angles but left carina easily recogniz-

able in dorsal view through left wing); dorsum shiny, minutely punctate (punctures one to two diameters apart), with no median (longitudinal) or oblique carinae and no defined enclosure; hindface with median groove and three transverse ridges above gastral articulation. Forewing hyaline, with three submarginal cells (Fig. 10); media diverging from M+Cu well beyond crossvein cu-a; marginal cell acute apically, extending well beyond vein 2r-m; submarginal cell II: height less than length of petiole; first and second recurrent veins received by submarginal cell I and III

(near its base), respectively. Hamuli of hindwing divided into two groups of six each. Legs of usual shape, minutely setose. Hindcoxal dorsum with complete inner carina; outer carina present only posteriorly. All tibiae with short, sparse spines on outer side. Plantulae present on fore- and midtarsomeres II-IV and hindtarsomeres III-IV; largest plantula on tarsomere IV (Fig. 5). Gaster sessile, moderately constricted between terga I and II. Tergum I not humped posteriorly, with appressed microsetae; terga IV-VI with semi-erect microsetae. Pygidial plate absent. Sternum I with basomedian carina that bifurcates at middle. Length 9.0 mm (amber sample $19.3 \times 7.3 \times 7.0$ mm). Body black, without yellow markings.

Male unknown.

## ACKNOWLEDGMENTS

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# Contribution to the Bionomics of *Ceramius tuberculifer* Saussure (Hymenoptera, Vespidae, Masarinae)

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*Abstract.*—Three nesting aggregations of *Ceramius tuberculifer* Saussure were investigated in the French Alps. *C. tuberculifer* inhabits submediterranean calcareous grassland. The nest consists of a one- to multi-cellular burrow surmounted by a mud turret. The main shaft descends obliquely into the ground and terminates in a cell. Secondary shafts are short. Brood-cells are built of mud within an excavated cell. Nests are probably perennial. Imagines are polylectic, collecting primarily pollen from *Teucrium montanum* L. (Lamiaceae), *Helianthemum* (Cistaceae) and an unidentified Fabaceae. There are additional flower visiting records from *Lavandula* (Lamiaceae) and *Ononis*. (Fabaceae). The imagines employ a specialized method to gather pollen from *Teucrium*-flowers, which can be interpreted as a behavioural adaptation to a nototribic pollen presentation. Males patrol along flight paths in the foraging area of the females. They interrupt their flight regularly in order to perch for short periods. *Chrysis emarginatula* Spinola (Chrysididae) is a common parasitoid. Larvae of *Zodion* (Conopidae) and Mermithidae (Nematoda) were identified as endoparasites of the imagines.

## INTRODUCTION

The genus *Ceramius* Latreille is a monophyletic subgroup of the honeywasps (Masarinae) (Carpenter 1993). All species studied so far are solitary (Gess & Gess 1989, 1990). They nest in the ground in excavated burrows, which are surmounted by a mud entrance turret. The brood-cells are provisioned with a mixture of pollen and nectar (Gess & Gess 1989, 1990). Based on morphological characters and biogeographical evidence *Ceramius* has been divided into eight species groups (Richards 1962) one of which has recently been subdivided (Gess & Gess 1988). Moreover, Gess & Gess (1986, 1988, 1990) have shown for the Afrotropical taxa (the species groups 2, 3, 4, 5, 6, 8 of Richards 1962) that there are specific differences between the species groups in regard to nest-construction and flower visiting. Hitherto, comparable information on the bionomy of the palaearctic *Ceramius*-species (groups 1 and 7) has not been been record-ed (cf. Gess & Gess 1988). *Ceramius tuberculifer* is a member of species group 7 (Richards 1962). The species has been found in southern France and in the northeastern parts of the Iberian Peninsula (Richards 1963). It is closely related to *C. lusitanicus* Klug, *C. vechti* Richards and *C. bischoffi* Richards, with which it had been united under the name *C. lusitanicus* until the revision by Richards (1962, 1963). Giraud (1871) and Ferton (1901) described habitat and nest-construction of *Ceramius tuberculifer* in the French Alps and the Pyrenees, respectively. Whether Ferton's account really refers to *C. tuberculifer*, as supposed by Richards (1962), is uncertain. The observations of Giraud (1871) and Ferton (1901) are to some extent at variance with each other.

In the following data about habitat, nest construction, flower visiting, pollen collecting, mating and parasites of *C. tuberculifer* are presented which were obtained at nesting aggregations in South France.

The results are compared with descriptions of other *Ceramius*-species.

## MATERIAL AND METHODS

Investigations were carried out from 19 to 29 July 1994. Weather conditions were almost uniform throughout the whole period. Until about midday it was sunny and temperatures rose to 25°–30°C. Later in the day it clouded over, and more than once there were fairly heavy thunderstorms. In the upper valley of the Verdon river (Département Alpes Haute Provence), open habitats in the vicinity of la Foux d'Allos, Allos, Colmars, Beauvezer, Peyresq, Thorame-Haute, Thorame-Basse and la Valette were sampled for imagines and nests. The nesting area at Peyresq was visited on July 19, 21, 25 and 28, July, that on the Montagne de Boules on 26 and 29 July. Observations were noted in the field and documented using a 35 mm camera with 100 mm lens (scale up to 1:1) and flash. Time is Central European Time. Positions of the nests in the nesting aggregations were recorded as sketches, which were retouched later by comparing them with photos taken at the time. Five nests were excavated. Their construction was outlined as accurately as possible, although exact measurements could not be taken due to the nature of the soil. Entire brood-cells were collected and later studied under a dissecting microscope. Plants which had been visited by adults were preserved both dried and in 70% ethanol. Samples of *C. tuberculifer* were collected, 10 males and 29 females at Peyresq and one male and one female on the Montagne de Boules. The metasomata of all specimens were dissected under a dissecting microscope and examined for endoparasites. The alimentary tracts of six females from Peyresq were fixed according to the formula of Pabst & Crailsheim (1990). Then pollen samples from the ventriculus and the rectum were prepared using the method of Westrich & Schmidt (1986). The pollen was determined under a light mi-croscope and compared with pollen from the anthers of the ethanol-fixed plants prepared in the same way. Only pollen-types that existed in large quantities were considered for the evaluation. Quantitative indications were estimated. In each case, five of the ethanol preserved males and females were selected at random to investigate the pollen-distribution on the exoskeleton. The number of grains on the clypeus, the vertex + frons, the rest of the head, the dorsal, left, right and ventral part of the mesosoma, the fore-, middle- and hind-legs and the metasomal-tergites and -sternites were counted separately under a dissecting microscope. From these data, the total number of pollen grains was summed up for each specimen and the proportional number of grains on vertex + frons, the dorsal part of the mesosoma and the rest of the body was calculated. Finally, the arithmetic means and their standard errors of the proportional numbers for males and females were calculated.

## BIONOMIC ACCOUNT

*Description of the Habitats.*—*Ceramius tuberculifer* was found at two localities in the vicinity of Thorame-Haute, which are characterized in more detail in Table 1. Both were in submediterranean calcareous grassland (Brometalia Br.-Bl.). The ground cover was about 60–70%. In both localities *Teucrium montanum* (Lamiaceae) was strikingly more abundant than in the surrounding areas. The soil, in which the burrows were excavated, contained some clay and was somewhat friable.

At Peyresq the ground was partially covered with clusters of approximately 0.3 m high *Sarothamnus*-(Fabaceae) and *Lavandula angustifolia* Miller (Lamiaceae) shrubs and a few pines of 1–(3)m in height (Fig. 1). Among the dwarf shrubs, the soil was sparsely covered with low vegetation dominated by *T. montanum* and grasses. One nesting aggregation (= aggregation P) with 77 nests was located on an area of

Table 1. Characters of two localities with nesting aggregations of *Ceramius tuberculifer* in the vicinity of Thorame-Haute (France: Département Alpes Haute Provence)

| Parameter | Peyresq | Montagne de Boules |
|---|---|---|
| location | a little up-hill from the D.32 about 400 m before Peyresq | about 2 km NNW from la Valette |
| co-ordinates (Gauß-Krüger) | 44°4'22''N 6°36'46''E | 44°9'29''N 6°30'31''E |
| altitude above sea-level | 1520 m | 1560 m |
| exposition of the slope | 250° | 150° |
| approx. steepness of the slope | 10° | 45° |
| outset from sun-irradiation | 9h00 | 6h00 |
| minimal distance towards the next water-site | 300 m (stream in the valley) | 200 m (stream in the valley) |

about 10 m², where the soil contained slightly more clay than in the surroundings. Most of the nests were in sparsely covered soil, only five were under a little *Sarothamnus* bush (Fig. 3). In the centre of the aggregation, the nest-entrances were close to one another, with minimum distances of approximately 50 mm. Towards the edges the space between nests increased (Fig. 3). About 15 m northeast of the aggregation an isolated nest was found. The adults visited flowers mainly in an area that extended 30–100m in a northeasterly direction from the aggregation (Fig. 1), where *T. montanum* occurred abundantly and *Helianthemum oelandicum* L. (Cistaceae) less so.

On the Montagne de Boules two nesting aggregations (= aggregations B1 and B2) were found on a steep slope, which was cut by numerous bare, dry erosion-rills, many of which were filled with gravel (Fig. 2, Table 1). Vegetation was more diverse than at Peyresq. Predominantly 0.3–0.5 m high grasses, *Sarothamnus*, *Lavandula* and a yellow flowered species of Asteraceae were growing among scattered pines of 0.5–3 m in height. Furthermore, *T. montanum* and on a smaller scale *H. oelandicum*, *Ononis fructicosa* L. (Fabaceae) and *Campanula* spec. (Campanulaceae) occurred. The calcareous grassland was bordered by pine-forest at three sides. Obliquely up hill it continued into a steep

open area of larger dimensions. The aggregations were located in the middle of the slope (Fig. 2). The distance between them was about 10 m. The more westerly aggregation B1 consisted of 25 nests, B2 of 13. Most of the nests were established at restricted spots directly below plants, which were protected against erosion (Fig. 4). At these places, the root-system detained weakly clayey soil, in which the burrows were excavated. At suitable sites the shortest distances between the nests were approximately 50 mm. Foraging adults were observed about 25 m northeast of aggregation B2, where *Teucrium montanum* was flowering in abundance.

*Nest Construction.*—Some of the nest-entrances were surmounted by a more or less damaged cylindrical turret which was constructed from mud pellets cemented together. The best preserved turret was approximately 15 mm long (Fig. 5). Initially it was subvertical, but after half of its length it curved over becoming horizontal. The walls had no interstices. Often only remnants of a turret were present. Frequently, there was no indication of a turret at all (e.g. in 34 nests of B1 and B2). During the observation period neither construction nor repair of a turret was seen.

Vertical plans of the burrows are presented in Fig. 6 and the contents of each nest are listed in Table 2. In all nests the

Figs. 1–2. Fig. 1. Nesting area of *Ceramius tuberculifer* at Peyresq, 28.7.1994; view from the southwest. The nesting aggregation P was situated in front of the two little pines a bit to the right from the centre (arrow). The foraging area of the imagines extended in front of the pine forest fringe on the left. Fig. 2. Habitat of *Ceramius tuberculifer* on the Montagne de Boules, 26.7.1995; view from southeast. The nesting aggregations B1 and B2 were in the centre of the steep slope. Flower visiting females were commonly observed in an adjacent open area obliquely uphill to the right.

**aggregation P**



Fig. 3. Positions of the nests in the nesting aggregation P of *Ceramius tuberculifer* at Peyresq, 21.7.1994. For key see Fig. 4.

entrance was followed by a shaft of constant diameter descending 50–70 mm obliquely into the ground. Whenever brood-cells were present, the shaft terminated in a cell (Fig. 6). When there was more than one cell, they were closely grouped. Most of the cells lay sub-horizontally, one cell was orientated downwards. All cell-openings were directed towards the end of the shaft.

**aggregation B1**



0.5 m

**aggregation B2**



0.5 m
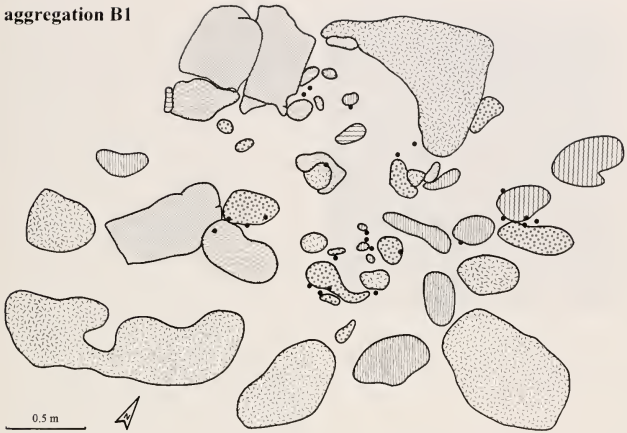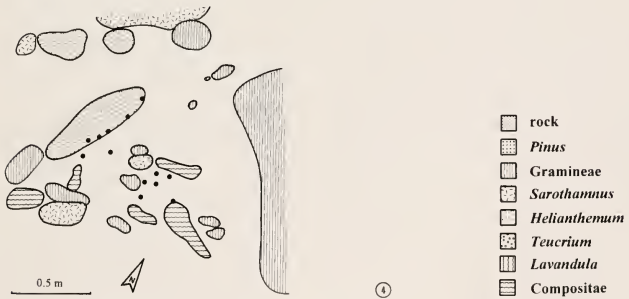
| | rock |
| | *Pinus* |
| | Gramineae |
| | *Sarothamnus* |
| | *Helianthemum* |
| | *Teucrium* |
| | *Lavandula* |
| | Compositae |

Fig. 4. Positions of the nests in the nesting aggregations B1 and B2 of *Ceramius tuberculifer* on the Montagne de Boules, 26.7.1994.

The constructed mud brood-cells were easily separated from the adherent soil. They varied from nearly cylindrical to bean-shaped (Fig. 9). They had a rough, irregular outer surface on which separate applications of mud were discernible. The inner surface was regular and smooth but dull. Fragments of fibrous tissue and

Fig. 5. Mud turret surmounting the entrance of a *Ceramius tuberculifer* nest; Peyresq 21.7.1994 (length of the turret approximately 15 mm, its distal parts are slightly damaged).

threads corresponding in structure and colour to cocoon-material (see below) were embedded in the walls and mud-plugs of two cells of nest 5. Similar fragments and fibres mixed with crumbly soil were found within the cocoon of nest 4.

Three cells of nest 5 were studied in detail (Fig. 7). They measured 18–23 mm in length and had a maximum outer diameter of approximately 11 mm. Their walls were 1.1–1.9 mm thick. The cells were sealed with a 3.0–3.5 mm long mud plug at the proximal end. The cocoon-cap was located close behind the plug, but separated from it by a very short empty space. The cap was a circular weakly biconcave plate, from 4.3 to 4.7 mm in diameter. The cocoon consisted of reddish to brownish, slightly shining fibrous tissue. It was 14–17 mm long and 5.8–6.6 mm wide at its greatest, and the distal end was rounded. The cocoon was in intimate contact with the inner walls of the mud cell from which it could be parted only with difficulty. There were small black brownish shining pellets on the inner surface of the cocoon in an annular zone of 1 mm in length, 2–

4 mm distal from the cocoon-cap. The hollow hemispherical pellets had thin brittle walls which consisted of a substance that was homogeneously brownish and translucent under the light microscope. In their outer appearance the pellets resembled the "fecal pellets" from *Pseudomasaris edwardsii* (Cresson) (Masarinae) (cf. Torchio 1970). In one case these pellets were in addition present at the distal end on the inner surface of the cocoon. Starting at 6.0–7.5 mm distal from the cap and extending from there over the whole distal portion of the cocoon a thin, yellowish, slightly granular and brittle layer covered the inner wall of the cocoon. The light microscope revealed that it consisted of pollen-exines, which were tightly compressed and united with a secretion.

*Behaviour of the Females.*—Females were regularly observed excavating their nests. They backed up the shaft with a soil-pellet held by their mandibles. The pellets were nearly half as large as their heads (Fig. 8). As soon as they had left the nest entrance, the females turned 90°–180° on their vertical axis and discarded the pellet (cf. Fig. 8). Then they turned back and re-entered the nest head first. The earth was always dropped at the same spot a few centimetres from the entrance, where a small heap was formed. Judging from its appearance, the soil on the heap was moist. I did not discover if or to what extent liquid was used in order to soften the ground in the course of nest excavation. Transport of water in the crop was not observed but the crops of two females collected at aggregation P were tensely filled with a clear liquid of high viscosity, probably nectar.

Before activity started in the morning and during times of unfavourable weather the females rested in the upper part of the shaft, each with its head directed to the entrance and completely plugging the shaft. As an exception one female was observed crawling under the twigs of a *Teucrium* plant as the sky became overcast. It remained there, lying more or less on its
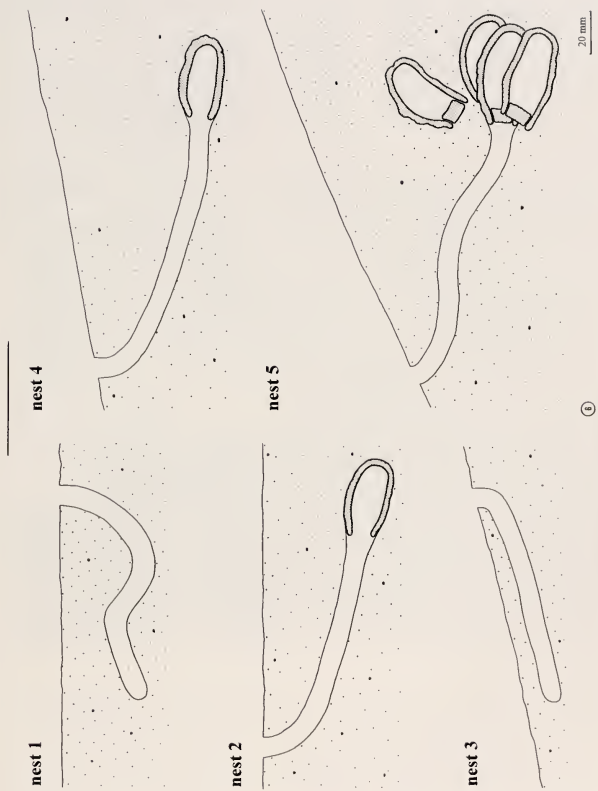
Fig. 6. Vertical plans of 5 nests of *C. tuberculifer*. For further information see Table 2.

Table 2. Details pertaining to the five nests of *Ceramius tuberculifer* excavated on July 25, 1994 at Peyresq (P) and on July 26, 1994 on the Montagne de Boules (B) respectively. The cell of nest 2 was damaged during excavation. It appeared as if it had not been plugged

| Aggregation | Nest No. | Σ females | Σ cells | Condition of the cells | Content of the cells |
|---|---|---|---|---|---|
| P | 1 | 1 | 0 | — | — |
| P | 2 | 1 | 1 | open? | large larva; rests of pollen |
| B1 | 3 | 1 | 0 | — | — |
| B1 | 4 | 1 | 1 | open | rest of a cocoon filled with crumbly earth mixed with cocoon-fragments |
| B2 | 5 | 1 | 4 | sealed with a mud plug | prepupa in a cocoon |

left side (Fig. 10). Flight activity of the females started at about 10h00 and on all days was terminated more or less abruptly when the weather became cloudy. Active females were observed until 14h00 at the latest.

The females always entered the nests head first. Wasps that were departing left
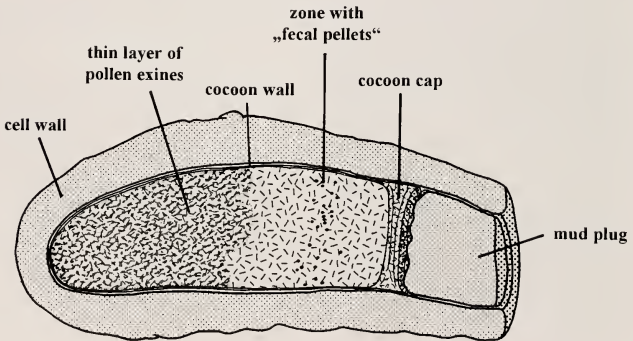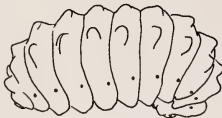


Fig. 7. Schematic representation of a longitudinal section through a mud-cell of *Ceramius tuberculifer* from nest 5. The cocoon contained a prepupa.

Figs. 8–13. Fig. 8. *Ceramius tuberculifer* during nest excavation at Peyresq, 28.7.1994. The female is turning round with a soil-pellet held in her mandibles after she had backed out of the entrance. The pellet-dropping area in the foreground is marked with an arrow. Fig. 9. Constructed mud-cells of *Ceramius tuberculifer* from nest 5 from aggregation B2, 26.7.1994 (length of each side of the squares is 5 mm). Fig. 10. Female of *Ceramius tuberculifer* sheltering under twigs during a period of unfavourable weather at Montagne de Boules, 29.7.1994. Fig. 11. Male of *Ceramius tuberculifer* perching on a sun-exposed stone at Peyresq, 28.7.1994 (arrow pointing at the shadow of the widely opened mandibles). Fig. 12. Female of *Ceramius tuberculifer* visiting a flower of *Teucrium montanum* at Peyresq, 28.7.1994. The anthers touch frons and vertex of the wasp (arrow). Fig. 13. Left foretarsus of a *Ceramius tuberculifer* female from posterior (scale bar = 0.3 mm).

Table 3. Flower visiting records for males and females of *Ceranius tuberculifer* on five days of observation at Peyresq (P) and on the Montagne de Boules (B). (O = >5 observations o = 2–5 observations + = single observation)

| Plant taxon | 19.7.P | | 21.7.P | | 25.7.P | | 26.7.B | | 28.7.P | | 29.7.B | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ |
| **Lamiaceae** LINDL. | | | | | | | | | | | | |
| *Teucrium montanum* L. | O | O | O | O | O | O | O | | O | + | O | |
| *Lavandula angustifolia* MILLER ssp. *angustifolia* | | | | | | | o | | + | | O | |
| **Cistaceae** JUSS. | | | | | | | | | | | | |
| *Helianthemum oelandicum* (L.) DC. ssp. *alpestre* (JACQU.) BREISTR. | | | | | O | O | | | | | | |
| **Fabaceae** LINDL. | | | | | | | | | | | | |
| *Ononis fructicosa* L. | | | | | | | o | | | | | |

the shaft, likewise, running forward. More than once it was observed that an individual which had vanished into the burrow running forward left the nest head first or was soon afterwards resting in the anterior part of the shaft with its head directed towards the entrance, indicating that they had turned around inside the burrows.

*Behaviour of the Males.*—Males of *C. tuberculifer* were regularly observed in the area to the northeast of the nesting aggregation P, an area commonly visited by foraging females. Activity of the males started about 10h30. They were moving over the *Teucrium* clumps in a slow, constant flight approximately 0.1 m above the ground. Every few metres (usually 1–3 m, at most 20 m) they interrupted their flight and alighted on sun-exposed stones or dry twigs lying on the ground, where perched for brief periods (less than a minute). On the perch they maintained a characteristic posture; antennae and wings were raised at about 45° to the median axis of the body and mandibles were opened wide (Fig. 11). Often the males simultaneously rubbed the ventral side of their metasoma with the hind-legs. Sometimes in addition they cleaned the head and the dorsal part of the thorax with the fore-legs. When disturbed, for example by a passing insect, the males resumed their

flight. In other cases they started flying anew without an obvious stimulus. After a few metres in flight they alighted on another perch. In this way, they seemed to patrol along more or less constant paths. The same perches were repeatedly visited by males. One particular male covered a complete oval course of approximately 40 m for one and a half times, alternating between flying and perching, before sight of it was lost. Matings were not observed, but frequently the males briefly approached other insects during the patrol flights and from perches. On one occasion a patrolling male flew rapidly towards another flying male, chased it for about 0.5 m before returning to its course. The patrolling behaviour was irregularly interrupted by periods in which the males visited flowers. Around midday males were occasionally observed in the range of the nesting aggregations, where they alighted for a short while on the ground close by the nest entrances. On one morning a male was resting in the shaft of a nest with its head directed towards its nest entrance.

*Flower Visiting.*—Flower visiting records for imagines of *C. tuberculifer* are presented in Table 3. The most frequently visited plant was *T. montanum* but there was no fidelity to flowers and several times both males and females changed from one

Table 4. Distribution of pollen grains on the exoskeleton of males and females of *Ceramius tuberculifer*. The arithmetic means and the standard errors for the total number of pollen grains per individual and for the percentage of grains found on different parts of the body are given

| | n | Σ pollen grains per individual | Percentage of pollen-grains on | | |
| | | | Vertex and frons | Dorsal part of the mesosoma | Rest of the body |
| --- | --- | --- | --- | --- | --- |
| Males | 5 | 368 (±57) | 67 (±6) % | 12 (±5) % | 21 (±4) % |
| Females | 5 | 132 (±40) | 66 (±14) % | 10 (±7) % | 23 (±8) % |

plant species to another during a single foraging trip.

*Pollen Gathering.*—The crop of three females was distended with pollen, which was suspended in some liquid. Ventriculus and rectum of all dissected individuals contained pollen grains in variable quantities. The pollen-content of ventriculus and rectum of six females consisted of a mixture of pollen from *Teucrium*, *Helianthemum*, a species of Fabaceae and on a smaller scale also *Lavandula*; species of Liguliflorae and additional unidentified plant taxa. Individual differences existed, however, in regard to the proportion of particular plant taxa. The ventriculus and rectum of four females contained mostly pollen of *Teucrium*, whereas the other samples were dominated either by *Helianthemum* or by an unidentified species of Fabaceae.

When the imagines visited the nototribic flowers of *T. montanum* (i.e. the anthers have a dorsal position in a monosymmetric flower so that regular pollinators are dusted with pollen on their back) their frons and vertex made contact with the anthers (cf. Fig. 12). In consequence the main proportion of pollen on the exoskeleton was located on these parts of the head (Table 4). After having visited several flowers the adults alighted regularly on sun-exposed stones or plants. There they groomed the dorsal and frontal parts of the head with the fore-legs which alternately were moved over it from dorsal/posterior to ventral/anterior. In two cases it was possible to observe that the distal parts of the fore-legs were brought

between the mandibles each time after the leg had been wielded over the head and that the mouthparts were moving simultaneously. Fore-tibiae and -tarsi of the females and to a lesser extent of the males form a pollen brush as they are short, thick and densely covered with stiff hairs (Fig. 13).

*Parasites.*—Imagines of the chrysidid wasp *Chrysis emarginatula* Spinola were common at all nesting aggregations, where they were observed on repeated occasions entering the burrows. The species was not found beyond the close vicinity of the nests. The activity of the adults was influenced to a lesser extent by irradiation and/or temperature than was that of *C. tuberculifer*.

Two female *C. tuberculifer* from Peyresq had the metasoma nearly completely filled with a larva of *Zodion* (Conopidae).The atrial domes of each larva were orientated towards the ventral side of the wasp and had immediate contact with the tracheal sacs of its host. The posterior end of the larva was situated in the first metasomal segment, the anterior end in the sixth. In relation to the median axis of the host the slender fore-end of the larva was orientated to the right. The alimentary tract and the ovaries of the host were compressed on its left ventral side.

A male from Peyresq contained, in the metasoma, a parasitic stage of an unidentified representative of the Mermithidae (Nematoda).

DISCUSSION

The aggregations investigated were smaller than those described by Giraud

(1871) and Ferton (1901), each of which had a few hundred individuals. Other *Ceramius*-species also exhibit a remarkable variation with regard to both nest dispersion and the number of nests in an aggregation (cf. Gess & Gess 1980, 1986, 1988, 1990). Both localities of *C. tuberculifer* were covered with calcareous grassland, which is in accord with the sketchy habitat descriptions of Giraud (1871) and Ferton (1901). At all aggregations investigated the nesting substrate was somewhat friable whereas in the Pyrenees the species was found nesting on solid, clay soil (Ferton 1901).

Afrotropical *Ceramius* use water for softening the soil in nest construction (Gess & Gess 1986, 1988, 1990). The same behaviour was shown by females of *Ceramius* in the Pyrenees (Ferton 1901). In agreement with Giraud (1871) *C. tuberculifer*, nesting in the French Alps, likewise uses a liquid at least for the construction of turret and cells, but this is not necessarily water. Nectar may conceivably be used instead, since none of the dissected females carried water (cf. also Giraud 1863, 1871), but two had their crops completely filled with nectar.

As already indicated by Giraud (1871) and Ferton (1901), *C. tuberculifer* constructs a mud entrance turret. Building a turret probably belongs to the ground pattern (in the sense of Ax 1984: 156) of *Ceramius*, since it has been recorded for members of all species-groups (cf. Gess & Gess 1992) and for all other ground-nesting Masarinae studied to date (cf. Gess & Gess 1980, Houston 1984). Ferton (1901) mentioned that the turrets were always repaired as soon as they had been damaged, whereas reconstruction or repair of a turret was not observed in the Verdon valley, which is in agreement with Giraud (1871).

As described by Giraud (1871) the shafts of the nests in the present study were 50–70 mm long but in contrast to his account they descended obliquely into the ground not vertically. This oblique descent of the shaft is remarkably different from the condition present in the nests of the Afrotropical species of *Ceramius*, the shafts of which are always almost vertical (Gess & Gess 1986, 1988, 1990). In most of the Afrotropical species the shaft has a short bulbous enlargement ("bulb") in the upper part, which allows the imagines to turn round in the burrow (Gess & Gess 1988). Such a bulb is lacking in the nests of *C. tuberculifer*.

The observations regarding the behaviour of the wasps, when excavating their burrows, correspond well with the account by Giraud (1871). Like other *Ceramius* species the females of *C. tuberculifer* back up the shaft with a soil pellet held by their mandibles (cf. Gess & Gess 1980, 1986, 1988, 1990). However, in contrast to the other taxa they do not fly up to discard the pellet but move to the pellet dropping area on foot. The existence of a clearly defined pellet dropping area has only been reported for two members of species group 8 (Gess & Gess 1980, 1988). In other *Ceramius*-species the pellets are spread out over a larger area (Gess & Gess 1980, 1988).

The brood-cells are constructed within a previously excavated cavity, that is they are "mud-cells" in the sense of Gess & Gess (1986). This is in agreement with the descriptions by Giraud (1871) and Ferton (1901). The construction of such mud-cells is probably plesiomorphic within *Ceramius* and occurs in all Afrotropical taxa except for members of species group 8 (cf. Gess & Gess 1992) where it must have been lost secondarily. The variable, more or less asymmetrical shape of the mud-cells of *C. tuberculifer* contrasts with the regular shape recorded for the mud-cells of other *Ceramius* species (cf. Gess & Gess 1980, 1986, 1988, 1990). As reported by Giraud (1871), the first cell terminates the main shaft of the burrow, a character shared with most of the other *Ceramius* species with the exception of *C. lichtensteinii* (cf. Gess & Gess 1988). Perennial nests have

been recorded for most species which construct mud-cells (Gess & Gess 1988). Two findings suggest that this is also the case in *C. tuberculifer*: Firstly, two cells had fragments of cocoon-material embedded in their walls and mud-plugs, which indicates that they were constructed after imagines had already emerged from this nest. Secondly, one nest contained a female along with an old cell, from which an imago had already emerged.

Ferton (1901) reported that the provisioned cells were sealed with a mud-plug. In contrast, Giraud (1871) found all cells to be open, irrespective of their pollen content and the development of the larvae. Furthermore, the cell of nest 2 was probably not sealed, although it contained a large larva. Open cells with larvae occur occasionally also in *C. lichtensteinii* (Gess & Gess 1980). This may be due to unfavourable foraging conditions which bring about delayed provisioning after deposition of the egg. The effect of this delay would be that the larva hatches and starts feeding before provisioning and sealing of the cell is completed (Gess & Gess 1980).

Brood-cells of *Ceramius* containing prepupae have been described only in *C. lichtensteinii* (Gess & Gess 1980) and *C. rex* Saussure (Gess & Gess 1988). With 4–8 mm and 3 mm respectively the space between the mud-plug and the cocoon cap is much longer in both species than in *C. tuberculifer*. The thin brittle yellowish layer of pollen-exines on the inner wall in most of the lower half of the cocoon of *C. tuberculifer* is probably the meconium. A similar thin faecal layer is deposited over the distal three-fifths of the cocoon of *Paragia tricolor* Smith (Masarinae), though there are often also thick scales deposited at its distal end (Houston 1984). A comparably thin meconium occurs in *Euparagia scutellaris* Cresson (Euparagiinae) (cf. Torchio 1970). In contrast the meconium of *Pseudomasaris* is restricted to the posterior end of the cocoon, where the excrements form a compressed cake, about half

as deep as wide, with a flat surface, which is perpendicular to the walls of the cocoon (Torchio 1970, cf. Hicks 1927).

Although pairing was not observed, it can be assumed that the males were seeking mates in the foraging area of the females. Likewise males of the Afrotropical *Ceramius* search for potential mates at resources that are regularly visited by females, for example water (cf. Gess & Gess 1980, 1988) and forage plants (cf. Gess & Gess 1990). Males of *C. tuberculifer* interrupt their patrol flights regularly in order to perch for brief periods. The characteristic behaviour of *C. tuberculifer* males on the perch, especially the opened mandibles, and the rubbing of the ventral surface of the gaster with the hind-legs, may conceivably indicate the release of a pheromone. Comparable behaviours are shown by males of some species of *Polistes* (Vespidae) which chemically marking their territorial perches (cf. e.g. Beani & Calloni 1991, Wenzel 1987). The use of pheromones in courtship behaviour has not been reported for any representative of the Masarinae (cf. e.g. Alcock et al. 1978, Alcock 1985, Gess & Gess 1988, 1990, Hicks 1929, Houston 1984, Longair 1987). Males of *Pseudomasaris maculifrons* (Fox) (Alcock 1985: Fig. 2) and *P. vespoides* (Cress.) (Hicks 1929), however, also perch and whilst so doing slightly spread their wings. At least in this respect their behaviour is similar to that of *C. tuberculifer*.

The Afrotropical taxa of *Ceramius* are oligolectic to a high degree. They obtain pollen from either Mesembryanthemaceae, Asteraceae or Fabaceae (Gess & Gess 1989, 1990). Members of the same species group exhibit a marked fidelity to flowers of a single plant family (Gess & Gess 1989). This does not seem to be the case in species group 7, with *Ceramius tuberculifer* being obviously polylectic. In addition other members of the species group have been recorded visiting flowers of Lamiaceae, Fabaceae and Apiaceae (Richards 1963). These records can be misleading,

however, since they do not verify that the visited plants are utilized as a pollen source (Gess & Gess 1988).

The occurrence of *Teucrium montanum* seems to be of particular importance for *Ceramius tuberculifer*. At both nesting sites the plant was strikingly more abundant than in the surrounding areas, its flowers were visited most frequently and it was most common in the majority of the pollen samples from the alimentary tract. During the visits to the nototribic *Teucrium* flowers the anthers come into close contact with the vertex and frons of the imagines, so that most of the pollen is deposited on these parts of the body. Afterwards it is drawn towards the mouth by grooming movements of the brush-like forelegs and is finally ingested. This behaviour differs remarkably from the pollen gathering methods employed by other *Ceramius* species and most of the other Masarinae, which either use their forelegs to agitate the anthers and draw the pollen towards their mouth or ingest pollen directly from the anthers (Gess & Gess 1989, 1990b, cf. Neff & Simpson 1985, cf. Torchio 1970). *Celonites abbreviatus* Villers is an exception for the imagines gather pollen from nototribic flowers of different Lamiaceae in a manner which is quite similar to the behaviour of *C. tuberculifer* (cf. Schremmer 1959, cf. Müller in press). The similarities are probably due to convergent behavioural adaptations to a nototribic pollen presentation (cf. Müller in press). Comparable pollen-harvesting methods have also been independently developed several times in some taxa of Apiformes, which likewise collect pollen at nototribic flowers (Müller in press). In contrast to these taxa, imagines of *C. tuberculifer* neither show specialized behaviours to improve the release of pollen from the anthers nor do they have particular morphological devices (cf. Schremmer 1959, cf. Müller in press). The brush-like forelegs of *C. tuberculifer* cannot be interpreted as a morphological adaptation to pollen

gathering from nototribic flowers, since they occur in all Masarini (Richards 1962: 35) and therefore probably represent a plesiomorphic character.)

*Chrysis emarginatula* has already been reported as a parasitoid of *C. tuberculifer* by Ferton (1901). In addition Linsenmaier (1968) found this chrysidid associated with an undeterminated *Ceramius* species in Spain. Likewise the second member of the *C. emarginatula* group, *C. tingitana* Bischoff, has exclusively been established together with *Ceramius* (Linsenmaier 1968). Larvae of *Zodion* (Conopidae) have not been recorded as endoparasites of any representative of the Masarinae before (cf. Smith 1966). Previously, the taxon has mainly been associated with various species of Apiformes and only rarely with *Podalonia* ("Sphecidae") and *Odynerus* (Eumeninae) (Smith in litt. 1994).

## ACKNOWLEDGEMENTS

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# Inter-Generic Variation in the External Male Genitalia of the Subfamily Microgastrinae (Hymenoptera, Braconidae), with a Reassessment of Mason's Tribal System

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*Abstract.*—External male genitalia of 39 genera of Microgastrinae, 2 of Cardiochilinae and one of Miracinae were examined to reappraise Mason's tribal system of the braconid subfamily Microgastrinae. Volsellar structures of the male genitalia came to provide useful new characters. On the basis of morphological characters including those of the male genitalia, monophyly of Mason's tribes and their groups was reassessed. The tribes Apantelini and Microgastrini (except for *Sathon*) most likely form a monophyletic group, although monophyly of each tribe is not supported by the evidence. The placement of *Prasmodon* and *Sathon* in the Microgastrini is doubtful, and the latter may belong to the monophyletic assemblage composed of the Cotesiini, Microplitini and Forniciini. The Cotesiini is probably paraphyletic since some of the members seem to be close to the Microplitini and Forniciini.

## INTRODUCTION

With about 1300 described species worldwide, the Microgastrinae is the second largest braconid subfamily in terms of number of species (Shaw and Huddleston, 1991), and it is one of the most important components of the parasitoid complex of many lepidopteran pests in forestry and agriculture (e.g., Gauld and Bolton 1988, Austin and Dangerfield 1992). Members of the subfamily are koinobiont endoparasitoids of lepidopteran larvae and are associated with symbiotic polydnaviruses (Shaw and Huddleston 1991, Stoltz and Whitfield 1992, Sharkey 1993, Wharton 1993).

The monophyly of the Microgastrinae is firmly established by the unique flagellum with invariably 16 articles, most of which typically have 2 ranks of longitudinal placodes (Mason 1981). Also, Mason (1981, 1983) suggested some additional autapomorphies to define this subfamily. It is widely accepted that the Microgastrinae forms a monophyletic group with the Car-

diochilinae, Khoikhoiinae and Miracinae, though the relationships among them have not been firmly resolved (Mason 1983, Quicke and van Achterberg 1990, Wharton et al. 1992, Whitfield and Mason 1994).

Current framework of the generic and tribal systematics of the Microgastrinae was proposed by Mason (1981), who split the large genus *Apanteles* (*sensu* Nixon 1965) into 23 genera and recognized 50 extant genera arranged in five tribes, Apantelini, Microgastrini, Forniciini, Cotesiini and Microplitini. His generic concept was quite close to the species groups of *Apanteles* defined by Nixon (1965), which had been largely taken from the idea of Wilkinson (1932).

Mason's generic classification has been adopted by many taxonomists (e.g., Williams 1985, 1988, Marsh et al. 1987, Papp 1988, Austin and Dangerfield 1992), though Tobias (1986) and Shaw and Huddleston (1991) withheld total approval of his generic proposals. Mason's phylogenetic analysis and suprageneric classifica-

tion of the Microgastrinae, however, have been criticized by Walker et al. (1990), who concluded that Mason's tribes are not established on the basis of synapomorphies. Recent authors (Shaw and Huddleston 1992, Austin and Dangerfield 1992) also hesitated to adopt Mason's tribal system of the Microgastrinae. There is a need of further intensive research to understand the phylogenetic framework of this large and economically important subfamily.

Mason's classification is principally based on structures of the female genitalia. As shown by Tobias (1967), Marsh (1965), Quicke (1988) and Quicke and van Achterberg (1990), the male genitalia can provide useful characters for the higher level classification of braconids. Except for Williams' (1988) revisional study of *Sathon*, however, most systematic studies on the Microgastrinae have given little attention to the male genitalia. The present paper reports on the volsellar structures of the external male genitalia in the Microgastrinae to elucidate their inter-generic variations. I have examined 39 out of 53 extant genera of the Microgastrinae, and also several genera of the Cardiochilinae and Miracinae as outgroups. On the basis of morphological data including those of the male genitalia, I will reappraise Mason's tribal system.

## MATERIALS AND METHODS

The species examined are listed in Table 1. The microgastrines are arranged in Mason's tribal system; *Austrocotesia* is tentatively placed in the Apantelini. As outgroups of the Microgastrinae, *Cardiochiles* and *Hartemita* (Cardiochilinae) and *Mirax* (Miracinae) were examined.

Metasomata of the dried specimens were immersed for 2–3 days in 5% KOH at 40°C. Genitalia were removed from the rest of the metasoma and rinsed with 70% ethanol.

Volsellae were torn away from surrounding cuticle and mounted in glyceri-

ne on slides. They were measured and photographed with a Nikon light microscope.

Terms for male genitalia are taken from Snodgrass (1941). The volsella of the Braconidae consists of lamina volsellaris (l) and two distal lobes, digitus (digitus volsellaris, d) and cuspis (cuspis volsellaris, c) (Figs. 1, 3). At the apex of a median longitudinal ridge (volsellar ridge, r), the lamina volsellaris is distally articulated with the digitus. The cuspis is continuous with the lamina volsellaris in the Microgastrinae and related subfamilies (Quicke and van Achterberg 1990).

Length of the lamina volsellaris was measured from the basal end of the lamina volsellaris to the apical end of the volsellar ridge. Digital length was measured from the apical end of the volsellar ridge to the apex of the digitus.

## RESULTS AND DISCUSSION

### Descriptions of Volsellae

**Microgastrinae: Apantelini.** Lamina volsellaris with 1–8 (usually 2–5) setae or setal alveoli (Table 1). Cuspis glabrous, separated from digitus except for *Miropotes*, in which they were fused with each other and so volsella became a single plate (Figs. 7–8). Relative length of digitus to lamina volsellaris 0.39 to 0.69 (Table 1). In *Apanteles, Austrocotesia, Dolichogenidea, Papanteles, Pholetesor, Promicrogaster* and *Sendaphne*, digitus arched dorsally or crescent-shaped, distinctly convex ventrally, with a pointed apex directed dorsally or laterally (Figs. 1–5, 9, 11–13); in *Illidops*, digitus tubiform apically and strongly arched dorsally (Fig. 6); in *Miropotes*, digitus convex ventrally with the apex rather round (Fig. 7) or crescent-shaped (Fig. 8); in *Pelicope*, digitus only slightly convex ventrally, not crescent-shaped, while the apical portion obviously bent dorsally (Fig. 10). Apex of digitus with 1–4 (usually 2–3) teeth (Table 1).

**Microgastrinae: Microgastrini.** Lamina

Table 1. Lamina volsellaris and digitus of Microgastrinae, Cardiochilinae and Miracinae.

| Taxon | Origin and number of specimens | Length of lamina volsellaris (mm) | No. of setae on lamina volsel- laris[a] | Digitus/ lamina volsellaris length | No. of apical teeth of digitus | Shape of digitus[b] |
|---|---|---|---|---|---|---|
| **MICROGASTERINAE** | | | | | | |
| Apantelini | | | | | | |
| *Apanteles baldufi* Muesebeck | USA (1) | 0.16 | 3 | 0.58 | 2 | A, C (Fig. 1) |
| *Apanteles conopiae* Watanabe | Japan (2) | 0.22–0.25 | 6–8 | 0.46–0.52 | 2 | A, C |
| *Apanteles crassicornis* (Provancer) | Canada (1) | 0.3 | 3–4 | 0.51 | 2 | A, C |
| *Apanteles cypris* Nixon | Japan (5) | 0.17–0.20 | 2–5 | 0.44–0.51 | 2 | A, C (Fig. 2) |
| *Apanteles murinanae* Capek & Zwoelfer | Switzerland (1) | 0.23 | 3–4 | 0.48 | 2 | A, C |
| *Apanteles nephoptericis* (Packard) | Canada (1) | 0.22 | 3 | 0.41 | 2 | A, C |
| *Apanteles xanthostigma* (Haliday) | Europe (1) | 0.17 | 3 | 0.55 | 1 | A, C |
| *Austrocotesia delicata* Austin & Dangerfield | New Guinea (1) | 0.11 | 3 | 0.45 | 1–2 | A, C (Fig. 3) |
| *Dolichogenidea absona* (Muesebeck) | Canada (1) | 0.20 | 3 | 0.44 | 2 | A, C |
| *Dolichogenidea conspersae* (Fiske) comb. nov. = *Apanteles conspersae* Fiske, 1911 | Japan (5) | 0.15–0.17 | 3–4 | 0.44–0.54 | 2 | A, C |
| *Dolichogenidea dilecta* (Haliday) | Slovakia (1) | 0.20 | 4 | 0.42 | 2 | A, C |
| *Dolichogenidea infima* (Haliday) | Hungary (1) | 0.18 | 2–3 | 0.49 | 2 | A, C (Fig. 4) |
| *Dolichogenidea nixosiris* (Papp) | Mongolia (1) | 0.16 | 2 | 0.54 | 2 | A, C (Fig. 5) |
| *Dolichogenidea* sp. (*laevigata* species-group) | Japan (5) | 0.18–0.21 | 3–4 | 0.48–0.55 | 2 | A, C |
| *Illidops* sp. | Canada (1) | 0.26 | 7 | 0.39 | 2 | T, C (Fig. 6) |
| *Miropotes kilkulunis* Austin | Australia (1) | 0.15 | (1) | 0.52 | 2 | O–R, C (Fig. 7) |
| *Miropotes thuraris* Austin | New Hebridis (1) | 0.17 | 2 | 0.46 | 2 | A, C (Fig. 8) |
| *Papanteles peckorum* Mason | Ecuador (1) | 0.21 | 3–4 | 0.69 | 3 | A, C (Fig. 9) |
| *Pelicope yuccamica* Mason | USA (1) | 0.28 | 2 | 0.57 | 3–4 | O, S (Fig. 10) |
| *Pholetesor bicolor* (Nees) | Hungary (2) | 0.13 | 2 | 0.48–0.54 | 2 | A, C |
| *Pholetesor circumscriptus* (Nees) | Hungary (1) | 0.13 | 2 | 0.49 | 2 | A, C |
| *Pholetesor salalicus* (Mason) | USA (1) | 0.14 | 2 | 0.48 | 1 | A, C |
| *Pholetesor viminetorum* (Wesmael) | USA (1) | 0.17 | 3 | 0.46 | 2 | A, C (Fig. 13) |
| *Promicrogaster* sp. | Brazil (1) | 0.17 | 3–4 | 0.55 | 3 | A, C (Fig. 11) |
| *Sendaphne* sp. | Ecuador (1) | 0.20 | 5–6 | 0.60 | 2 | A, C (Fig. 12) |
| Microgastrini | | | | | | |
| *Choeras consimilis* (Viereck) | Canada (1) | 0.19 | 3 | 0.42 | 2 | A, C |
| *Choeras psarae* (Wilkinson) | Nepal (1) | 0.23 | 2 | 0.54 | 2 | A, C (Fig. 14) |
| *Choeras takeuchii* (Watanabe) comb. nov. = *Microgaster takeuchii* Watanabe, 1937 | Japan (6) | 0.23–0.28 | 2–3 | 0.46–0.57 | 2–3 | A, C (Fig. 15) |
| *Hygroplitis melligaster* (Provancher) | Canada (1) | 0.25 | 4 | 0.34 | 2 | O, C–S |
| *Hygroplitis russatus* (Haliday) | Japan (3) | 0.28 | 2–4 | 0.46–0.48 | 3 | O, C (Fig. 19) |
| *Hypomicrogaster ecdytolophae* (Muesebeck) | Canada (1) | 0.18 | 3 | 0.48 | 2–3 | A, C (Fig. 16) |
| *Iconella etiellae* (Viereck) | Mexico (1) | 0.26 | 4–5 | 0.49 | 2 | A, C (Fig. 17) |
| *Iconella* sp. | Japan (2) | 0.23 | 3–4 | 0.58 | 2 | A, C |
| *Microgaster australis* Thomson | Spain (1) | 0.23 | 3 | 0.46 | 2–3 | A, C (Fig. 18) |
| *Microgaster canadensis* Muesebeck | Canada (1) | 0.23 | 2 | 0.46 | 2–3 | O, C |
| *Microgaster gelechiae* Riley | Canada (1) | 0.30 | 2 | 0.45 | 4 | O, C |
| *Microgaster hospes* Marshall | Hungary (1) | 0.23 | 2 | 0.50 | 3 | O, C |
| *Microgaster kuchingensis* Wilkinson | Japan (2) | 0.28 | 3 | 0.50–0.52 | 3 | O, C (Fig. 20) |
| *Microgaster subcompleta* Nees | Japan (2) | 0.26–0.28 | 2–3 | 0.45–0.52 | 2–3 | O, C |
| *Microgaster tibialis* Nees | Hungary (2) | 0.24 | 2–3 | 0.45–0.47 | 3 | O, C |
| *Paroplitis* cf. *wesmaeli* (Ruthe) | Japan (1) | 0.14 | 3–4 | 0.62 | 2 | A, C (Fig. 21) |

Table 1. Continued

| Taxon | Origin and number of specimens | Length of lamina volsellaris (mm) | No. of setae on lamina volsellaris | Digitus/ lamina volsellaris length | No of apical teeth of digitus | Shape of digitus |
|---|---|---|---|---|---|---|
| *Prasmodon* sp. | Brazil (1) | 0.27 | 2 | 0.46 | 4–5 | A–R, S (Fig. 22) |
| *Pseudapanteles annulicornis* Ashmead | Panama (1) | 0.15 | 2 | 0.45 | 2 | A, C (Fig. 23) |
| *Rhygoplitis aciculatus* Ashmead | St. Lucia (1) | 0.17 | 3 | 0.51 | 2 | A, C (Fig. 25) |
| *Sathon lateralis* (Haliday) | Ireland (1) | 0.20 | 3 | 0.44 | 2 | R, S (Fig. 24) |
| *Sathon masoni* Williams | USA (1) | 0.22 | 7 | 0.44 | 2 | N, C–S (Fig. 27) |
| *Sathon neomexicanus* (Muesebeck) | USA (1) | 0.52 | 7 | 0.50 | 2 | T, C (Fig. 26) |
| *Xanthomicrogaster* sp. | Ecuador (1) | 0.21 | 1 | 0.46 | 2 | A, C–S (Fig. 28) |
| Forniciini | | | | | | |
| *Fornica arata* (Enderlein) | Taiwan (1) | 0.27 | 2 | 0.46 | 3–4 | R, C |
| *Fornica ceylonica* Wilkinson | Taiwan (1) | 0.21 | 2 | 0.53 | 3 | R, C–S (Fig. 29) |
| Cotesiini | | | | | | |
| *Buluka achterbergi* Austin | Pen. Malaysia (1) | 0.13 | (3) | 0.49 | 2 | R, C (Fig. 34) |
| *Cotesia affinis* (Nees) | Japan (5) | 0.15–0.17 | 12–15 | 0.47–0.51 | 3–4 | R, S |
| *Cotesia ancilla* (Nixon) | Japan (1) | 0.13 | 8–10 | 0.49 | 3 | R, S |
| *Cotesia flavipes* Cameron | Japan (3) | 0.16–0.19 | 6–7 | 0.27–0.35 | 2 | R, S |
| *Cotesia glomerata* (L.) | Japan (4) | 0.14–0.16 | 6–9 | 0.37–0.46 | 2–3 | R, S |
| *Cotesia kariyai* (Watanabe) | Japan (2) | 0.20 | 8–10 | 0.35 | 3 | R, S |
| *Cotesia melanoscelus* (Ratzeburg) | Canada (1) | 0.13 | 13 | 0.45 | 4 | R, S (Fig. 36) |
| *Cotesia ofella* (Nixon) | Italy (1) | 0.15 | 10–13 | 0.40 | 3 | R, S |
| *Cotesia plutellae* (Kurdjumov) | Japan (3) | 0.12 | 10–13 | 0.42–0.47 | 3 | R, S |
| *Cotesia rubecula* (Marshall) | Canada (1) | 0.15 | 10–12 | 0.43 | 3 | R, S |
| *Cotesia tatehae* (Wesmael) | Japan (5) | 0.17–0.20 | 7–8 | 0.38–0.46 | 4–6 | R, S (Fig. 37) |
| *Cotesia tenebrosa* (Wesmael) | Iraq (1) | 0.13 | 8–9 | 0.42 | 4 | R, S |
| *Deuterixys carbonaria* (Wesmael) | Sweden (1) | 0.10 | 2 | 0.47 | 2 | R, S (Fig. 38) |
| *Deuterixys pacifica* Whitfield | USA (1) | 0.09 | 2 | 0.46 | 2 | R, S |
| *Diolcogaster abdominalis* (Nees) | Hungary (1) | 0.20 | 6–7 | 0.46 | 4 | R, S (Fig. 39) |
| *Diolcogaster duris* (Nixon) | Mexico (1) | 0.18 | 5–6 | 0.50 | 2 | R, S |
| *Diolcogaster* cf. *spreta* (Marshall) | Japan (5) | 0.13–0.15 | 3–5 | 0.49–0.52 | 3–4 | R, C (Fig. 40) |
| *Distatrix papilionis* (Viereck) | India (2) | 0.16 | 1 | 0.40–0.44 | 2 | R, C–S (Fig. 41) |
| *Exix mexicana* Mason | Mexico (1) | 0.18 | 6–7 | 0.49 | 2–3 | R, S (Fig. 42) |
| *Glyptapanteles aliphera* (Nixon) | Netherlands (1) | 0.17 | 4–5 | 0.45 | 2 | R, S (Fig. 46) |
| *Glyptapanteles fulvipes* (Haliday) | Japan (5) | 0.16–0.18 | 6–7 | 0.36–0.41 | 2 | R, S |
| *Glyptapanteles liparidis* (Bouche) | Japan (5) | 0.20–0.24 | 9–13 | 0.44–0.51 | 4–5 | R, S (Fig. 47) |
| *Glyptapanteles websteri* (Muesebeck) | Canada (1) | 0.11 | 2 | 0.49 | 2 | R, S |
| *Lathrapanteles fuscus* Williams | Canada (1) | 0.20 | 7–8 | 0.45 | 2 | N, C–S (Fig. 35) |
| *Protapanteles alaskensis* Ashmead | Canada (1) | 0.14 | 7 | 0.43 | 2 | R, S |
| *Protapanteles anchisiades* (Nixon) | Slovakia (1) | 0.17 | 7 | 0.42 | 2 | R, S |
| *Protapanteles lymantriae* (Marsh) | Japan (2) | 0.16 | 6–9 | 0.37–0.45 | 2–3 | R, S (Fig. 43) |
| *Protomicroplitis calliptera* (Say) | USA (1) | 0.23 | 4–6 | 0.54 | 2 | R, S |
| *Protomicroplitis mediatus* (Cresson) | Cuba (1) | 0.27 | 6–7 | 0.43 | 2 | R, C (Fig. 44) |
| *Rasivalva rugosa* (Muesebeck) | USA (1) | 0.17 | 2–3 | 0.41 | 2 | R, S (Fig. 45) |
| *Rasivalva stigmatica* (Muesebeck) | Canada (1) | 0.18 | 4–5 | 0.47 | 2 | R, S |
| *Venanides xeste* Mason | Canada (1) | 0.15 | 1–2 | 0.37 | 3 | R, C–S (Fig. 48) |
| *Venanus pinicola* Mason | USA (1) | 0.09 | (1) | 0.46 | 2 | R, S (Fig. 49) |
| *Wilkinsonellus striatus* Austin & Dangerfield | New Guinea (1) | 0.15 | (2) | 0.52 | 2 | R, C–S (Fig. 50) |
| Microplitini | | | | | | |
| *Alloplitis completus* Nixon | Pen. Malaysia (1) | 0.17 | 2 | 0.47 | 2 | R, S (Fig. 33) |
| *Microplitis ataniensis* Ashmead | Japan (4) | 0.17–0.22 | 2–4 | 0.42–0.49 | 2–3 | R, S (Fig. 30) |
| *Microplitis deprinator* (Fabricius) | Japan (3) | 0.19–0.22 | 3–4 | 0.36–0.43 | 2 | R, S |

Table 1. Continued

| Taxon | Origin and number of specimens | Length of lamina volsellaris (mm) | No. of setae on lamina volsellaris[a] | Digitus/ lamina volsellaris length | No. of apical teeth of digitus | Shape of digitus[b] |
|---|---|---|---|---|---|---|
| *Microplitis manilae* Ashmead | Taiwan (2) | 0.16 | 2–3 | 0.42–0.46 | 2 | R, S |
| *Microplitis ratzeburgii* (Ruthe) | Japan (1) | 0.27 | 5 | 0.39 | 2 | R, C–S |
| *Microplitis sispes* Nixon | Canada (1) | 0.30 | 3–4 | 0.33 | 2 | R, S (Fig. 31) |
| *Snellenius theretrae* (Watanabe) | Japan (2) | 0.30–0.32 | 4–5 | 0.41–0.45 | 2 | R, S (Fig. 32) |
| CARDIOCHILINAE | | | | | | |
| *Cardiochiles japonicus* Watanabe | Japan (2) | 0.43–0.50 | 4–5 | 0.44–0.51 | 8 | R, C–S (Fig. 51) |
| *Cardiochiles nigriceps* Viereck | USA (1) | 0.39 | 3–4 | 0.52 | 10 | R, S (Fig. 52) |
| *Cardiochiles szepligetii* Enderlein | Taiwan (2) | 0.30 | 4–6 | 0.44–0.49 | 7 | R, C–S |
| *Hartemita muirii* (Fullaway) | Japan (1) | 0.29 | 7–8 | 0.48 | 5 | R, S (Fig. 53) |
| MIRACINAE | | | | | | |
| *Mirax captodiscae* Walley | Canada (1) | 0.10 | (5) | 0.43 | 2 | R, S (Fig. 54) |
| *Mirax insularis* Muesebeck | Dominica (1) | 0.09 | (4–5) | 0.46 | 2 | R, S |
| *Mirax mogrus* Papp | Japan (3) | 0.12–0.16 | (4–6) | 0.40–0.44 | 2 | R, S (Fig. 55) |

[a] Number of alveoli without a seta is indicated in parentheses.
[b] Apex: A = acute and directed dorsally, O = somewhat obtuse and directed dorsally, N = narrowly truncated, not strongly directed dorsally, R = round or broadly truncated, T = tubiform and curved dorsally. Ventral edge: C = strongly convex, S = almost straight or slightly convex.

volsellaris with 1–7 (usually 2–4) setae (Table 1). Cuspis glabrous, separated from digitus. Relative length of digitus to lamina volsellaris 0.34 to 0.62 (Table 1). In *Choeras, Hypomicrogaster, Iconella, Paroplitis* and *Pseudapanteles*, digitus arched dorsally or crescent-shaped, distinctly convex ventrally, with a pointed apex directed dorsally or laterally (Figs. 14–17, 21, 23); in *Hygroplitis, Microgaster* and *Rhygoplitis*, digitus arched dorsally as in the preceding genera but the apex somewhat obtuse (Figs. 18–20, 25); in *Prasmodon* and *Xanthomicrogaster*, digitus not or only slightly convex ventrally, not crescent-shaped, but the apical portion obviously bent ventrally (Figs. 22, 28). In *Sathon*, digitus slightly convex ventrally, not crescent-shaped, with a round or narrowly truncated apex (Figs. 24, 27), or slender, tubiform and abruptly curved dorsally (Fig. 26). Apex of digitus with 2–4 teeth, but the number of the apical teeth up to 5 in *Prasmodon* (Table 1).

**Microgastrinae: Forniciini.** Lamina volsellaris with 2 setae (Table 1). Cuspis glabrous and separated from digitus. Relative

length of digitus to lamina volsellaris 0.46 to 0.53. Digitus weakly convex ventrally, not crescent-shaped, with a round apex bearing 3–4 teeth (Fig. 29).

**Microgastrinae: Cotesiini.** Lamina volsellaris with 1–15 setae or setal alveoli, usually with less than 8 setae except for *Cotesia*, in which it has 6–15 setae (Table 1, Fig. 56). Cuspis glabrous and separated from digitus, but the intermediate membranous area is narrow in *Deuterixys* (Fig. 38) and *Vananus* (Fig. 49). Relative length of digitus to lamina volsellaris 0.27 to 0.54 (Table 1). Digitus almost straight or weakly convex ventrally, not crescent-shaped, with a round apex (Figs. 34, 36–50), or with a narrowly truncated apex in *Lathrapanteles* (Fig. 35). Apex of digitus with 2–6 (usually 2–4) teeth (Table 1).

**Microgastrinae: Microplitini.** Lamina volsellaris with 2–5 setae (Table 1). Cuspis glabrous and separated from digitus. Relative length of digitus to lamina volsellaris 0.33 to 0.49 (Table 1). Digitus almost straight or weakly convex ventrally, not crescent-shaped, with a round apex bearing 2–3 teeth (Figs. 30–33).

**Cardiochilinae.** Lamina volsellaris with 3–8 setae (Table 1). Cuspis separated from digitus, and bearing a group of alveoli without seta (Fig. 52). Relative length of digitus to lamina volsellaris 0.44–0.52. Digitus round apically and not or weakly arched dorsally (Figs. 51–53), with 5–10 apical teeth.

**Miracinae.** Lamina volsellaris with 4–6 alveoli, invariably without seta. Cuspis glabrous, separated from digitus. Relative length of digitus to lamina volsellaris 0.40–0.46. Digitus broadly truncated apically, slightly arched dorsally, and invariably with 2 apical teeth (Figs. 54–55).

### Polarity of Character States

Based on the conditions observed in the outgroups, Cardiochilinae and Miracinae, the polarity of character states in the Microgastrinae is suggested as follows:

1. **Number of setae (or setal alveoli) on lamina volsellaris.** The plesiomorphic condition is perhaps 3–6. Loss and acquisition of setae are found both in the Microgastrini and Cotesiini. *Cotesia* is aberrant in always having numerous volsellar setae (Fig. 56), and also some other genera of the Cotesiini (*Glyptapanteles, Lathrapanteles, Protapanteles*) and *Sathon* (Microgastrini) often have 7 or more setae.
2. **Articulation of digitus with cuspis.** Separation of the digitus from the cuspis is apparently plesiomorphic. The fusion of these lobes is found only in the genus *Miropotes* (Apantelini).
3. **Relative length of digitus to lamina volsellaris.** Medium sized digitus, 0.4–0.5 of the lamina volsellaris in length, is probably plesiomorphic. A comparatively long digitus (0.55 or more times as long as the lamina volsellaris) was found in some genera of the Apantelini and Microgastrini.
4. **Shape of digitus.** The digitus, not distinctly arched dorsally, with a round or broadly truncated apex is probably ple-

siomorphic. The digitus found in the Apantelini and Microgastrini is apomorphic, being crescent-shaped with a sharp (occasionally slightly obtuse) apex directed dorsally or laterally.
5. **Number of apical teeth of digitus.** A plesiomorphic condition cannot be defined, because the teeth vary in number from 2 in the Miracinae to 5–10 in the Cardiochilinae.

### Reassessment of Mason's Tribal System

Although Mason (1981) postulated that his tribes Apantelini and Microgastrini form a monophyletic group, he did not suggest any credible synapomorphies for the assemblage (Walker et al. 1990). Austin (1990), however, pointed out that the ventromedially membranous, folded and often expandible hypopygium is probably a synapomorphy for a clade including most, definitely not all, of Mason's Apantelini + Microgastrini.

Moreover, the monophyly of Apantelini + Microgastrini is most likely to be supported by the crescent-shaped or arched digitus with its sharp (or slightly obtuse) apex being directed dorsally or laterally. In some aberrant genera (*Illidops, Miropotes, Pelicope* and *Xanthomicrogaster*), the digitus is not typically crescent-shaped, but the apical portion tends to be pointed dorsally or laterally.

Mason's tribe Apantelini has been distinguished from his Microgastrini by having no percurrent median carina on the propodeum. Most genera of the Apantelini doubtless form a monophyletic group supported by the anteriorly projecting lateral lobe of the metanotum (Mason 1981). However, some genera (*Miropotes, Sendaphne, Pelicope,* etc.) of the Apantelini are devoid of the apomorphy. At the same time, some genera (*Choeras, Clarkinella, Iconella*) of the Microgastrini show a similar if not homologous character state (Mason 1981). The percurrent median propodeal carina of the Microgastrini may be apomorphic, but the same condition is found
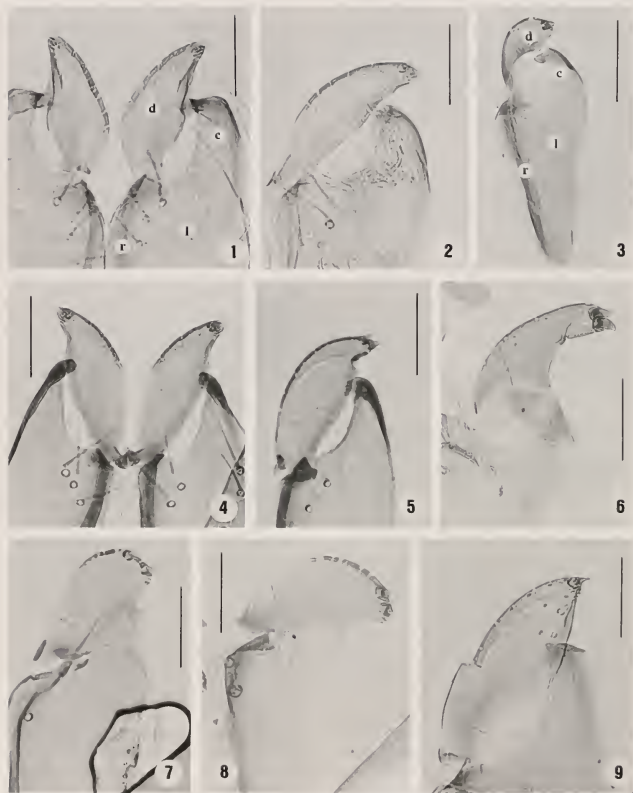
Figs. 1–9. Apical portion of volsella in the Apantelini. 1, *Apanteles baldufi*. 2, *Apanteles cypris*. 3, *Austrocotesia delicata* (the whole of volsella). 4, *Dolichogenidea infima*. 5, *Dolichogenidea nixosiris*. 6, *Illidops* sp. 7, *Miropotes kilkulunis*. 8, *Miropotes thuraris*. 9, *Papanteles peckorum*. Abbreviations: **c**, cuspis; **d**, digitus; **l**, lamina volsellaris; **r**, volsellar ridge. Scale lines = 0.05mm.
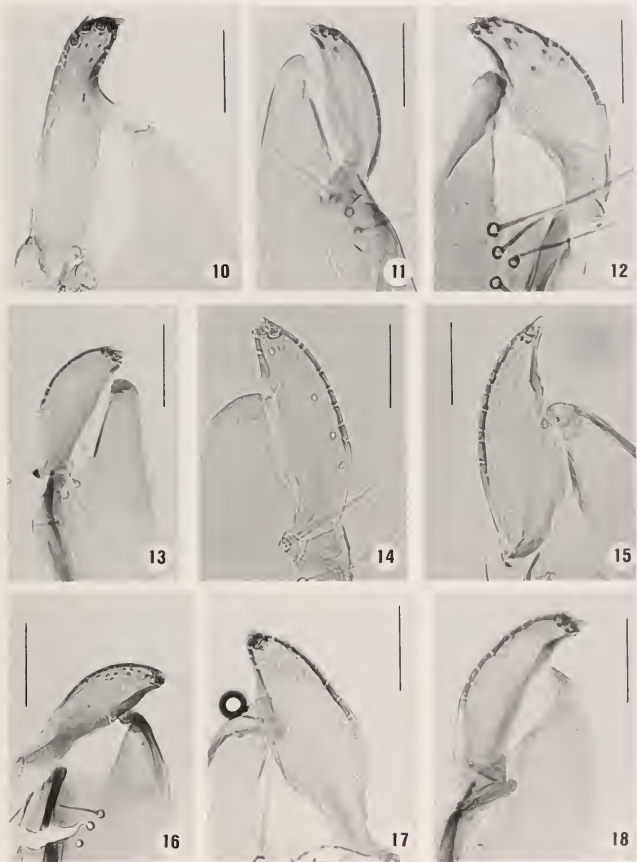
Figs. 10–18. Apical portion of volsella in the Apantelini (10–13) and Microgastrini (14–18). 10, *Pelicope yuccamica*. 11, *Promicrogaster* sp. 12, *Sendaphne* sp. 13, *Pholetesor viminetorum*. 14, *Choeras psarae*. 15, *Choeras takeuchii*. 16, *Hypomicrogaster ecdytolophae*. 17, *Iconella etiellae*. 18, *Microgaster australis*. Scale lines = 0.05mm.
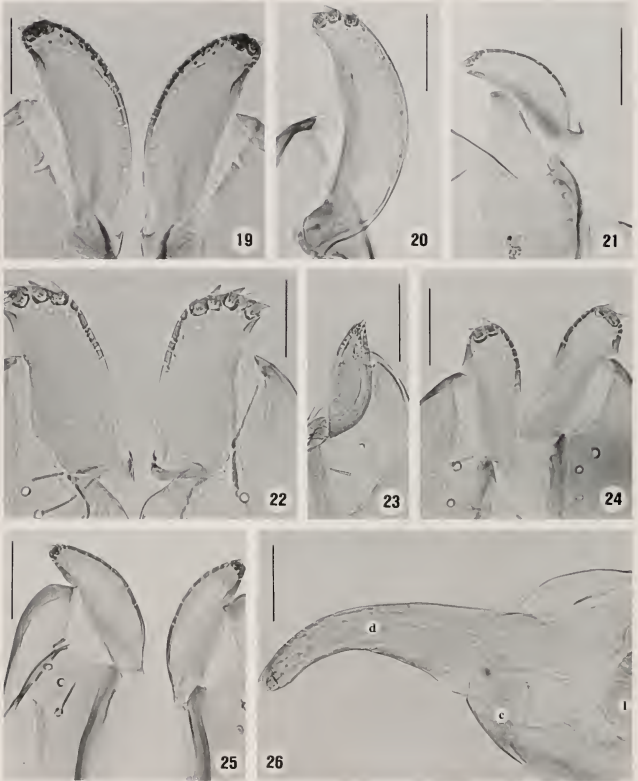
Figs. 19–26. Apical portion of volsella in the Microgastrini. 19, *Hygroplitis russatus*. 20, *Microgaster kuchingensis*. 21, *Paroplitis* cf. *wesmaeli*. 22, *Prasmodon* sp. 23, *Pseudapanteles annulicornis*. 24, *Sathon lateralis*. 25, *Rhygoplitis aciculatus*. 26, *Sathon neomexicanus*. Abbreviations: c, cuspis; d, digitus; l, lamina volsellaris. Scale lines = 0.05mm

Figs. 27–35. Apical portion of volsella in the Microgastrini (27–28), Forniciini (29), Microplitini (30–33) and Cotesiini (34–35). 27, *Sathon masoni*. 28, *Xanthomicrogaster* sp. 29, *Fornica ceylonica*. 30, *Microplitis atamiensis*. 31, *Microplitis sispes*. 32, *Snellenius theretrae*. 33, *Alloplitis completus*. 34, *Buluka achterbergi*. 35, *Lathrapanteles fuscus*. Scale lines = 0.05mm.
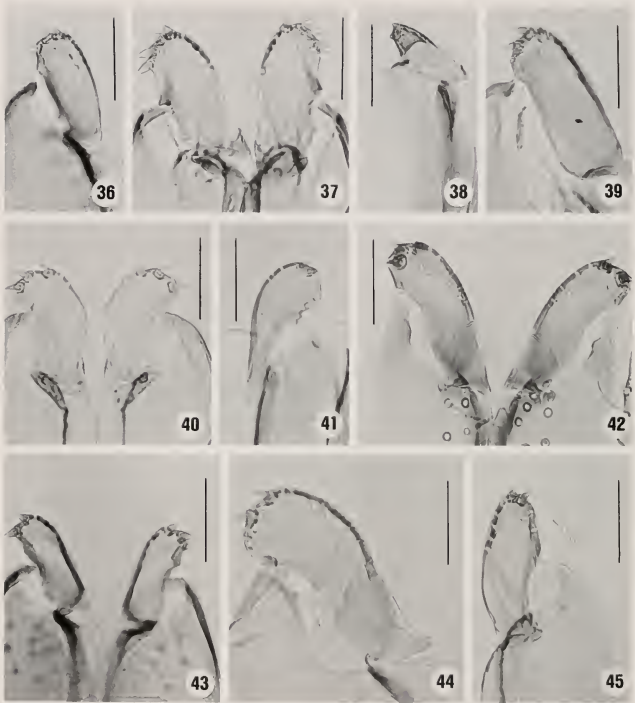
Figs. 36–45. Apical portion of volsella in the Cotesiini. 36, *Cotesia melanoscelus*. 37, *Cotesia tatehae*. 38, *Deuterixys carbonaria*. 39, *Diolcogaster abdominalis*. 40, *Diolcogaster* cf. *spreta*. 41, *Distatrix papilionis*. 42, *Exix mexicana*. 43, *Protapanteles lymantriae*. 44, *Protomicroplitis mediatus*. 45, *Rasivalva rugosa*. Scale lines = 0.05mm.

in many other Microgastrinae as well as in the Cardiochilinae and Miracinae. Therefore, the sister-group relationship of the Apantelini and Microgastrini is unsupported.

Although the hypopygium of *Austrocotesia*, *Hygroplitis* and most *Pholeteor* is evenly sclerotized (plesiomorphic), their digitus is apomorphic in shape. They may be basal lineages of the clade Apantelini + Microgastrini, or they may have secondarily lost the membranous median fold of the hypopygium. The placement of *Prasmodon* in this clade is uncertain, be-
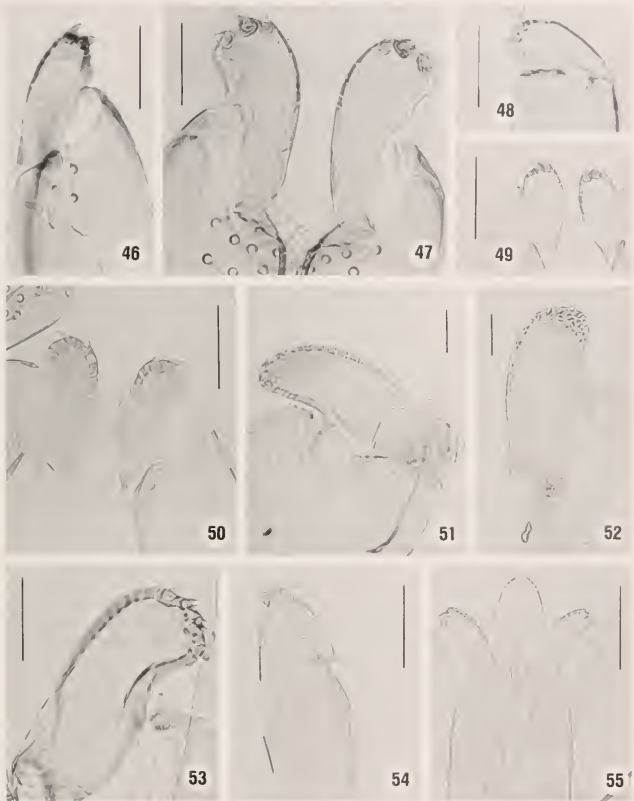
Figs. 46–55. Apical portion of volsella in the Cotesiini (46–50) and in the Cardiochilinae (51–53) and Miracinae (54–55). 46, *Glyptapanteles aliphera*. 47, *Glyptapanteles liparidis*. 48, *Venanides xeste*. 49, *Venanus pinicola*. 50, *Wilkinsonellus striatus*. 51, *Cardiochiles japonicus*. 52, *Cardiochiles nigriceps*. 53, *Hartemita muirii*. 54. *Mirax captodiscae* (the whole of volsella). 55, *Mirax mogrus* (including aedeagus). Scale lines = 0.05mm.

Fig. 56. Number of setae or setal alveoli on lamina volsellaris in the Microgastrinae and its outgroups, Cardiochilinae and Miracinae.

cause it lacks the membranous hypopygium and also its digitus is not evidently apomorphic.

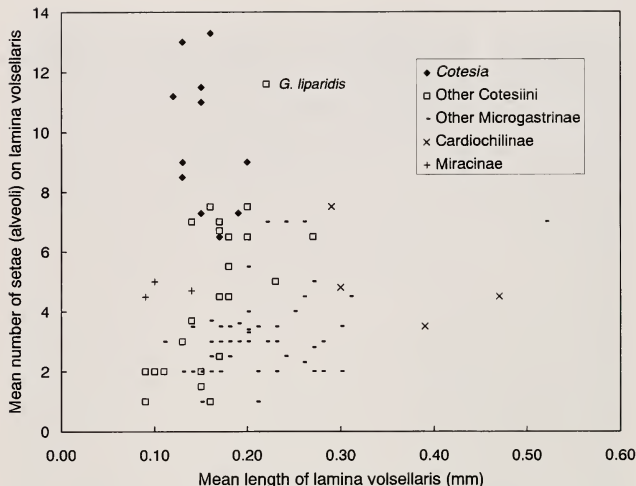Also, *Sathon* has been placed in the Microgastrini even though its hypopygium is evenly sclerotized (Mason 1981, Williams 1985, 1988). The digitus of *Sathon* varies in shape but is always different from the crescent-shaped digitus of most Apantelini and Microgastrini; it is round apically in *S. lateralis* like in many of the Forniciini + Cotesiini + Microplitini, narrowly truncated in *S. masoni* very similar to that of *Lathrapanteles fuscus* (Cotesiini), or aberrantly tubiform in *S. neomexicanus*. Hence, *Sathon* shares no definite synapomorphies with the rest of Apantelini + Microgastrini. On the other hand, the metanotum of *Sathon* shows a simple and glabrous anterior margin, along with a widely exposed scutellar phragma (Williams 1988); such an apomorphic state is frequently found in the Cotesiini (e.g., *Glyptapanteles, Lathrapanteles, Protapanteles*) but not in the Apantelini nor Microgastrini (Mason 1981). Moreover, the larval papules of the larval skin lack long spines (apomorphic state) in *Sathon* as in most Cotesiini and Microplitini. These circumstantial pieces of evidence suggest that *Sathon* belongs to the Cotesiini instead of to the Microgastrini.

Mason's tribes of Forniciini, Cotesiini and Microplitini are commonly characterized by several apomorphies: ovipositor sheath (3rd valvula) attached to 2nd valvifer subbasally, 2nd valvifer widened apically, larval mandible with no teeth or with less than 15 (usually a few weak) teeth subapically, and papules of larval

skin without long spines (Short 1953, Mason 1981, Williams 1985, Walker et al. 1990). Mason (1981) indicated additional apomorphies (e.g., setae of ovipositor sheath restricted apically, ovipositor abruptly narrowed subapically) while these may be related to the reduction of the ovipositor in length. In fact, the genus *Lathrapanteles*, which has a long ovipositor, lacks some of the apomorphies (Williams 1985). Besides the morphological apomorphies, absence of the final ectophagous stage of larvae may be also autapomorphic for the Cotesiini and Microplitini, because the ectophagous phase is common in the Apantelini and Microgastrini as well as in the Cardiochilinae and Cheloninae (Huddleston and Walker 1988, Shaw and Huddleston 1991).

Mason (1981) divided this clade into the Forniciini, Cotesiini and Microplitini, without indicating any reliable autapomorphies for the Cotesiini (Walker et al., 1990). In the Forniciini, Microplitini, and the *Diolcogaster* genus-group of the Cotesiini, the apical smooth band of the scutellum is almost always interrupted medially by a punctate or rugose area (Nixon, 1965, Mason 1981, Austin 1992); this condition is possibly apomorphic within the clade Forniciini + Cotesiini + Microplitini because, as in the remainder of this clade, the apical smooth band of the scutellum is continuous in the Apantelini and Microgastrini (except for *Illidops*). Moreover, females of *Fornicia* (Forniciini), *Alloplitis* (Microplitini) and at least two genera, *Diolcogaster* and *Exix*, of the *Diolcogaster* genus-group (Cotesiini) share apomorphic, ventral sensory fields on the middle and subapical flagellomeres in common (Mason 1981). Therefore, it is most likely that the Cotesiini is paraphyletic when the Forniciini and Microplitini are not included.

In conclusion, Mason's framework of two main clades (Apantelini + Microgastrini, and Forniciini + Cotesiini + Microplitini) in the Microgastrinae is essentially supported while monophyly of each tribe is not sustained.

## ACKNOWLEDGEMENTS

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# *Horcomutilla* Casal: Description of Previously Unknown Males, New Distribution Records, and Comments on the Genus (Hymenoptera: Mutillidae)

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*Abstract.*—The previously unknown male of the genus *Horcomutilla* Casal is described, based on sex associations in two species, *H. krombeini* Casal, 1965 and *H. maracayi* Fritz & Martínez, 1993. These males are unique among American Sphaeropthalminae in having the distal third of their parameres bifid. *Horcomutilla krombeini* Casal, previously known from Panama, is recorded from Venezuela. A generic discussion is presented.

## INTRODUCTION

The pseudomethocine genus *Horcomutilla* Casal, 1962 is known from 14 species, all known from females only, distributed from the Province of Chiriquí (near Costa Rica), Panama, south into Argentina (Casal 1962, 1965, 1970; Cambra & Quintero 1992; Fritz 1992; Fritz & Martínez 1993). Females of *Horcomutilla* range from 6 to 12 mm in body length and are quite variable in the color of the integument. We comment on the somatic variation we have observed in two species of *Horcomutilla*: *H. krombeini* Casal and *H. maracayi* Fritz & Martínez.

We here describe the first males known for the genus *Horcomutilla* and associated them with females of *H. krombeini* Casal and *H. maracayi* Fritz & Martínez from material collected in Panamá (19 males) and Venezuela (2 males). Descriptions are followed by additional material examined, new distributional data and taxonomic notes. We recently incorporated the males of *Horcomutilla* into a generic key for Peruvian mutillids (Quintero & Cambra 1996). Their genitalia are unique among Sphaeropthalminae from America that we have examined, including males of *Calo-*

*mutilla* Mickel, 1952, and *Pertyella* Mickel, 1952 (Quintero & Cambra, unpublished), in having the distal third of the parameres bifid. Scanning electron microscopy was done with a JEOL model JSM 5300LV. The following acronyms are used: U.S. National Museum of Natural History at Smithsonian Institution (USNM); University of Minnesota Insect Collection (UMIC), and Museo de Invertebrados G. B. Fairchild at Universidad de Panamá (MIUP).

## HORCOMUTILLA Casal, 1962

Type species: *Sphinctomutilla fronticornis* var. *glabriceps* André, 1908 (Museo Argentino de Ciencias Naturales); female lectotype designation by Casal (1962).

*Generic characters of males.*—Proboscidal fossa not extending to base of mandibles (Figs. 3–4); genal carinae absent; proximal two-thirds of mandibles broad, then narrowed, forming a conspicuous tooth on the inner margin, the distal third slender and edentate (Fig. 6); scape with a single sharp carina beneath; first and second flagellomeres equal in length; antennal scrobes slightly carinate above (Fig. 1); humeral angles of pronotum rounded (Figs. 7–8); par-
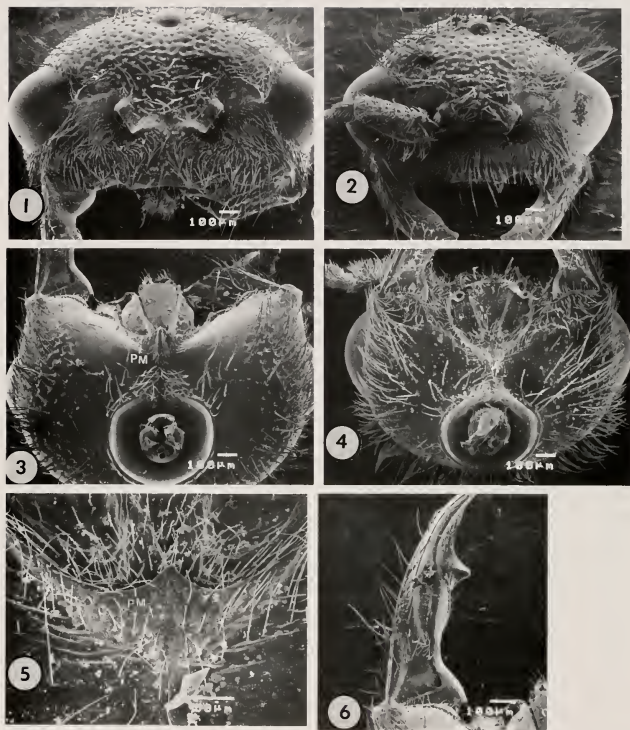
Figs. 1–6.   Head details of *Horcomutilla*, males. 1, *krombeini*, head, frontal view (× 75). 2, *maracayi*, head, frontal view (× 75). 3, *krombeini*, head, ventral view (× 75); PM = posterior margin of proboscidal fossa. 4, *maracayi*, head, ventral view (× 75). 5, *maracayi*, posterior margin of proboscidal fossa, triangular projection without a middle longitudinal ridge (× 350); PM = posterior margin of proboscidal fossa. 6, *krombeini*, mandible (ventral face), lateral view (× 100).

apsidal lines nearly obliterated (Fig. 7); dorsum and posterior face of propodeum rounded into one another, without an enclosed space, reticulate throughout (Fig. 7–8); abdomen with segment one completely sessile with second; tergum two with felt lines; sternum two without felt lines; marginal cell of front wings rounded distally

and acute at the apices (Figs. 11–12); third submarginal cell present but less distinct than the second; parameres with the distal third bifid (Figs. 13–19).

*Discussion of the Genus Horcomutilla.*— Species of *Horcomutilla*, as well as those of *Pseudomethoca* Ashmead, are present in a range of environments, from those highly degraded by humans to primary humid tropical lowland forests. We have found species of both genera living sympatrically in Panama and Brazil. *Horcomutilla* is closely related to *Pseudomethoca* Ashmead and *Mickelia* Suárez. The latter is at present separated only by its "flattened" flagellomeres, but we consider that the valid diagnostic character is the outline of the thorax: rectangular in *Mickelia* and violin shaped in *Horcomutilla*. We have examined the female paratype of *Mickelia cressoni* Suárez, 1966 (same data as the holotype), and two females of that species from Goiás and Sao Paulo, Brazil. We found that their flagellomeres are not distinctly flattened, but that 4–12 are slightly compressed, looking much like a preservation artifact commonly found among many different mutillid taxa. Moreover, the compression of flagellomeres 1–3 is bilaterally asymmetric.

Preliminary results of a generic phylogenetic analysis of Sphaeropthalminae (Quintero, unpublished) indicate that the monophyly of *Horcomutilla* is supported by the single synapomorphy of the bifid distal third of the parameres. It appears to be a highly derived character within the Aculeata, not mentioned by Brothers and Carpenter (1993). Bifid parameres (biramous gonostyles) are known from a few species in three genera of Sphecidae (Bohart and Menke 1976, p. 21), but is used as a generic character in only one of those genera, *Entomosericus* Dahlbom. The function and structural correspondence of the bifid parameres with the female genitalia is unknown, as is true for most other parts of the male genitalia of aculeate wasps. O'Toole (1975) suggested a locking action

of the parameres (= gonoforceps) for *Timulla oculata* (Fabricius). Instead, we consider that they might function as stimulators, their known function in other insect groups (Eberhard 1985). We have searched and have not been able to find any distinctly modified mating behavior associated with these unique male genitalia (except for the lack of wing tremor during courtship). Neither have we been able to find any special structural modifications on the distal abdominal segments of females of *Horcomutilla* (cf. Figs. 25, 26), except for a slightly wider integumental smooth stripe on the female's abdomen, probably massaged by the male parameres. These lateral stripes are visible on abdominal tergum VI of the female of *H. krombeini* (cf. Fig. 25, 26); no other structural modifications are recognizable. The corresponding smooth stripe is slightly narrower in females of *Pseudomethoca*, whose males have simple parameres (Fig. 26).

Based on females, we can recognize two groups of species in *Horcomutilla*: 1. species (*krombeini*, *maracayi* and *reichi*) with two transverse integumental spots on tergum two, which lack lateral bands of pale pubescence on the dorsum of the thorax, and which are distributed in the northern part of South America, above the Equator. Only one species enters Panama, *krombeini*; 2. species (includes eleven nominal species) with two longitudinally ovate integumental spots on tergum two. Most of these species present lateral bands of pale pubescence on the dorsum of the thorax, except *denticeps* (Spinola), *suis* Casal, *taliata* (Kohl) and *tonocote* Casal. The second group of species is exclusively South American, south of the Equator. We describe here the males of two of the species in the first group.

Nothing is known about the hosts parasitized by *Horcomutilla*, but females have the last abdominal tergum with a well-defined pygidial plate, defined by carinae (Fig. 25), and presumably they parasitize
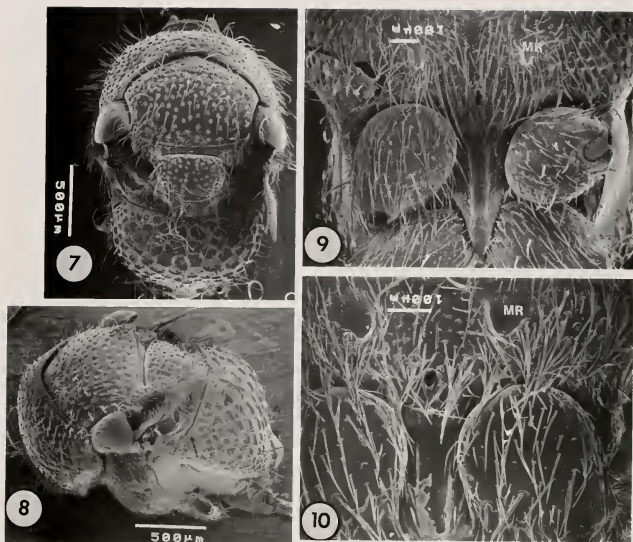
Figs. 7–10. Thorax details of *Horcomutilla*, males. 7, *maracayi*, thorax, dorsal view (× 50). 8, *maracayi*, thorax, laterodorsal view (× 50). 9, *krombeini*, thorax, ventral view (× 100); MR = mesosternal ridge. 10, *maracayi*, thorax, ventral view (× 150); MR = mesosternal ridge.

ground-nesting aculeates as do other fossorial forms (Naumann 1991, page 923). Numerous females of *H. krombeini* have been collected near aggregations of ground-nesting bees, *Melitoma* sp. (Río Perequeté, Chorrera), and sphecids, *Cerceris* sp. (Cruce de Mono Station, Parque Nacional Darién), and we suspect they parasitize their nests.

Here we present brief observations on the mating behavior of *Horcomutilla krombeini*, made by Rodolfo Contreras on four couples captured on January 17 and February 23 1992 in Capira, Panama Province. The male approached from behind and mounted the female without the stereo-typed wing tremor we have observed during the courtship of other genera of Sphaeropthalminae and Mutillinae (Quintero and Cambra, unpublished). Once mounted onto the female, with both individuals facing the same direction, the male grasps the female's "neck" (anterior pronotal area) with his mandibles. The sequence lasts less than two minutes. No observations were made on how the male uses his modified genitalia.

**Horcomutilla krombeini** Casal, 1965
Figs. 1, 3, 5, 6, 9, 11, 13, 15, 17,
20, 22, 23, 25

*Horcomutilla krombeini* Casal, 1965: 81–84. Holotype female: PANAMA: Barro Colorado
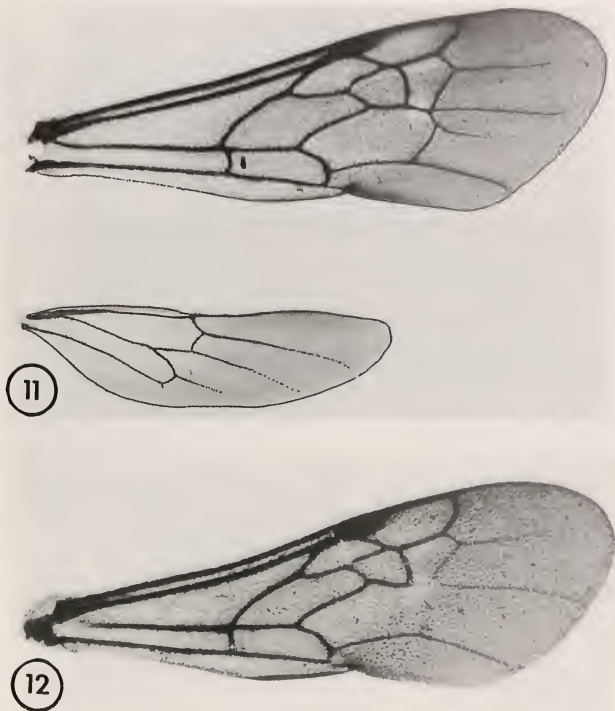
Figs. 11–12. Wings of *Horcomutilla*, males. 11, *krombeini*, fore and hind wing. 12, *maracayi*, fore wing.

(USNM, No. 67707), examined; Cambra & Quintero 1992: 472–473 (9 additional females).

*Male.*—Capira [Panama Province], Panama, 1 Feb 1992, R. Contreras, deposited MIUP.

*Description of Male.*—Integument black, except clypeus pale yellow, and mandi-

bles pale yellow with red tips. Head subrectangular in dorsal view, as wide as thorax; row of six or seven long, erect, dark setae near inner eye orbit; clypeus without tubercles or teeth (Fig. 1); clypeal disk sparsely punctate. Frons, vertex, and genae with shallow, close punctures, not confluent (Fig. 1). Posterior margin of probos-

Figs 13–18.
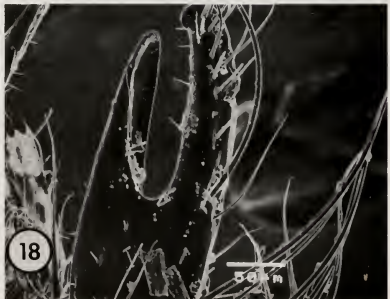
cidal fossa with triangular projection that is bisected by longitudinal median ridge (Fig. 3).

Head and thorax clothed with long, erect, white setae. Pronotum, mesonotum, and scutellum shallowly, closely punctate, punctures not confluent, about the size of those on head. Tegula glabrous, mostly impunctate; mesopleuron with moderate close punctures, except small area near the metapleuron, which is almost smooth, micropunctate; metapleuron glabrous, unsculptured. Mesosternum with a pair of small ridges, produced posteriorly (Fig. 9).

Legs covered with long, erect, white setae; mid coxae without teeth or carinae; hind coxae carinate on inner margin. Tibial spurs pale.

Abdomen setose throughout, setae sparse, white, mostly erect. Tergum I with small, sparse punctures on disk; posterior margin of terga I and II fully covered with moderate size, nearly contiguous punctures; abdominal segments III–VII with small, very close punctures throughout.

Genitalia with parameres and penis valve as figured (Figs. 13, 15, 17, 20, 22, 23). Body length: 6.5 mm.

*Known Distribution.*—Panama, Venezuela.

*Additional Material Examined.*—The finding of *Horcomutilla krombeini* in Venezuela represents a new distribution record, as this species was previously known only from Panama. [Specimens deposited in MIUP, acronymy omitted]. VENEZUELA: Carabobo, 8 May 1990, J. García, 1 female. PANAMA. DARIEN PROVINCE: Cruce de Mono, Estación INRENARE, Parq[ue] Nac[ional] Darién, 6 Feb 1993, R. Cambra & J. Coronado, 2 females; same loc. and collectors but: 7 Feb 1993, 1 female (UMIC); 8 Feb 1993, 1 female (UMIC); 9 Feb 1993, 2 females; 10 Feb 1993, 3 females; 11 Feb 1993, 2 females; 12 Feb 1993, 1 female; 13 Feb 1993, 8 females; 14 Feb 1993, 7 females; 15 Feb 1993, 4 females; 16 Feb 1993, 7 females; 17 Feb 1993, 5 females; 18 Feb 1993, 2 females; 19 Feb 1993, 7 females; 20 Feb 1993, 8 females; 21 Feb 1993, 2 females; 22 Feb 1993, 2 females; 23 Feb 1993, 5 females; 24 Feb 1993, 1 female; 25–28 Feb 1993, 4 females; 1–4 Mar 1993, 2 females. Trocha Yaviza-Pinogana, 27–29 Mar 1990, R. Cambra, 4 males, 1 female. El Real, 4 Feb 1993, R. Cambra & J. Coronado, 4 females. PANAMA PROVINCE: Rio Perequeté, Correg. Playa Leona, Chorrera, 27 Feb 1991, R. Cambra & D. Quintero, 6 females, 1 male; same loc.: 18–20 Mar 1991, R. Cambra, 4 males; 13 Feb 1991, R. Cambra, 3 males; 25 Jan 1992, I. Henry & Castillo, 3 females, 2 males 8 (one male without head); 26 Feb 1991, R. Cambra, 1 male (UMIC). Capira, 22 Feb 1992, R. Contreras, 2 females, 2 males (USNM); Capira, 2 Feb 1992, R. Contreras, 1 male. LOS SANTOS PROVINCE: Guararé, 14 Nov 1994, R. Pérez, 1 female. CHIRIQUI PROVINCE: Las Lajas, 24 Mar 1992, R. Contreras, 2 females.

*Variation of H. krombeini.*—After examining 119 females and 19 males of this species, we found color variation only among females: head integument black (75 per cent of specimens: one female from Venezuela, and the most common color form in the eastern part of Panama) to red (only one specimen); other females have the head black except the frons, vertex (below the white pubescence lines) and gena which are red. The thoracic integument varies from bright red to dark red.

*Comments on Sex Associations.*—Male and female conspecificity was established

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Figs. 13–18. Male genitalia of *Horcomutilla.* 13, *krombeini*, genitalia, dorsal view (× 75). 14, *maracayi*, genitalia, dorsal view (× 100). 15, *krombeini*, genitalia, laterodorsal view (× 100). 16, *maracayi*, genitalia, laterodorsal view (× 100). 17, *krombeini*, distal arms of parameres, dorsal view (× 200). 18, *maracayi*, distal arm of paramere, laterodorsal view (× 350).
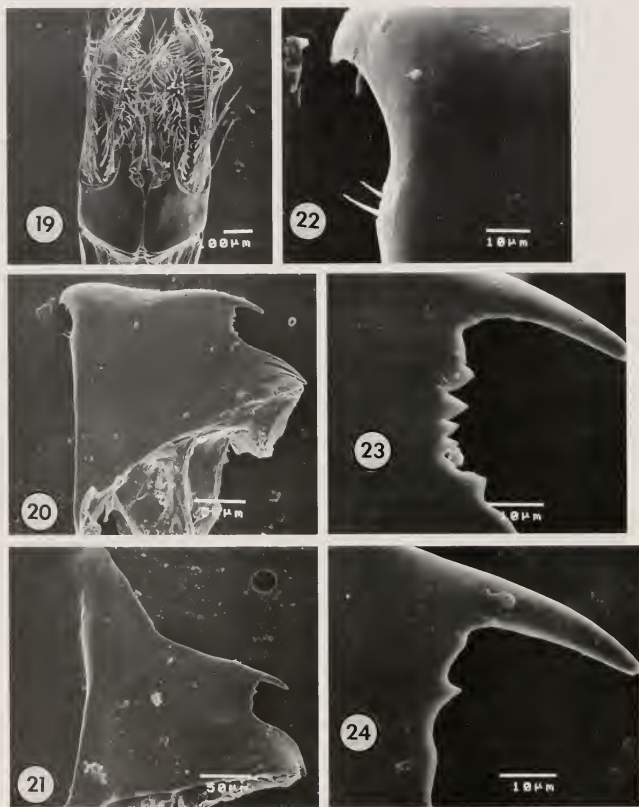
Figs. 19–24. Male genitalia of *Horcomutilla*. 19, *maracayi*, genitalia, ventral view (× 100). 20, *krombeini*, penis valve (anterior half), lateral view (× 350). 21, *maracayi*, penis valve (anterior half), lateral view (× 350). 22, *krombeini*, penis valve, anterior dorsal margin (× 1500). 23, *krombeini*, anterior ventral margin (× 2000). 24, *maracayi*, penis valve, anterior ventral margin (× 2000).
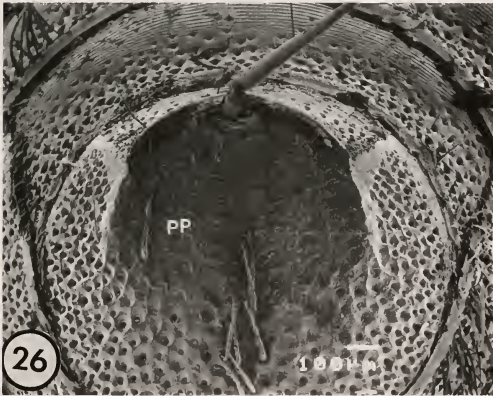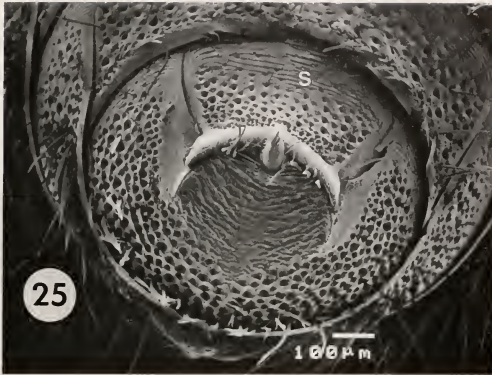
Figs. 25–26. Female distal abdominal segments, posterior view. 25. *Horcomutilla krombeini* (× 100); S = sternite VI; PP = pygidial plate. 26. *Pseudomethoca chontalensis* (Cameron) (× 75).

by experimental attraction, in nature, of six males flying upwind to one caged female (not visible from the outside), releasing airborne pheromones, and later obtaining, in a closed container, one positive experimental mating with one of those six males. Although some eager males might attempt to mate with any virgin female inside a close container, we have found that they are never able to force an unreceptive female to mate. Females with which the males are not conspecific are always unreceptive, thus the technique is highly reliable.

### Horcomutilla maracayi
Fritz & Martínez, 1993
Figs. 2, 4, 5, 7, 8, 10, 12, 14, 16,
18, 19, 21, 24

*Horcomutilla maracayi* Fritz & Martínez, 1993: 105–106. Holotype female: VENEZUELA: Aragua, El Limón (Maracay), 450 m (Martínez personal collection).

*Male.*—VENEZUELA: Aragua, El Limón, 450 m, 27 Apr 1973, C. J. Rosales, deposited MIUP.

*Description of Male.*—Integument dark red, except clypeus and mandibles, pale yellow. Head subrectangular in dorsal view, as wide as thorax, covered with long, erect, white setae; row of six or seven long, erect, dark setae near inner eye orbit; clypeus without tubercles or teeth (Fig. 2); clypeal disk sparsely punctate. Frons, vertex, and genae with shallow, close punctures, not confluent (Fig. 2). Posterior margin of proboscidal fossa with triangular projection not bisected by longitudinal median ridge (Figs. 4, 5).

Thorax with long, erect, white setae. Pronotum, mesonotum and scutellum (Fig. 7) shallowly, closely punctate, punctures about the size of those on head. Tegula glabrous, mostly impunctate (Fig. 7, 8); mesopleuron with moderate close punctures, except small area near metapleuron, which is almost smooth, micropunctate; metapleuron glabrous, unsculp-

tured (Fig. 8). Mesosternum with a pair of conspicuous tubercles (Fig. 10).

Legs covered with long, erect, white setae; fore and mid coxae without teeth or carinae; hind coxae carinate on inner margin. Tibial spurs pale.

Abdomen setose throughout, setae sparse, white, mostly erect. Tergum I with small, sparse punctures on disk; posterior margin of terga I and II fully covered with moderate size, nearly contiguous punctures; abdominal segments III-VII with small, very close punctures throughout.

Genitalia with parameres and penis valve as figured (Figs. 14, 16, 18, 19, 21, 24). Body length: 7 mm.

*Known Distribution.*—Venezuela.

*Additional Material Examined.*—[All specimens deposited in MIUP].-VENEZUELA. Aragua, El Limón, 450 m, 27 Apr 1973, C. J. Rosales, 1 male; same loc, 15 Sep 1955, F. Fernández & C. J. Rosales, 1 female; same loc, 15 Apr 1975, F. Fernández, 1 female.

*Variation of H. maracayi.*—Only four specimens of this species were examined (two females and two males), and no variation was recognized in that small sample.

*Comments on Sex Associations.*—Horcomutilla reichi (Mickel) is known only from the Venezuelan female holotype, deposited in the Spinola collection, but lacking further collection data. Male and female conspecificity of *H. maracayi* was established by coincident distribution; both females and males were collected from the same locality. No other species of *Horcomutilla* has been reported from the State of Aragua.

*Diagnosis, Males of Horcomutilla.*—Males of *Horcomutilla krombeini* and *maracayi* are very similar in most external features. However, three distinctive differences are valuable in separating these species reliably: the form of the penis valves (cf. Figs. 20, 21), the shape of the arms of the parameres (cf. Figs. 17, 18), and the shape of the mesosternal ridges (cf. Figs. 9, 10). Mesosternal processes or ridges are rather

uncommon among males of the subtribe Pseudomethocina (present in *Horcomutilla krombeini* and *H. maracayi* and some species of *Pseudomethoca*).

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# A Review of the Genus *Psenobolus* (Hymenoptera: Braconidae) from Costa Rica, an Inquiline Fig Wasp with Brachypterous Males, With Descriptions of Two New Species

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*Abstract.*—Biological observations and a description of two new species of the braconid genus *Psenobolus* are presented. These wasps were reared from the syconia (figs) of *Ficus* (*Urostigma*) spp. in San Jose, Costa Rica where they appear to develop as inquilines with chalcid fig wasps. No indication of parasitism was found. The sexes of the new species are dimorphic: the females are typical braconids; the males, however, are brachypterous with many characters in common with males of the chalcodoid *Idarnes*, also found in the figs.

## INTRODUCTION

The braconid genus *Psenobolus* was described by Reinhard in 1885 from wasps reared from a fig fruit collected in St. Catharina, Brazil. Reinhard's description included normal winged females and males. No biological information was given.

In 1965, the senior author (Ramirez) sent to the late C. F. W. Muesebeck at the U. S. National Museum, Washington, DC, specimens of winged females and brachypterous males of a braconid wasp reared from the figs of *Ficus* (*Urostigma*) *velutina* Willd. in Costa Rica which he thought were parasitizing *Blastophaga torresi* Grandi (presently in the genus *Pegoscapus*). The females were identified as a new species of *Psenobolus*. Muesebeck stated that there were "no braconid males in the sample" adding that the "males present were some species of Idarninae (Chalcidoidea), which presumably developed as an inquiline." Ramirez continued to collect and rear *Psenobolus* from *F.* (*U.*) *velutina* and other *F.(Urostigma)* species and the females were always associated with extremely dimorphic brachypterous males. In 1991, he sent more specimens to

the junior author (Marsh) at the U. S. National Museum who also identified the females as a new species of *Psenobolus* but considered the brachypterous males to be bethylids or tiphiids if not idarnine chalcids. Even Marsh's colleagues in the Hymenoptera Unit could not identify this unusual males. Undauntedly, in 1993 Ramirez sent another sample to Marsh that contained females and brachypterous males as before. However, one male was actually gynandromorphic: the head and metasoma were typical male but the mesosoma had one side with male brachypterous wings and swollen femora while the opposite side was female with normal wings and legs! This was convincing evidence that the brachypterous males did belong to the females and that the species was possibly developing in the figs as an inquiline with the males being highly modified similar to the idarnine chalcids also present (see below). Further evidence that these males are those of the female braconid is that the males of the type species, *P. pygmaeus* Reinhard, and males of another species in the U. S. National Museum are fully winged but have similar

antennae and swollen femora to those of the brachypterous males.

Many of the chalcidoid wasps that develop in the syconia (figs) of *Ficus* are brachypterous or wingless: the males of Agaoninae are completely wingless while those of other agaonids (non-pollinators) are brachypterous or wingless. Hamilton (1979) observed that of the more than 18 species of fig wasps found in two Brazilian *Urostigma* fig species, many had wingless males and several showed extreme sexual dimorphism. He also found that there was lethal combat among several types of these wingless males. Additionally, Murray (1989) found 25 species with flightless males among the fig wasps he collected.

### BIOLOGY OF *PSENOBOLUS* IN FIGS

**(Biological information presented below based primarily on study of *P. ficarius* n. sp.)**

Species of *Psenobolus* appear to be inquiline wasps that develop in the syconia of the genus *Ficus* subgenus *Urostigma* section *Americana* only. The female probably pierces the fig wall with her long ovipositor and lays the eggs in the female flowers of the figs ("gall flowers") which were recently oviposited into and pollinated by the symbiotic agaonid wasps. The larval and pupal stage occur inside the gall flowers. The adult brachypterous males emerge from the galls before the females but simultaneously with the agaonid and *Idarnes* males. The *Psenobolus* males apparently then mate with the "inactive" females while they are still inside the galls, although this was not observed. This is similar to other New World fig inquiline wasps such as the genera *Idarnes* and *Critogaster*. According to Hamilton (1979), "the great majority of male fig wasps are wingless" and this, along with precocious mating, has been well documented. After mating, the females emerge from the galls and escape from the syconia through the

exit holes in the fig wall made by males of the agaonid pollinators. *Idarnes* females also depend on the agaonid males for escape from the syconia. The sex ratio of *Psenobolus* was found to be 1:1.

The brachypterous males of these species of *Psenobolus* from Costa Rica are soldier males. With their prognathous heads and large mandibles they have been observed to fight to the death with other males of their own species. Many specimens we have seen have lost most of their antennae apparently from this fighting activity as well as while searching for females, gnawing through the galls and mating. Only a few authors have reported fighting in other fig wasps. Joseph (1958) observed fighting in *Philotrypesis* and Murray (1989) described intensive fighting in *Philotrypesis* and *Apocrypta bakeri*. The extreme dimorphism and dwarfing of male fig wasps may be partially attributable to fighting. According to Hamilton (1979), apart from the large heads and mandibles and perhaps the shield-like head and pronotum, the other modifications, such as winglessness, are probably not connected with selection for fighting. We feel, however, that many characters of the fig wasp males are, in fact, associated with fighting, such as brachyptery or winglessness, reduction in number of antennal segments and mating inside the galls.

The polymorphism and dwarfing of male *Psenobolus*, absent in the female, is probably associated with the amount of "vegetable food" left by the agaonid larva in each gall as suggested by Joseph (1984) rather than caused by a supergene (or a switched set of genes) that controls size and morphology as suggested by Hamilton (1979). According to Joseph (1984), male fig wasps survive as dwarf individuals, increasing the proportion of males.

### THE "AGAONIDIZATION" OF *PSENOBOLUS*

The brachypterous males of *Psenobolus* have many characters in common with

males of *Idarnes* (Torymidae in the sense of Gordh 1975 or Agaonidae in the sense of Boucek 1988) which also develop as inquilines in New World *Ficus (Urostigma)* figs. The common morphological and biological characters are listed below. We compared the brachypterous *Psenobolus* males with the description of *Idarnes* presented by Gordh (1975).

Morphological characters shared between brachypterous *Psenobolus* and *Idarnes* males:

Head

  Extreme polymorphism, soldier type males
  Prognathous heavily sclerotized heads
  Head wider or as wide as long
  Reduced eyes
  Ocelli absent
  Reduced antennae, large scape
  Large mandibles, articulated in horizontal plane

Mesosoma

  Dorsoventrally compressed
  Large pronotum
  Short legs with swollen femora

Biological characters shared between *Psenobolus* and *Idarnes*:

Males

  Polymorphic
  Non flying
  Emerge before females
  Lethal fighting between males
  Mating with inactive females
  Do not abandon fig in which they developed
  Probably do not feed as adults (not observed)

Females

  Ovipositors longer than body
  Oviposit after pollination of syconium
  Oviposit through syconial wall
  Mated while inside gall and inactive
  Abandon gall after mating

  Depend on agaonid males to escape from fig
  Similar fig hosts—*Ficus (Urostigma)* section *Americana*
  Occur only in New World.

The most significant similarities are that both groups are inquilines in *Ficus (Urostigma)* section *Americana* figs and that the males are often extremely polymorphic and flightless with depressed bodies. Although these are remarkable similarities between these two unrelated groups of wasps, there are differences which make it easy to distinguish *Psenobolus* and *Idarnes*. Males of *Psenobolus* have a two-segmented trochanter, typical for braconids, whereas *Idarnes* males have a one-segmented trochanter fused to the femur. The antenna of male *Psenobolus* has 9–12 distinct antennomeres with a swollen scape and pedicel (Fig. 8); *Idarnes* antenna has 4–5 antennomeres, a swollen scape and a distal club formed by the fusion of the last three antennomeres. The *Idarnes* males do not have a developed labiomaxillary complex indicating that they do not feed, whereas the *Psenobolus* males have distinct mouth parts although they also probably do not feed. Wing reduction in fig wasps may be related to fighting and mating inside the syconial cavity or inside the galls. According to Hamilton (1979), "wing reduction (in some fig wasps) is probably partly in the interest of redirection of growth into greater sperm production and (sometimes) into fighting adaptations, and partly simply because wings are an encumbrance for the male activities inside the figs." He also felt that the coincidence of winglessness, fighting and dimorphism is not accidental.

We suspect that the genus *Psenobolus* is still in a process of adaptation to development in the gall flowers of figs because the type species, *P. pygmaeus*, and several winged males of an unknown species from Trinidad, have winged males with modified antennae and swollen femora

similar to the brachypterous males. Much more study needs to be done on the biology of these unusual braconids to establish their exact biological relationship with the other wasps in figs. An interesting study would be to revisit near the type locality of *P. pygmaeus* in Brazil to study the biology of the more normal males.

## TAXONOMY OF NEW WORLD PSENOBOLUS
### Genus **Psenobolus** Reinhard

*Psenobolus* Reinhard, 1885, in Mayr, Verh. Zool.-Bot. Ges. Wien 35:246. Type species: *Psenobolus pygmaeus* Reinhard (monotypic).

*Diagnosis.*—A cyclostome braconid in subfamily Doryctinae; female normal, occipital carina present, fore tibia with row of short stout spines on anterior edge, fore wing with three submarginal cells, first subdiscal cell open at apex, vein 2–1A absent or indistinct at apex, hind wing with vein M+CU about equal to length of 1M, vein m-cu slightly curved toward wing apex, hind coxa rounded at base without tubercle, ovipositor usually much longer than body; male either similar to female but with basal flagellomeres stalked and scape and femora swollen, or often extremely dimorphic, brachypterous (see description below).

*Comments.*—Females of this genus can be identified by using the key to Western Hemisphere Doryctinae presented by Marsh (1993). Reinhard included a single species in the genus; subsequently Enderlein (1912) and Szépligeti (1902) added four species but these have all been transferred to the genus *Notiospathius* (see Shenefelt and Marsh 1976). In addition to the two new species described below the junior author has seen several new species from the Neotropical Region and these will be dealt with in a future revision of the genus now in preparation.

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KEY TO NEW WORLD SPECIES OF *PSENOBOLUS*

Females

1. First metasomal tergum wider at apex than at base, not parallel sided  . . *pygmaeus* Reinhard
– First metasomal tergum as wide at apex as at base, parallel sided (Fig. 5) . . . . . . . . . . . . .  2
2. Flagellum entirely brown; propodeum brown  . . . . . . . . . . . . . . . . . . . . *ficarius* new species
– Flagellum yellow on basal half; propodeum yellow . . . . . . . . . . . *parapygmaeus* new species

Males

1. Winged, similar to female  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *pygmaeus* Reinhard
– Brachypterous, extremely dimorphic (Figs. 6–9) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .  2
2. Head wider than long in dorsal view (Fig. 7); 9–10 antennomeres, scape and pedicel very large and swollen (Fig. 8) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *ficarius* new species
– Head about as wide as long; 12 antennomeres; scape and pedicel less swollen . . . . . . . . . .
 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *parapygmaeus* new species

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### **Psenobolus pygmaeus** Reinhard

*Psenobolus pygmaeus* Reinhard, 1885, in Mayr, Verh. Zool. Bot. Ges. Wien 35:247. Lectotype female, "St.Catharina in Brasilien," deposited in Zoological Museum, Humboldt University, Berlin, Germany.

*Diagnosis.*—Female: body color honey yellow, propodeum dorsally, first metasomal segment and median-basal spot on second metasomal tergum brown, scape, pedicel and first 3–4 flagellomeres yellow, remainder light brown; 20-antennomeres; head cubical, wider than high in anterior view; eyes large, malar space shorter than basal width of mandible; ocelli small, ocellocular distance about four times diameter of lateral ocellus; frons excavated; vertex,

frons and temple smooth, face smooth medially, rugulose laterally; mesosoma flattened dorsoventrally, smooth except propodeum weakly rugulose dorsally; notauli shallow, weakly crenulate anteriorly, absent before scutellum, not meeting; sternaulus smooth, about as long as mesopleuron; metasoma petiolate, first tergum narrow at base, suddenly widened at apex, apical width about twice basal width, carinate rugose, rugulose at base; remainder of terga smooth except second tergum in middle at base carinate, groove between second and third terga very weak and smooth; ovipositor about 1⅓ times longer than body; fore wing with three submarginal cells, stigma nearly as broad as long, vein m-cu interstitial with 2RS, vein 1cu-a slightly beyond 1M, second subdiscal cell open at apex, vein 2–1A absent at apex; hind wing with vein M+Cu nearly equal to 1M, vein m-cu weakly curved toward wing apex; fore tibia with row of 4–5 short stout spines an anterior edge, hind coxa without basal tubercle, femora at least 4 times as long as wide.

Male: similar to female except as follows; flagellomeres 1–4 stalked at base, swollen at apex; all femora swollen, about 2 times as long as wide.

Comments.—This species differs from the two new species described below by having the first metasomal tergum of the female wider at apex than long and by having winged males. It is presently known only from Brazil. The type series was reared from "Feigenfrüchten" but no indication of which genus or species of figs.

**Psenobolus ficarius** Ramirez and Marsh, new species
(Figs. 1–10)

*Female.*—Body color: honey yellow except flagellum, ocellar triangle, propodeum, first metasomal segment and basomedial spot on second tergum which are dark brown, propodeum occasionally light brown; wings hyaline, veins light brown but becoming clear yellow toward base and apex of wing, stigma brown with small yellow area at extreme base and apex; ovipositor sheaths brown. **Body length**: 2.5–3.0 mm. **Head**: entirely smooth; frons excavated, with short carina between antennae; face broader than high; hypoclypeal depression small and oval, diameter slightly greater than malar space; malar space short, about ⅐ eye height; temple narrow, about ⅓ eye width; occipital carina complete; ocelli very small, ocellocular distance about 5 times diameter of lateral ocellus, ocellar triangle isoceles-shaped; 21–25 antennomeres, all flagellomeres longer than scape and pedicel. **Mesosoma** (Fig. 4): pronotum smooth and polished, with deep longitudinal smooth groove laterally; mesonotum and scutellum smooth and polished, notauli complete and finely impressed, scutellum flattened; mesopleuron smooth and polished, sternaulus smooth, about ¾ length of mesopleuron; propodeum without carinae, with two basal lateral semicircular smooth and polished areas, rugulose medially, apically and laterally. **Metasoma** (Fig. 5): petiolate; tergum 1 rugulose carinate, slender, parallel sided, apical and basal widths equal, basal width about ⅓ width of propodeum; remainder of terga smooth and shining except a small basal medial rugose area on tergum 2, terga 2–5 each with sparse row of long white setae at apex, tergum 2 with sparse row of long white setae at base; ovipositor very long, at least as long as entire body and usually about twice as long. **Legs**: fore tibia with row of 4–6 short stout spines on anterior edge (Figs. 2–3); hind coxa round at base without distinct tooth; inner spine at apex of hind tibia strongly curved. **Wings**: fore wing (Fig. 10) with stigma short and broad, breadth greater than length of vein r, vein r-m present, thus three submarginal cells present, vein r about ¾ as long as 3RSa, vein m-cu interstitial with 2RS, second subdiscal cell open at apex, vein 2–1A weak or absent apically; hind wing with
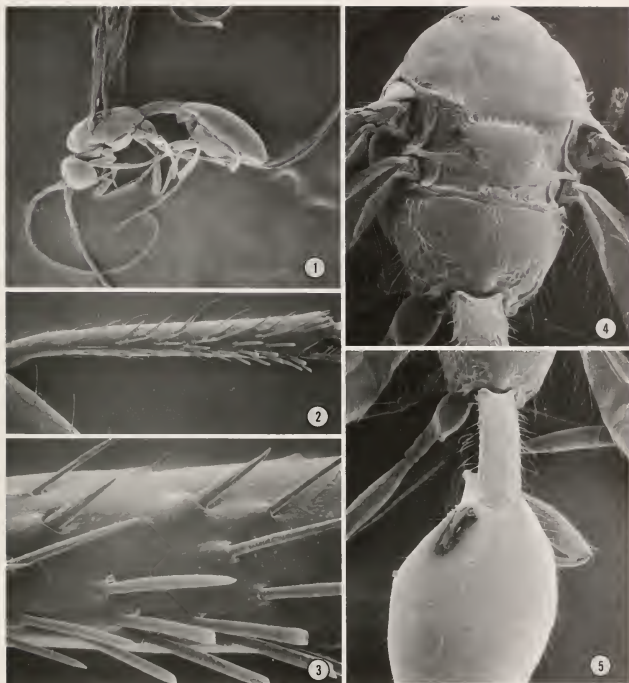
Figs. 1–5. *Psenobolus ficarius* new species. 1, habitus; 2, fore tibia showing chaetobothria; 3, same, enlarged; 4, mesosoma, dorsal view; 5, metasoma, dorsal view.

vein M+Cu about ¾ length of 1M, vein m-cu curved toward wing apex.

*Male.*—**Body color**: honey yellow except mandibles, scape, pedicel, trochanters and base of tibiae brown. **Body length**: 2.0–2.5 mm. **Head**: prognathous, wider than long in dorsal view, smooth and shining (Figs. 7, 9); 9–10 antennomeres, scape and pedicel large and swollen, width of scape greater than diameter of eye, flagellomeres 1–5 stalked, very narrow at base and wide at apex (Fig. 8); mandibles large, tips crossing when closed (Fig. 8); clypeus very narrow, concave; hypostomal depression oval; labrum concave; eyes small, temple behind eye about 5 times length of eye; ocelli absent; occipital carina absent. **Mesosoma** (Figs. 7, 9): smooth and polished,

Figs. 6–9. *Psenobolus ficarius* new species, males. 6, ventral view; 7, dorsal view; 8, head, ventral view; 9, lateral view.

flattened dorsoventrally; mesonotum sharply declivous to pronotum; notauli and scutellum absent; propodeum without any carinae; mesopleuron small, sternaulus absent. **Metasoma**: all terga smooth and polished; tergum 1 short, broad, oval shaped, dorsoventrally flattened (Fig. 7); remainder of terga similar to female. **Legs** (Fig. 9): all femora short and swollen; all tibiae narrow basally, swollen apically; fore and middle tarsi with tarsomeres 1–4 extremely short, api-
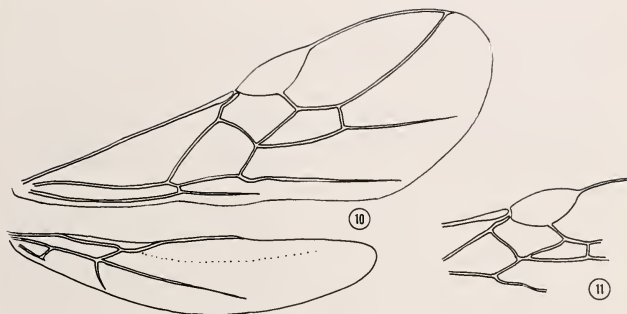
Figs. 10–11. Wings of *Psenobolus* species. 10, *P. ficarius* new species; 11, *P. parapygmaeus* new species.

cal tarsomere longer than tarsomeres 1–4 combined, claws large and simple; hind tarsomeres 1 and 5 equal in length and equal to length of 2–4 combined. **Wings**: brachypterous with few short veins near base (Figs. 7, 9).

*Holotype female.*—COSTA RICA, San Jose, El Tornillal, San Geronimo de Moravia, February 18, 1983, W. Ramirez. Deposited in Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica.

*Paratypes.*—COSTA RICA: 1 female, 11 males, 1 gyandromorph, same data as holotype; 6 females, 11 males, same data as holotype with date February 28, 1983, ex *Ficus velutina* Willd.; 5 females, 45 males, same data as holotype with date February 29, 1993, from fig; 14 females, 11 males, same data as holotype with date December 30, 1992; 3 females, La Canada, Cartago, January 31, 1964, W. Ramirez, ex. *Blastophaga torresi* Gir. in *Ficus velutina*; 3 females, San Jose, Zurqui de Moravia, 1600 m, August 1994 and March 1992, col. Paul Hanson. Deposited in: Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica; U. S. National Museum, Washington, DC; Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie, WY; Canadian National Collection, Ottawa, Canada; Natural History Museum, Leiden, The Netherlands.

*Comments.*—The above host record of *Blastophaga torresi* is in error as mentioned in the introduction and biology sections. The original assumption when these wasps were first collected in 1964 was that they were parasitoids of fig wasps which has since been disproved.

*Etymology.*—The species name is Latin for "of figs" in reference to the biology of the species.

**Psenobolus parapygmaeus** Ramirez and Marsh, new species
(Fig. 11)

*Female.*—Differs from *ficarius* as follows: basal 4–5 flagellomeres yellow, remainder gradually becoming brown to apex, propodeum yellow, second metasomal tergum entirely yellow; fore wing with vein m-cu meeting RS+M before 2RS (Fig. 11).

*Male.*—Differs from *ficarius* as follows: head as wide as long in dorsal view; 12 antennomeres; scape not as swollen as in *ficarius*, width about equal to eye diameter.

*Holotype female.*—COSTA RICA: Route to La Suize, Turrialba, August 29, 1973, *Fi-*

*cus (Urostigma)* sp., one fruit, coll. W. Ramirez. Deposited in Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica.

*Paratypes.*—COSTA RICA: 3 females, 1 male, same data as holotype. Deposited in Museo de Insectos, Universidad de Costa Rica, San Jose, Costa Rica; U. S. National Museum, Washington, DC.

*Etymology.*—The species name is from the Greek *para* meaning "near" in reference to the similarities of this species to *pygmaeus*.

## Other *Psenobolus* Species

The U. S. National Museum contains one female from Panama, one male from Mexico collected in wild figs and two males from Trinidad. The three males are fully winged and have stalked antennae and swollen femora as in *pygmaeus*. The junior author has also seen females of several apparently undescribed species from Mexico, Central America and northern South America which indicates that the genus is probably wide spread throughout the Neotropics where figs are growing. A revision of the entire genus is in preparation.

## ACKNOWLEDGEMENTS

Möllhof, Zoologisches Museum, Humboldt Universität, Berlin, kindly loaned the type series of *Psenobolus pygmaeus* Reinhard for study.

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# Recto-tergal Fusion in the Braconinae (Hymenoptera: Braconidae): Structure and Distribution

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*Abstract.*—A unique morphological feature is described, in which the rectum in the males of some genera of the braconid wasp subfamily Braconinae is fused with the 7th metasomal tergum. The area of the tergum overlying the area of recto-tergal fusion has a sponge-like structure in transverse section, and pores are visible using scanning electron microscopy, suggesting that this may permit volatile substances produced in the gut to escape when the wasp exposes the dorsal surface of the tergum. The distribution of this structure among the genera of Braconinae is discussed from a phylogenetic perspective.

## INTRODUCTION

The braconid wasp subfamily Braconinae is a diverse group containing more than 250 valid genera and 2000 described species (Shenefelt 1978; Quicke 1987; Shaw & Huddleston 1991), the majority from the Old World tropics. Members of the subfamily are almost exclusively idiobiont ectoparasitoids of concealed hosts, principally belonging to the Coleoptera and Lepidoptera, though Diptera and Hymenoptera are also attacked by some species. During surveys of the male genitalia (Quicke 1988a) and metasomal glands (Quicke 1991), we encountered an apparently unique feature of the digestive tract in members of several genera: the rectum of the male being fused dorsally to the eighth abdominal (7th metasomal) tergum. In this paper we describe the structure and ultrastructure of this anatomical feature, which we term recto-tergal fusion, and provide data on its distribution within the subfamily.

## MATERIALS AND METHODS

Morphology of the region showing the recto-tergal fusion (RTF) was studied us-ing *Atanycolus ulmicola* (Viereck). Live males of this species were collected around dead tree trunks in Boston, Massachusetts in August of 1987, and at College Station, Texas, in September of 1987. Specimens used for light, scanning (SEM) and transmission electron microscopy (TEM) were first dissected in sterile insect saline (Ephrussi and Beadle 1939) to isolate the posterior metasomal terga and digestive tract. Terga used for SEM were separated to expose the region fused to the rectum, dried through 100% ethanol, and coated with gold-palladium, prior to scanning. Additional SEM studies were performed on pinned specimens of several other genera (*Hemibracon* Szépligeti, *Rhadinobracon* Szépligeti, *Rhytimorpha* Szépligeti).

Preparations for TEM and light microscopy were fixed for approximately 5 hours in a mixture of 2% glutaraldehyde, 2% paraformaldehyde, 2% acrolein and 1.5% dimethyl sulphoxide in 0.133 M sodium cacodylate buffer (pH 7.4). After three rinses in 0.1 M sodium cacodylate, material was post-fixed in 1% osmium tetroxide for TEM (Hayat 1989). Following fix-

ation, the material was embedded in Araldite 502-EMBED 812 Embedding Medium (Mollenhauer 1964). Semi-thin sections of 1 μm thickness for light microscopy were stained with 0.1% toluidine blue in 1% aqueous sodium borate, and photographed with a Zeiss Axiophot using Ektachrome 160 Tungsten film. Ultrathin sections (50–70 nm) were post-stained with alcoholic uranyl acetate solution for 30 minutes followed by Reynolds' lead citrate (Reynolds 1963) for 10 minutes. Sections were examined and photographed using a Zeiss 10C transmission microscope at 60 kV on Kodak Electron Microscope Film 4489 (ESTAR Thick Base).

For a survey of the presence or absence of RTF across the subfamily, we used both live material and pinned museum specimens. Live material from field collections or from colonies maintained at Texas A&M were dissected in physiological saline. Metasomata were removed from dry specimens and soaked overnight in aqueous 10% potassium hydroxide, the sternites and tergites teased apart, and the chitinous lining of the hind gut stained with 1% aqueous Chlorazol Black. Gross dissections of all material, when performed carefully, did not disrupt the RTF, and the rectum remained tightly bound to the eighth abdominal tergum. Specimens in which RTF did not occur were unambiguously identifiable.

Suprageneric classification follows Quicke (1987). Voucher specimens of *A. ulmicola* are housed in the Texas A&M University Collection. Names of species in the genera surveyed for the presence of RTF, and their repository, are available from the senior author.

## RESULTS AND DISCUSSION

### Morphology

In living *A. ulmicola*, RTF is evident externally as a pale, circular region anteromedially on the otherwise reddish eighth abdominal tergite. Scanning electron mi-

crographs of this region in all genera examined showed the region of RTF to be sculptured differently from adjacent parts of the tergum, having numerous tiny pores (Figs 1, 2), but no other evidence of differentiation was noted. Light microscopy shows the digestive tract to be intimately associated with the tergum in the RTF region, with pores visible in the epicuticle at high magnification (Fig. 4). The cuticle over most of the region of RTF is markedly thicker in cross-section than in adjacent, lateral portions of the tergum (Figs 3 & 4). Transmission electron microscopy of the RTF region (Figs 5, 6) shows that the thickening of the cuticle is due to the development of a thick spongiform layer below a thin, more or less normal fibrous layer at the dorsal surface. This spongy layer appears at higher magnification (Fig. 6) to consist largely of empty space with a three-dimensional latticework of chitinous rods. Whilst none of our ultrathin sections showed it, we suspect that the lumens of the dorsal pores connect directly with the spaces in this spongy layer. Towards the inner side of the tergum, the chitin becomes more coherent and the spaces are reduced, but the chitin does not reach the same density as at the outer surface (Figs 4, 5). Immediately below, and normally firmly attached to, the RTF region of the tergum is the thin chitinous membrane of the rectum; in Figure 4 the membrane has become partially detached from the tergum due to the mechanical stresses imposed by dissection and sectioning. TEM shows unambiguously that there is no living tissue between the thin cuticle of the rectum and that of the tergum within the RTF region, though elsewhere, the chitinous cuticle and the rectum wall are both lined with cells.

### Distribution

More than 20 individual males of *A. ulmicola* were dissected and no intraspecific variation was detected, all displaying RTF. We have never observed RTF in females,
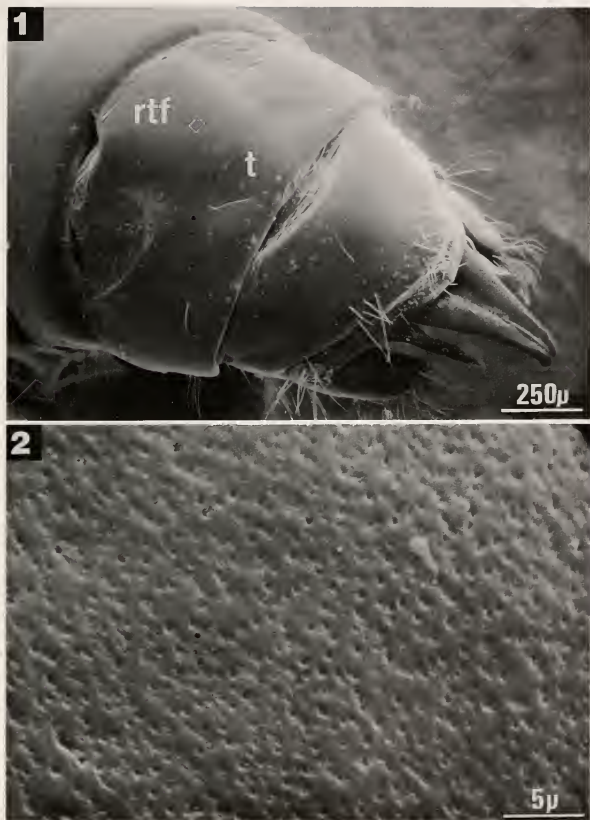
Figs. 1, 2. Scanning electronmicrographs of the 7th metasomal tergum of a male *Hemibracon* sp. 1, whole tergum with area of recto-tergal fusion exposed and apparent as a weakly raised oval area; 2, detail of area indicated by white rectangle in Fig. 1. Abbreviations: rtf, recto-tergal fusion; t, 7th metasomal tergum.

Table 1. Genera of Braconinae with males that display recto-tergal fusion. Genera are arranged according to tribes and generic groups, numbers of species examined (N)

| Taxon | Author | N | Taxon | Author | N |
|---|---|---|---|---|---|
| Aphrastobraconini | | | Euurobraconini (part) | | |
| *Aphrastobracon* | Ashmead | 2 | *Archibracon* | Saussure | 2 |
| *Curriea* | Ashmead | 1 | *Fraterarchibracon* | Quicke | 1 |
| *Ligulibracon* | Quicke | 1 | *Serraulax* | Quicke | 1 |
| *Megalommum* | Szépligeti | 2 | *Sororarchibracon* | Quicke | 1 |
| *Undabracon* (part) | Quicke | 1 | Glyptomorphini | | |
| *Vipiellus* | Roman | 2 | *Glyptomorpha* s.s. | Holmgren | 3 |
| Atanycolus group | | | *G.* (*Teraturus*) | Kokujev | 1 |
| *Alienoclypeus* | Shenefelt | 1 | *G.* (*Zanporia*) | Sarhan & Quicke | 1 |
| *Atanycolus* | Foerster | 3 | *Rhytimorpha* | Szépligeti | 2 |
| *Calobracon* | Szépligeti | 1 | *Vipio* | Latreille | 5 |
| *Chaoilta* | Cameron | 2 | Unplaced genera | | |
| *Hemibracon* | Szépligeti | 3 | *Campyloneurus* | Szépligeti | 3 |
| *Monilobracon* | Quicke | 1 | *Cordibracon* | Achterberg | 1 |
| *Nedinoschiza* | Cameron | 2 | *Cratobracon* | Szépligeti | 1 |
| *Neohelcon* | Szépligeti | 1 | *Digonogastra* (part) | Viereck | 3 |
| *Odontoscapus* | Kriechbaumer | 2 | *Nesaulax* (part) | Roman | 1 |
| Bathyaulacini (part) | | | *Pachybracon* | Cameron | 1 |
| *Bathyaulax* | Szépligeti | 2 | *Plaxopsis* | Szépligeti | 1 |
| *Euvipio* | Szépligeti | 2 | *Shelfordia* | Cameron | 1 |
| *Ischnobracon* | Baltazar | 1 | *Soter* (part) | Saussure | 1 |
| *Nundinella* (part) | Szépligeti | 1 | *Sylvibracon* | Quicke | 1 |
| *Odesia* | Cameron | 2 | *Vomeribracon* | Quicke | 1 |
| *Stenobracon* | Szépligeti | 2 | *Zaglyptogastra* | Ashmead | 2 |

although females of the great majority of braconine genera were examined. Further, RTF appears to be restricted to the Braconinae, members of virtually all other subfamilies of Braconidae having been dissected. Within the Braconinae, RTF has been found in somewhat fewer than half of the genera investigated (cf. Tables 1, 2). Within most genera it is either universally present or consistently absent, but variation was found in a few genera (*Digonogastra* Viereck, *Nesaulax* Roman, *Nundinella* Szépligeti, *Soter* Saussure, *Undabracon* Quicke). Of these, *Soter* may be polyphyletic as currently constituted, and this may also be the case with *Digonogastra* which is a very large and diverse genus. However, *Nesaulax*, *Nundinella*, and *Undabracon* are well supported monophyletic taxa (Quicke 1987; Quicke & Tobias 1990; Chishti & Quicke 1995), and therefore, it appears that RTF can be lost or perhaps

independently gained in some clades. At a higher level, the distribution of RTF appears to agree well with tribes and supra-generic groupings based on other characters (Quicke, 1987), being present, for example, in virtually all members of the *Atanycolus* Foerster group, the Bathyaulacini, Euurobraconini, and Glyptomorphini, while it is absent in all the Braconini, and the *Compsobracon* Ashmead, *Mesobracon* Szépligeti, and *Virgulibracon* Quicke groups.

## DISCUSSION

The apparent absence of RTF in all other braconid subfamilies suggests that it should be regarded as a synapomorphy within the Braconinae. Unfortunately, tribal boundaries within the Braconinae are far from settled at present, and although there are a small number of fairly clearly defined tribes, the affinities of the

Table 2. Genera of Braconinae with males not displaying recto-tergal fusion. Genera are arranged according to tribes and generic groups; numbers of species examined (N)

| Taxon | Author | N | Taxon | Author | N |
|---|---|---|---|---|---|
| **Adeshini** | | | **Coeloidini** | | |
| *Indadesha* | Quicke | 1 | *Coeloides* | Wesmael | 1 |
| **Aphrastobraconini (part)** | | | **Euurobraconini (part)** | | |
| *Undabracon* (part) | Quicke | 1 | *Euurobracon** | Ashmead | 6 |
| **Bathyaulacini (part)** | | | **Iphiaulacini s.s.** | | |
| *Nundinella* (part) | Szépligeti | 1 | *Iphiaulax* | Foerster | 6 |
| **Braconini sensu Achterberg** | | | *Hybogaster* | Szépligeti | 1 |
| *Aspidobraconina* | | | *Compsobracon* group | | |
| *Aspidobracon* | Achterberg | 1 | *Compsobracon* | Ashmead | 2 |
| *Philomacroploea* | Cameron | 1 | *Compsobraconoides* | Quicke | 1 |
| *Braconina* | | | *Cyclaulacidea* | Quicke & Delobel | 1 |
| *Bracon* | Fabricius | 7 | *Cyclaulax* | Cameron | 1 |
| *Braconella* | Szépligeti | 1 | *Gracilibracon* | Quicke | 1 |
| *Cratocnema* | Szépligeti | 1 | *Sacirema* | Quicke | 1 |
| *Habrobracon* | Ashmead | 1 | *Mesobracon* group | | |
| *Kimavu* | Quicke | 1 | *Macrobracon* | Szépligeti | 1 |
| *Tropobracon* | Cameron | 1 | *Mesobracon* | Szépligeti | 1 |
| *Myosoma* group | | | *Mesobraconoides* | Sarhan & Quicke | 1 |
| *Myosoma* | Brullé | 3 | *Pseudoshirakia* | Achterberg | 1 |
| *Myosomatoides* | Quicke | 1 | *Unplaced genera* | | |
| *Calcaribracon* | Quicke | 2 | *Bacuma* | Szépligeti | 1 |
| *Physaraina* | | | *Baryproctus* | Ashmead | 1 |
| *Physaraia* | Shenefelt | 1 | *Callibracon* | Brullé | 2 |
| *Trispinaria* | Quicke | 1 | *Cervellus* | Szépligeti | 1 |
| *Pycnobracon* group | | | *Cyanopterus* | Haliday | 2 |
| *Bicarinibracon* | Quicke & Walker | 1 | *Digonogastra* (part) | Viereck | 2 |
| *Chelonogastra* | Ashmead | 1 | *Gammabracon* | Quicke | 1 |
| *Pycnobracon* | Cameron | 1 | *Gronaulax* | Szépligeti | 1 |
| *Pycnobraconoides* | Quicke | 2 | *Lasiophorus* | Brullé | 1 |
| *Virgulibracon* group | | | *Megabracon* | Szépligeti | 1 |
| *Mollibracon* | Quicke | 2 | *Nesaulax* (part) | Roman | 1 |
| *Virgulibracon* | Quicke | 1 | *Rhadinobracon* | Szépligeti | 1 |
| *Virgulibraconoides* | Quicke | 1 | *Soter* (part) | Saussure | 1 |
| | | | *Stigmatobracon* | Turner | 1 |

* In *Euurobracon* the rectum has a large number of small rectal pads rather than the four typical of all other Braconinae (Quicke 1989).

majority of genera are uncertain (Quicke 1987, 1988b; Chishti & Quicke 1995), and the relationships among tribes have not been established. Nevertheless, it is clear from our findings that RTF is not distributed randomly within the subfamily (Table 1), and it may be useful in helping define inter-generic relationships. The observed variability within some well-characterized genera such as *Nesaulax*,

*Nundinella* and *Undabracon* means that even its use in this respect must be treated cautiously, and that several species should be investigated before the absence of RTF within a taxon can be accepted with a reasonable degree of certainty.

The function of RTF can only be surmised at present. However, given its morphology, including the close proximity of the thin chitinous wall of the rectum to the
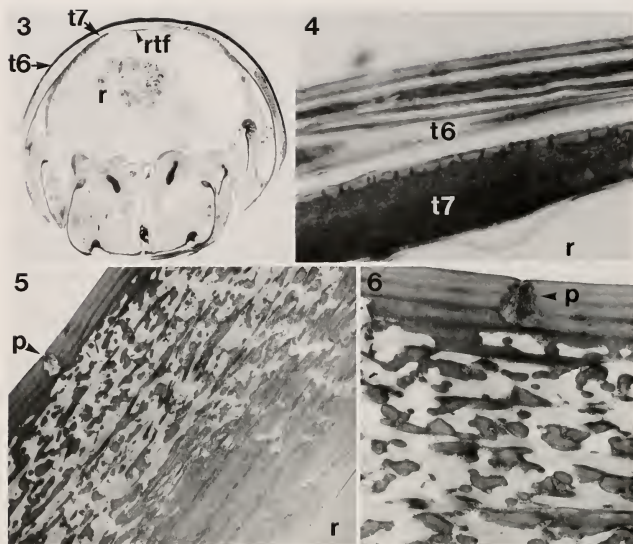
Figs 3–6. Transverse sections of 7th metasomal segment of *Atanycolus ulmicola* showing features of RTF. 3, photomicrograph of semithin section through whole tergum; 4, detail of tergal cuticle within region of recto-tergal fusion, showing pores in upper part of chitinous cuticle; 5, transmission electronmicrograph of tergal cuticle within region of recto-tergal fusion, showing pores in upper part of chitinous cuticle; 6, detail of a single pore. abbreviations, p, pore in 7th metasomal tergum; r, lumen of rectum; rtf, recto-tergal fusion; t6, 6th metasomal tergum; t7, 7th metasomal tergum. Note that in figures 3 and 4, the 6th metasomal tergum, which overlaps the 7th in normal resting position, is also sectioned.

highly modified, spongy and porous tergum in the RTF zone, together with the total loss of living rectum and epidermal cells, it seems very likely that the region has evolved to permit/facilitate passage of volatile compounds from the rectum through the tergum. If this is the case then RTF would be analogous to a gland, although no glandular tissue is present in the RTF region. Collectively, a considerable variety of true metasomal exocrine glands have also been discovered in brac-

onid wasps belonging to several subfamilies (Waseloh 1980; Tagawa 1983; Buckingham & Sharkey 1988; Williams et al. 1988; Quicke 1991; Field & Keller 1994), and as with RTF, many of these are limited to members of just one sex, often the males. Thus the distribution of RTF would be consistent in it having a pheromone-associated function possibly in relation to species recognition, courtship or aggregation. Much more work on pheromonal communication and pheromone glands in

braconids in general will be needed before the roles of the various glandular and non-glandular structures can be understood.

## ACKNOWLEDGEMENTS

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# Phylogenetic Relationships of the Thynnine Wasp Tribe Rhagigasterini (Hymenoptera: Tiphiidae)

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*Abstract.*—The thynnine tribe Rhagigasterini is reviewed, with an extensive reevaluation of generic groupings. Phylogenetic analyses of seven *Rhagigaster* species, two species of *Dimorphothynnus*, two *Aelurus* species, and fourteen species of *Eirone*, with Anthoboscinae and Thynnini s.s. as outgroups, reveal the relationships: Anthoboscinae + (Thynnini + [(Aelurus + Eirone) + (Dimorphothynnus + Rhagigaster)]). A consensus tree generated from all 27 taxa yielded a ci of 59. Analysis of only species representing genera (generic type species) resulted in a cladogram with the same topography and a ci of 73. *Rhagigaster* species were found to constitute a monophyletic unit despite suggestions that this genus may have been polyphyletic. The relationship between *Eirone* and *Aelurus* is problematic. *Aelurus*, the only South American genus, ends up embedded in *Eirone* in all of these analyses, and may indeed indicate that *Eirone* is a paraphyletic genus. However, derived features of the male terminalia in each group clearly separate them, and since females have been seen only for a few species in both genera, *Aelurus* will not be synonymized herein. Five new species of *Eirone* are described: *aquilonius* and *valokaensis* from New Britain, and *cheesmanae, schlingeri* and *speciosus* from Papua New Guinea.

## INTRODUCTION

Thynninae is the largest and most diverse subfamily in the Tiphiidae. Initially, Turner (1910b) treated this group as a discrete family, which he divided into three subfamilies, Diamminae, Rhagigasterinae and Thynninae, though the majority of genera and species were placed in the Thynninae. Subsequent studies (Pate 1947) and cladistic analyses (Brothers 1975, Brothers & Carpenter 1993, Kimsey 1991) clearly demonstrate that thynnines belong to the family Tiphiidae. This conclusion was based on a suite of characteristics including the presence of mesopleural lamellae, a quadrate pronotum, the unciform male subgenital plate found in most genera, and winged forms having the posterior angle of the pronotum reach the tegula. Argaman and Özbek (1992) made a retrograde proposal to restrict the family Tiphiidae to include only members of the Tiphiinae. However, this proposal is completely unsupported by any apomorphic characteristics or phylogenetic analyses, and is generally unaccepted.

The subfamily Rhagigasterinae was originally described by Turner (1910b) to include the genera *Rhagigaster* Guérin 1839, *Dimorphothynnus* Turner 1910b, *Eirone* Westwood 1844 and *Aelurus* Klug 1842. *Aelurus* is the only South American member of this group, all the rest are Australasian. This group is now treated as a tribe in the subfamily Thynninae (Given 1954, Salter 1954, Kimsey 1991).

Members of the Rhagigasterini lack a number of the derived features characteristic of other Thynninae, having instead the primitive character states as follow: 1. metasternum without apical medial ridge or truncation in both sexes, 2. male apical sternum apically rounded or with a linear uncus, 3. aedeagus simple and linear (except *Dimorphothynnus*), 4. female tergum I and II simple, without carinae or rugae (except *Dimorphothynnus*), and 5. female without discrete pygidial plate (except *Di-*

*morphothynnus*). Therefore they are treated as a basal lineage of the subfamily (Kimsey 1991). Derived features of rhagigasterines are: 1. male parameres with a dense apical row of elongate, often flattened setae, and 2. female mesopleuron with a discrete dorsal surface.

After examination of all of the rhagigasterine types in the British Museum (Natural History) it became apparent that the genera *Eirone* and *Aelurus* were very similar, and have very similar females, where known. There has also been the suggestion that the genus *Rhagigaster* is polyphyletic and should be further subdivided (G. Brown, personal communication). Finally, *Eirone* is a structurally diverse genus with some species groups apparently divergent enough to justify their separation into discrete genera. Therefore, previous treatments of the relationships among the Rhagigasterini are inadequate, and the entire group needed an objective reexamination.

## MATERIALS

Specimens were borrowed for this study or studied in situ from the following institutions and individuals: Australian National Insect Collection, CSIRO, Canberra, ACT; California Academy of Sciences, San Francisco, USA, W. Pulawski; California Department of Food and Agriculture, Sacramento, USA, M. S. Wasbauer; Canadian National Insect Collection, Ottawa, Ontario, L. Masner; Carnegie Museum, Pittsburgh, Pennsylvania, USA, J. E. Rawlins; Cornell University, Ithaca, N. Y., USA, J. K. Liebherr; Florida State Collection of Arthropods, Gainesville, USA; L. Stange; Charles Porter, personal collection; Gainesville, Florida, USA; Museo ed Istituto di Zoologia Sistematica, Universita di Torino, Italy, P. d'Entreves; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA, J. M. Carpenter, and D. Furth; Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands, C. van Achterberg; The Museum of Natural History, London,

England, M. C. Day; U. S. National Museum, Washington, D. C., K. V. Krombein and A. S. Menke; Zoologisches Museum, Humboldt-Universität, Berlin, F. Koch; Zoologisk Museum, Copenhagen, Denmark, B. Petersen. The species examined for this study are indicated below by an asterisk (*).

The following abbreviations are used: F = flagellomere, MOD = midocellus diameter, PD = puncture diameter, S = gastral sternum, and T = gastral tergum.

Parsimony analyses of the generic relationships were performed using the Hennig86 software (Farris 1988). The data matrix generated by detailed examination of the species listed in Table 1 was analyzed using explicit enumeration with branch swapping. All characteristics were treated as unweighted, and multistate characters as additive. These species were chosen because they represent very different groups within each genus or are types of published generic names. They were specifically chosen to test the notion that the current generic categories were either para- or polyphyletic. Character states were polarized using the Thynnini and Anthoboscinae as outgroups. Character polarities are discussed below, and are given in the data matrix provided in Table 1.

## RESULTS

### Tribal Characters

*Head.*—In the Thynninae a transverse carina extending across the frons is found only in males of *Rhagigaster* and *Dimorphothynnus*. The majority of *Rhagigaster* have at least a trace of a transverse carina. In *Dimorphothynnus* the carina is well-developed and extends from eye to eye across the frons, with a dorsal branch that forms an almost heart-shaped enclosure (Fig. 8). This feature is clearly a uniquely derived characteristic of these genera.

*Thorax.*—The dorsally bulging mesopleuron in female Rhagigasterini is diagnostic for this tribe. A hindcoxal carina,

extending along the dorsum of the coxa from the base nearly to the apex, is present in all male thynnines, and is generally undeveloped or is elevated and broadly rounded basally in rhagigasterines. However, in *Rhagigaster* and *Dimorphothynnus* it is elevated and toothlike (Fig. 11). Unlike most other thynnines, female *Eirone* have greatly reduced mesopleural lamellae.

In the majority of tiphiid subfamilies, including Myzininae, Anthoboscinae, and Tiphiinae, the metapostnotum is obscured medially by the scutellum. In the Rhagigasterini the metapostnotum is clearly visible as a band dorsally. This feature is found in no other Tiphiidae, and the pattern seen in the rest of the Aculeata suggests that the presence of a visible metapostnotum in the form seen in these genera is derived.

*Gaster.*—Sculpturing of the female T-II is a prominent feature in members of the Thynnini and Scotaenini (Kimsey 1992). In Rhagigasterini only *Dimorphothynnus* have sculpturing on this or any other gastral terga. In Anthoboscinae the subgenital plate is simple and evenly rounded, although in a few species such as *Anthobosca chilensis* Guérin, the apex may be spine-rimmed and thickened medially (Fig. 27) as is seen in some species of *Eirone* and in *Aelurus* (Fig. 31). This simple and evenly rounded apical sternum is assumed to be the primitive form in the Rhagigasterini. Based on the condition seen in Anthoboscinae and American Thynnini and Scotaenini, the lack of penis valves is primitive for Rhagigasterini. All Thynninae have a highly derived and distinctive aedeagus. Further modification can be seen in the Scotaenini where the aedeagus is relatively short with membranous lateral lobes and no apical loop, an autapomorphy for that group (Kimsey 1992). Within the Rhagigasterini, the majority of genera have an aedeagus with a basal bulb and slender apical neck (as in Figs. 43–53). The following characters were used to

analyze phylogenetic relationships. The resulting matrix is given in Table 1. Polarity is indicated in parentheses, and (0) is the primitive state, and (1) or (2) are derived.

1. **Male transverse frontal carina**: Absent (0), present (1) [*Rhagigaster*, *Dimorphothynnus*], joined by U-shaped dorsal carina forming a frontal enclosure (2) (Fig. 8) [*Dimorphothynnus*].

2. **Female maxillary palpus**: Four-segmented (0), three or two segmented (1). [*Aelurus* and *Eirone*]. Female *Aelurus* and *Eirone* have reduced palpi. Reduction in the number of palpal segments is common in aculeates; however, it appears to be a consistent generic feature in the Tiphiidae.

3. **Female labial palpus**: Five or 6-segmented (0), four segmented (1). [*Aelurus* and *Eirone*].

4. **Female mesopleural development**: Tapering evenly toward scutum (0), strongly bulging toward scutum with distinct dorsal surface (Fig. 4) (1) [Rhagigasterini].

5. **Female mesopleural lamella**: Well developed and apically rounded (0), strongly reduced to small point-like process (1) [*Eirone*].

6. **Male hindcoxal carina**: Present but evenly curved from apex to base (0). Abruptly expanded and angulate basally (Fig. 11) (1) [*Dimorphothynnus* and *Rhagigaster*].

7. **Male metapostnotal development**: Highly reduced and sunken medially (0). Broadly exposed dorsomedially (1) [*Eirone* and *Aelurus*].

8. **Female metasternum (first variable)**: With low medial ridge (0). Medial ridge modified into bilobate, apically flattened projection between midcoxae (1) [*Rhagigaster*].

9. **Female metasternum (second variable)**: Flat or carinate (0). Strongly expanded ventrally, appearing triangular in profile, with ventral apex (which may be bilobate) located considerably

Table 1. Character matrix for the genera of Rhagigasterini (Tiphiidae). Anthoboscinae (represented by *Anthobosca chilensis* (Saussure) and *A. crossicornis* Smith and Thynnini (represented by *Thynnus dentatus* Fabricius and *Zaspilothynnus interruptus* Westwood) are the outgroups used in this analysis

| Taxon | Characters | | | | | |
|---|---|---|---|---|---|---|
| Anthoboscinae | 00000 | 00000 | 00000 | 00001 | 00000 | 000 |
| Thynnini | 00000 | 00010 | 00010 | 00000 | 00001 | 250 |
| *Aelurus nasutus* | 01110 | 10101 | 00000 | 00002 | 01001 | 530 |
| *Aelurus septentrionalis* | 01110 | 10101 | 00000 | 00002 | 01001 | 530 |
| *Dimorphothynnus apicalis* | 21011 | 00012 | 10111 | 01113 | 21001 | 111 |
| *Dimorphothynnus morio* | 21011 | 00012 | 10111 | 01110 | 21001 | 111 |
| *Eirone aliciae* | 01110 | 10101 | 00000 | 00000 | 01001 | 320 |
| *Eirone aquilonius* | 00??0 | 10101 | 00000 | 00101 | 01001 | 420 |
| *Eirone cheesmanae* | 00??0 | 10102 | 00000 | 00101 | 01001 | 320 |
| *Eirone emarginatus* | 00??0 | 10102 | 00000 | 00100 | 01001 | 320 |
| *Eirone ferrugineicornis* | 01110 | 10101 | 00000 | 00100 | 01001 | 320 |
| *Eirone major* | 01110 | 10101 | 00000 | 00100 | 01001 | 320 |
| *Eirone mutabilis* | 00??0 | 10102 | 01000 | 00100 | 01101 | 420 |
| *Eirone parca* | 01110 | 10101 | 00000 | 00101 | 01001 | 320 |
| *Eirone rufopictus* | 01110 | 10101 | 00000 | 00001 | 01001 | 320 |
| *Eirone schizorhina* | 00??0 | 10102 | 01000 | 00100 | 01101 | 430 |
| *Eirone schlingeri* | 00??0 | 10101 | 00000 | 00101 | 01001 | 330 |
| *Eirone speciosus* | 00??0 | 10101 | 00000 | 00101 | 01001 | 340 |
| *Eirone valokaensis* | 00??0 | 10101 | 00000 | 00101 | 01001 | 430 |
| *Rhagigaster aculeatus* | 00011 | 01012 | 00000 | 01110 | 11001 | 030 |
| *Rhagigaster ephippiger* | 10011 | 01012 | 00000 | 01000 | 11011 | 030 |
| *Rhagigaster cinerellus* | 00011 | 01012 | 00000 | 10110 | 11011 | 030 |
| *Rhagigaster laevigatus* | 00011 | 01012 | 00000 | 10010 | 11001 | 030 |
| *Rhagigaster latisulcatus* | 10011 | 01012 | 00000 | 00010 | 11011 | 030 |
| *Rhagigaster lyelli* | 10011 | 01012 | 00000 | 11010 | 11011 | 030 |
| *Rhagigaster unicolor* | 10011 | 01012 | 00000 | 01010 | 110?1 | 030 |

behind mesocoxae (Fig. 5) (1) [*Aelurus, Eirone*].

10. **Male hindcoxal cavities closed**: Contiguous with the petiolar insertion (Figs. 12, 15) (0). Enclosed by converging metasternal and metapleural lobes (Figs. 14, 16, 17) (Kimsey 1991) (1) [*Rhagigaster, Dimorphothynnus*]. The hindcoxal cavities are open with the petiolar socket in *Aelurus* and *Eirone* (Figs. 12, 13), resembling the condition in Anthoboscinae (Fig. 18) and the majority of other Tiphiidae, but closed in *Rhagigaster* and *Dimorphothynnus* and Thynnini (Figs. 14, 16, 17).

11. **Male metasternal shape**: Apically flattened or medially emarginate (0). Projecting ventrally into two finger-like or conical lobes (1) [*Aelurus, Eirone*]. Metasternal lobes bending posteriorly

and overlapping the hindcoxal bases (Fig. 9) (2) [*Rhagigaster*, some *Eirone* species, *Dimorphothynnus*].

12. **Male propodeal shape**: Evenly rounded posteriorly and laterally (0). Strongly angulate laterally (1) [*Dimorphothynnus*].

13. **Male propodeal sculpturing**: Sculpturing continuous from apex to base (0). Dorsal and posterior surfaces of propodeum differentially sculptured, dorsal surface smooth and impunctate or shagreened, posterior surface extensively cross-ridged and punctate (1) [some *Eirone* species].

14. **Male propodeal carina**: Without transverse carina (0). Dorsal surface separated from posterior surface by transverse carina (1) [*Dimorphothynnus*].

15. **Female tergum III sculpturing**: Dorsally smooth, without cross-ridging (0). Extensively cross-ridged (Fig. 4) (1) [*Dimorphothynnus*].

16. **Male epipygial plate**: Absent (0). Present and carinate (1) [*Dimorphothynnus*]. The absence of a pygidial plate is assumed to be the primitive state since the Anthoboscinae lack one.

17. **Male gastral tergum VII lobate**: Gastral tergum VII evenly rounded (0). Tergum with apicomedial lobe (as in Fig. 26) (1) [some *Rhagigaster* species].

18. **Male gastral tergum VII carinate**: Tergum VII evenly rounded (0). Sublaterally carinate (1) [some *Rhagigaster* species].

19. **Male gastral sternum I (first variable)**: Evenly rounded with a single basal carina or ridge (0). With medial hook-like ridge (Figs. 20, 21, 23) (1) [*Dimorphothynnus*, some *Rhagigaster* species, some *Eirone* species].

20. **Male gastral sternum I (second variable)**: Sternum I simple basally (0). With shelf-like transverse carina, often connected to short but prominent medial longitudinal carina when the latter is present (Figs. 20, 21) (1) [most *Rhagigaster* species, *Dimorphothynnus*].

21. **Male subgenital plate (first variable)**: Simple and evenly curved, or somewhat thickened apically and spinose (0). With discrete, flat, spine-rimmed apicomedial plate (1) [*Aelurus*].

22. **Male subgenital plate (second variable)**: Simple, broadly and evenly curved (0). With long curved ventral spine (uncus) (Figs. 32–36) (1) [*Rhagigaster*, *Dimorphothynnus*]. Uncus protruding below broad flat shelf-like rim, fitting broad apical tergum in outline (Figs. 32, 33) (2) [*Dimorphothynnus*].

23. **Paramere setation**: Apical setae unmodified (0). Apical setae dense, elongate and most often flattened (Figs. 48, 52, 53) (1) [Rhagigasterini].

24. **Paramere shape (first variable)**: Para-

mere simple and evenly rounded apically (0). Apically with awl-like lobe (Fig. 48) (1) [several *Eirone* species]

25. **Paramere shape (second variable)**: Paramere simple and evenly rounded apically (0). Submedially with thumb-like lobe (Fig. 37) (1) [several *Rhagigaster* species]

26. **Digitus shape**: Digitus forming a setose, often small, rounded lobe (0). Digitus setose and C-shaped (1) [some *Rhagigaster* species]

27. **Penis valves**: Absent (0). Present, simple and foliaceous (as in Figs. 45, 46) (1) [Rhagigaster]. Elongate, spoon-shaped (2) [Thynnini *s.s*]. Extremely bilobate, with elongate dorsal and ventral lobes (3) [*Eirone s. s.*]. Bilobate with ventral lobe secondarily bifid (4) [some *Eirone* species]. Multilobate, without one or two unusually elongate lobes (5) [*Aelurus*].

28. **Aedeagal form**: Aedeagus consisting of two separate, simple, elongate lobes (0), Lobes separate, forming robust, basally lobed or angulate structure (Figs. 41, 42) (1) [*Dimorphothynnus*]. Aedeagal lobes fused into a structure with a distinct basal bulb and short apical neck (Figs. 45–48) (2) [some *Eirone* species]. Apical neck greatly elongate and linear (Figs. 49–53) (3) [some *Eirone* species, *Aelurus*]. Neck flattened and coiled (4) [one species of *Eirone*]. Aedeagus with basal column and neck (apical loop) flattened and coiled (5) [one species of *Rhagigaster*].

## Phylogenetic Relationships

The tiphiid subfamily Anthoboscinae and thynnine tribe Thynnini, are included in this analysis as outgroups. The resulting 14 trees found by implicit enumeration had a ci of 59. A Nelson Consensus Tree, shown in Fig. 1, produced the following relationships: Anthoboscinae + (Thynnini + [(*Aelurus*/*Eirone*) + (*Dimorphothynnus* + *Rhagigaster*)]). The ci was so low because there was relatively little resolution of re-
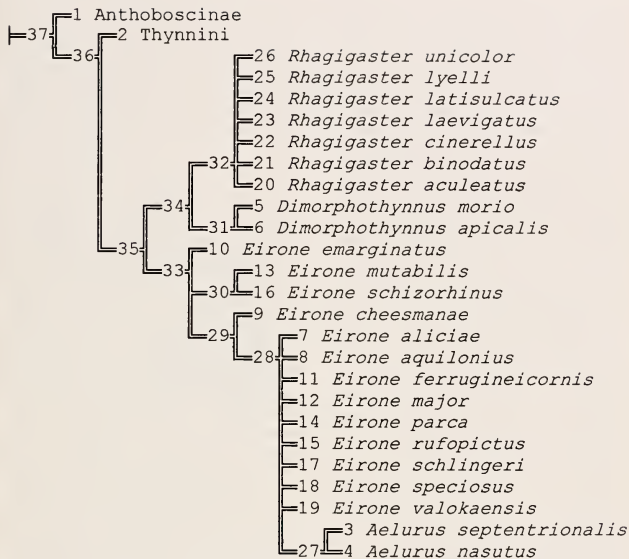
Fig. 1. Nelson Consensus Tree showing phylogenetic relationships of rhagigasterine species and generic groupings.

lationships among species of *Eirone* and *Rhagigaster*. However, implicit resolution of relationships among these species was less important than determining whether or not they actually represented sufficiently divergent groupings to constitute separate genera.

By eliminating all species but those with unique combinations of character states a single cladogram was generated with the same length and ci as the one using all taxa. This tree also had the same underlying topology as trees generated using all 27 taxa.

As discussed above, *Eirone* and *Aelurus* are very closely related groups sharing female palpal reduction, triangular female metasternum, and a broadly exposed metapostnotum and projecting lobate metasternum in males. In this analysis *Aelurus s.s.* fits readily within an assemblage of *Eirone* species. It is possible that *Aelurus s.s.* may represent a species group in this larger taxon. The females of both *Eirone s. s.* and *Aelurus s. s.* are thus far indistinguishable. In both groups the apical margin of the male subgenital plate varies from a thin, evenly curved, spineless rim to a discrete spine-rimmed apical platform. These modifications of the subgenital plate do not appear to correlate with any other modifications of the head or genitalia.

However, *Eirone* and *Aelurus* males can be consistently distinguished by unique elaboration of the penis valves in each. The valves in *Eirone* are strongly bilobed with one lobe extending ventrally and the other dorsally, with secondary subdivision of the dorsal lobe into a pincher-like structure in a few species. *Aelurus* males have the penis valves elaborately lobed, with dorsal, ventral, and even lateral lobes, which may themselves be secondarily lobate. Additionally, although *Aelurus* species based on males are largely described (Kimsey 1992), many *Eirone* species remain undescribed from either sex, and so few females are known for either genus, that further study is essential before making the decision to synonymize one with the other.

*Eirone s.s.* is a large structurally diverse group of species, but during the course of this study the only group that might justify generic status was a basal clade consisting of *Eirone mutabilis* and *schizorhinus*, and several as yet undescribed species. This clade is characterized by having the paramere terminate in a prong and the penis valve secondarily bifid. However, no females are known for these species, and each of these apomorphic characteristics turns up in other species of *Eirone*, for example, the penis valve structure also occurs in *cheesmanae*. As shown in the consensus tree this clade ends up embedded in *Eirone*, as it does in the majority of the iterations resulting from this analysis. Therefore there is no justification for treating this group of species as a discrete group.

*Dimorphothynnus* and *Rhagigaster* are sister groups based on the presence of a frontal carina on the face, unciform subgenital plate, and toothlike hindcoxal carina. However, *Dimorphothynnus* is highly modified and shares a number of features with many of the thynnine genera, including the transversely ridged female tergum, and a delineated pygidial plate. Synapomorphies for *Rhagigaster* include: the flattened and bilobate structure of the female metasternum, foliaceous penis valves, and male apical tergum apically narrowed and carinate or with thumblike lobe.

### Biogeography

Thynninae exhibit a typical trans-Antarctic distribution (Figs. 2, 3), with species occurring in South America and Australasia. Although there are currently no genera shared between these continental regions, *Aelurus* and *Eirone* show close phylogenetic links between the South American and Australasian faunas. *Aelurus s.s.* is restricted to the Neotropical Region, while *Eirone s.s.* is Australasian. *Eirone* is the most widespread member of the Australian rhagigasterines, and is one of the few genera with species occurring outside of Australia, on New Guinea, New Caledonia and New Britain. This genus is also the member of the Rhagigasterini with the largest number of primitive features resembling those of Anthobosciinae. The distribution and phylogenetic relationships of these genera suggest that the Thynninae evolved after the breakup of Gondwanaland, during the period when Australia and South America were connected to one another via Antarctica, between 70 and 30 mya (Fig. 3). Members of other thynnine tribes show no close phylogenetic relationships between the two regions, and in fact are divergent enough to suggest that the Australasian genera belong to one or more tribes and the South American genera in two other tribes (Kimsey 1991), with none of these occurring in both regions.

### KEY TO THE GENERA OF RHAGIGASTERINAE

1. Winged, with 7 gastral segments, and elongate slender antennae; males . . . . . . . . . . . . . . . 2
– Wingless, and ant-like, with 6 gastral segments, and short coiled antennae (as in Fig. 4); females . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

Fig. 2. World distribution of the tiphiid tribe Rhagigasterini.

2. Apical abdominal sternum unciform (Figs. 32–36), apical tergum broad and shovel-like or narrowed and sublaterally carinate (Figs. 25–26) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
− Apical abdominal sternum evenly rounded, unmodified or with a narrow platform margined with short spine (Fig. 31); apical tergum evenly rounded, or slightly indented and otherwise unmodified (Figs. 29, 30) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
3. Apical abdominal tergum broadly rounded apically and shovel-like (Fig. 25), apical sternum with broad dorsal platform above elongate curved apical spine (uncus) (Figs. 28, 32, 33) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Dimorphothynnus* Turner
− Apical abdominal tergum strongly narrowed or almost trilobate apically, often with accompanying sublateral carinae (as in Fig. 26); apical sternum with dorsal tooth or narrow rim above uncus (Figs. 34–36) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Rhagigaster* Guérin
4. Neotropical; apical abdominal sternum apically thickened with a discrete, narrow, spine-rimmed platform (Fig. 31), and penis valves elaborately pronged without an elongate dorsal lobe (Figs. 52, 53) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*Aelurus* Klug
− Australasian; apical abdominal sternum usually without a discrete apical, spine-rimmed platform (as in Figs. 29, 30), and penis valves strongly bi- or trilobed with well-developed apical lobe and single or bilobed dorsal one (Figs. 45–51) . . . . . . . . . . . . . . *Eirone* Westwood
5. Tergum III with numerous transverse carinae (Fig. 4); tergum VI with discrete, carinate pygidial plate; genal bridge strongly bulging in profile (Fig. 6); sternum I ventrally simple . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Dimorphothynnus* Turner
− Tergum III without carinae; tergum VI smooth, without carinae or discrete pygidial plate; genal bridge not bulging in profile; sternum I ventrally dentate . . . . . . . . . . . . . . . . . . . . . . . 6
6. Hindtarsal claws dentate; metasternum medially projecting, with an apically flattened and strongly bilobate structure . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Rhagigaster* Guérin

Fig. 3. Projection of continents in southern polar view 60 million years ago, with modern distribution of Rhagigasterini indicated by shading.

- Hindtarsal claws edentate; metasternum expanded and triangular in profile, apex of the triangle sharp apically (Fig. 5) .................................................. 7
7. Mesopleural lamella well developed, apically rounded; neotropical; propodeum usually with one or two ovoid depressions medially (Fig. 10); four maxillary and three or four labial palpal segments .................................................. *Aelurus* Klug
- Mesopleural lamella reduced to small pointed process; Australasian; four or fewer maxillary and three or fewer labial palpal segments; propodeum without ovoid medial depressions .................................................. *Eirone* Westwood

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## **Aelurus** Klug
(Figs. 10, 15, 31, 52, 53)

*Aelurus* Klug 1842:42. Type: *Aelurus nasutus* Klug 1842:43. Orig. desig.
*Cophothynnus* Turner 1908:79. Unnecessary replacement name for *Aelurus* Klug 1842.

*Male.*—Mandible simple, bidentate, or rarely tridentate; labrum broadly ovoid with narrowed base; maxillary palpus with 6 articles, labial palpus with 4; occipital carina faint dorsally; frons smooth without ridges or carinae; metasternum medially projecting and bilobate; propodeum evenly rounded, ecarinate; abdominal segments weakly punctate, without

subapical constriction, with anterior zone of coarse punctation; apical sternum thickened apically, with marginal row of spines along apex (Fig. 31); parameres generally broad, with row of long flattened setae on apical margin (as in Fig. 53); volsella usually apically bilobate; penis valves long, well developed; aedeagus basally bulbous and apically long and slender (Figs. 52, 53).

*Female.*—Head as long as broad or longer; eyes slightly larger than pedicel; mouthparts reduced, maxillary palpus with 4 or fewer articles and labial palpus with 3 or fewer; pronotum longer than broad; mesopleuron with clearly developed dorsal surface; propodeum with long flat sloping dorsal surface, often with 1 or 2 medial depressions (Fig. 10); terga relatively smooth without differentiated areas, carinae or rugosities; apical tergum smooth without carinae or defined pygidium; apical sternum with U-shaped apical lip having 2 infolded flaps.

*Distribution.*—*Aelurus* species have a patchy distribution in the Neotropical Region, occurring in Costa Rica, Panama, Colombia, Ecuador, Peru, Argentina, Chile and Brazil (Kimsey 1991).

*Discussion.*—*Aelurus* and *Eirone* are closely related genera, so much so that the females are virtually indistinguishable, except for the development of the mesopleural lamellae. There are other subtle differences, but whether these would separate all species in both genera is uncertain. *Aelurus* females have 5 maxillary and 4 labial palpal segments, the mesopleuron is strongly convex medially, and the propodeum is usually dorsally flattened with one or two medial depressions. In *Eirone* females there are usually 4 or fewer maxillary and 3 or fewer labial palpal segments, and the propodeum is dorsally gently convex without depressions. *Rhagigaster* females are also similar but they can be immediately separated from those of *Aelurus* and *Eirone* by the dentate hindtarsal claws.

*Included species.*—*Aelurus albofacies* Kimsey\*, *ater* Duran, *brasilianus* Kimsey\*, *clypeatus* Klug, *concava* Kimsey\*, *enigmaticus* Kimsey\*, *gayi* (Spinola), *grande* Kimsey\*, *nasutus* Klug\*, *nigrofasciatus* (Smith) \*, *penai* Kimsey\*, *septentrionalis* Kimsey\*, *tridens* (Spinola), *uncifer* Turner.

**Dimorphothynnus** Turner
(Figs. 4, 6, 8, 11, 17, 20, 24, 25, 28, 32, 33, 39, 41, 42)

*Dimorphothynnus* Turner 1910b:5. Type: *Rhagigaster haemorrhoidalis* Guérin 1842:2. Orig. desig.

*Male.*—Mandible slender and apically bidentate; labrum small and linear; maxillary palpus with 5 articles, labial palpus with 4; occipital carina dorsally obsolescent; frons with transverse carina joining carinae extending dorsally from the frontal lobes, forming a bell or heart-shaped enclosure (Fig. 8); region between antennal sockets strongly protruding; genal bridge protruding in lateral view; pronotum strongly angled laterally, transverse anterior carina strongly flared; mesopleuron sharply declivous anteriorly, with scrobe obsolescent; metasternum strongly ventrally bilobate; propodeum strongly angulate laterally, with transverse carina separating dorsal from posterior surfaces; tarsal claws dentate; hindcoxal carina strongly angulate (Fig. 11); abdominal segments often coarsely punctate, and somewhat constricted subapically; sternum II with Y-shaped basal carina, forming a large transverse ridge subbasally connected to a medial carina extending posteriorly (as in Fig. 20); apical sternum with slender curved uniform prong below a flat, often greatly expanded dorsal lip or rim that matches the margin of the apical tergum (Fig. 32); apical tergum apically broadly rounded and sometimes medially weakly indented as well, with short lateral carina (Fig. 25); parameres long and slender with elongate flattened apical setae (Fig. 39); volsella elaborately foliaceous,
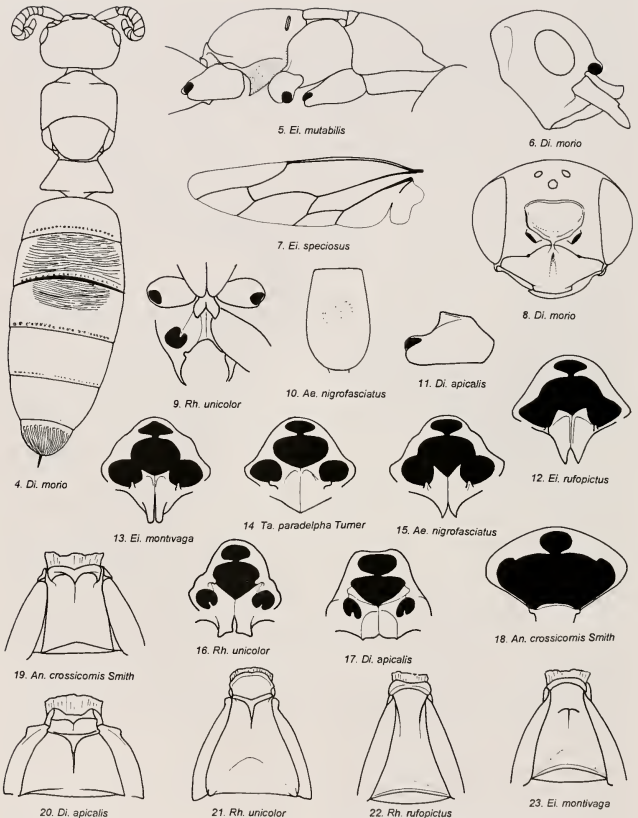
Figs. 4–23. Fig 4. Dorsal view of female head, thorax and abdomen. Fig. 5. Lateral view of female thorax. Fig. 6. Lateral view of female head, antennae removed. Fig. 7. Hindwing. Fig. 8. Front view of male face, antennae removed. Fig. 9. Ventral view of male metasternum, with one hindcoxa removed. Fig. 10. Dorsal view of female propodeum. Fig. 11. Male hindcoxa. Figs. 12–18. Arrangement of petiolar socket and hindcoxal cavities in males. Fig. 19–23. Ventral view of male gastral sternum I. Abbreviations: *Ae.* = *Aelurus*, *An.* = *Anthobosca*, *Di.* = *Dimorphothynnus*, *Ei.* = *Eirone*, *Rh.* = *Rhagigaster*, *Ta.* = *Tachynomia*.

with small setose lobe (Fig. 39); penis valves short, spoon-like and closely appressed to aedeagal base; gonobase short and broadly, closely appressed to parameres; aedeagal lobes separate, basally broadly angulate with slender, slightly curved apical neck (Figs. 41, 42).

*Female.*—Head considerably broader than long in front view; genal bridge protruding in lateral view (Fig. 6); eyes ovoid, one-half or more as long as head; mouthparts unmodified, labial palpus with 6 articles and maxillary palpus with 4; pronotum subquadrate, wider than long; mesopleuron flattened or slightly convex medially, somewhat angulate ventrally above midcoxa; scutum absent; metasternum with medial process short, subtriangular and apically bidentate, not widely separating the mid and hindcoxae; propodeum gently sloping posteriorly, sharply angled laterally and narrowed anteriorly (Fig. 4); tarsal claws dentate; terga broadly joined, not narrowed between segments; tergum III with numerous (about 8–15) cross ridges (Fig. 4); apical tergum descendingly carinate with marginally carinate pygidial plate (Fig. 24); apical sternum with broadly U-shaped apical lip.

*Distribution.*—Members of this genus are found only in Australia.

*Discussion.*—This genus is the most divergent and highly derived in the Rhagigasterini. Certain features including the development of penis valves and the female pygidium are more characteristic of the Thynnini and do not occur in the other Rhagigasterini. Other diagnostic features include the foreshortened female head and transversely carinate tergum III, and in males the carinate frontal enclosure on the face, angulate and carinate propodeum, and laterally angulate pronotum. In addition the females have dentate tarsal claws.

*Included species.*—*barnardi* (Turner)*, *conjugatus* (Turner)*, *deceptor* (Smith)*, *haemorrhoidalis* (Guerin), *integer* (Fabricius),

*morio* (Westwood)*, *ottonis* (Dalla Torre)*, *simillimus* (Smith), *testaceipes* (Turner), *trunciscutus* Turner*.

## Eirone Westwood
(Figs. 5, 7, 13, 23, 29, 30, 45–51)

*Eirone* Westwood 1844:144. Type: *Eirone dispar* Westwood 1844:144. Orig. desig.

*Male.*—Mandible slender and apically bidentate; labrum broad with short narrow basal neck; maxillary palpus with 5–6 articles, labial palpus with 3–4; occipital carina weakly developed to obsolescent dorsally; frons ecarinate and smooth, frontal lobes projecting to nearly flat; pronotum with well developed transverse carina; mesopleuron ecarinate with puncture like scrobe; metasternum with strongly projecting ventrally bilobate process; propodeum evenly curved and ecarinate or differentially sculptured dorsally versus posteriorly; abdominal segments smooth to punctate, and somewhat constricted subapically between segments II and III; apical sternum unmodified apically or with a spinose, apically thickened plate (Figs. 29, 30); apical tergum with wide, evenly rounded asetose and impunctate apical rim (Fig. 30); parameres generally broad and apically subtruncate or with apical awl-like lobe, with row of elongate, flattened apical setae (Fig. 48); volsella large and often apically multilobate, setose lobe attached subapically; penis valves strongly bilobate with elongate dorsal lobe and lobe extending alongside the aedeagus, each lobe may be secondarily subdivided (Figs. 45–51); gonobase short and broad, broadly attached to parameres; aedeagus flattened and linear with small basal bulb, or with large basal bulb and tapering slender apex (Figs. 45–51).

*Female.*—Head as broad as long or longer; eyes small and ovoid, usually less than one-fourth as long as head; mouthparts reduced, labial and maxillary palpi with 4 or fewer articles, maxillary palpus
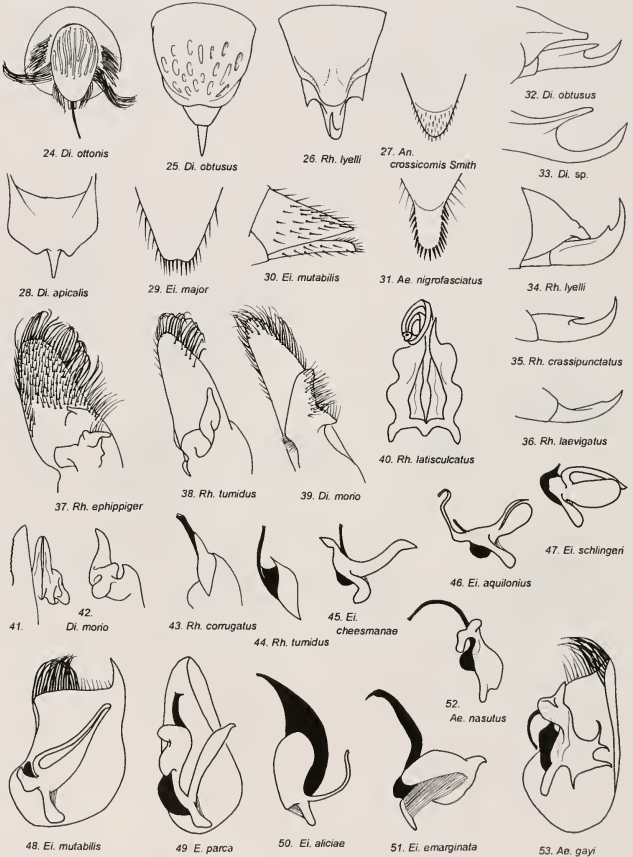
Figs. 24–53. Fig. 24. Posterior view of female abdominal apex. Figs. 25–26. Dorsal view of male abdominal apical segment. Figs. 27–29, 31. Male hypopygium. Figs. 30, 32–33. Lateral view of male abdominal apex. Figs. 34–36. Lateral view of male hypopygium. Figs. 37–39. Inner view of paramere and volsella. Fig. 40. Ventral-view of aedeagus and penis valves. Fig. 41. Ventral view of aedeagus. Fig. 42. Lateral view of aedeagus. Figs.

difficult to see without extending the tongue; pronotum subquadrate, evenly and shallowly convex dorsally; mesopleuron laterally flattened and usually angulate ventrally above midcoxa; mesopleural lamella represented by small pointed process; midcoxae widely separated from hindcoxae by elongate metasternum, which appears ventrally triangular in profile, and is apically bidentate or bilobate (Fig. 5); propodeum narrowed anteriorly, lateral margin compressed and somewhat sharp-edged; tarsal claws edentate; sternum II with one or two ventromedial denticles; tergum II with abrupt anterior declivity; terga without transverse striations, rugosities or carinae; apical tergum generally unmodified; apical sternum with U-shaped apical lip with two infolded flaps.

*Distribution.*—*Eirone* species occur throughout Australia and Tasmania, as well as in New Guinea, New Britain and New Caledonia.

*Discussion.*—Species of *Eirone* most closely resemble those of *Aelurus*, as discussed under that genus. Females are virtually indistinguishable except by the development of the mesopleural lamellae. Additionally, female *Eirone* never have the propodeal depressions seen in most female *Aelurus*. Males can be separated by a combination of features. *Eirone* have a relatively simple volsella and generally have strongly bilobate penis valves. In addition, most, but not all, species have the apical abdominal sternum simple or apically thickened, without a flat, thickened apical platform, or distinct row of marginal apical spines. In all *Aelurus* males, sternum VIII has a flattened and subtriangular apical platform, that is margined by a row of short spines. *Eirone* males also have elaborate penis valves, as in Figs. 45–51. Male *Eirone* appear to be divisible into several groups based on whether there is an indication of this apical platform, or at least marginal spines, and on features of the genital capsule. This difficulty is further enhanced by the utter lack of equivalent diagnostic features in the females. Without further study it appears to be impossible to further subdivide *Eirone* into additional genera, without creating paraphyletic groupings.

*Included species.*—*Eirone abdominalis* Westwood, *alboclypeata* Turner*, *aliciae* Turner*, *aquilonius* Kimsey*, *arenaria* (Turner)*, *basimaculata* Turner, *brumalis* Montet, *caroli* (Turner)*, *castaneiceps* Turner*, *celsissima* Turner*, *cheesmanae* Kimsey*, *colorata* Brown, *comes* Turner*, *crassiceps* (Turner)*, *cubitalis* (Turner), *denticulatus* Montet (*brumalis* ssp.), *dispar* Westwood*, *emarginata* Brown, *exilis* Turner*, *fallax* (Smith)*, *ferrugineiceps* Turner*, *ferrugineicornis* Turner*, *fulvicostalis* Turner*, *grandiceps* (Turner)*, *ichneumoniformis* (Smith), *impunctata* Brown, *inconspicua* Turner*, *leai* Turner*, *lucidus* (Smith)*, *lucidula* Turner*, *major* Turner, *marginata* Brown*, *marginicollis* Turner*, *mutabilis* Turner, *montivaga* Turner, *neocaledonica* Williams, *nigra* Brown, *obscurus* (Klug), *obtusidens* Turner*, *opaca* Turner*, *osculans* Turner*, *parca* Turner*, *pseudosedula* Turner*, *ruficornis* (Smith)*, *ruficrus* Turner*, *rufodorsata* Turner*, *salteri* Brown, *schizorhina* Turner, *schlingeri* Kimsey, *scutellata* Turner*, *speciosus* Kimsey, *subacta* Turner*, *subpetiolata* Turner*, *subtuberculata* Brown, *superestes* Cockerell, *tenebrosa* Turner*, *tenuipalpa* Turner*, *transversa* Brown*, *tristis* (Smith)*, *tuberculata* (Smith), *valokaensis* Kimsey*, *vitripennis* (Smith).

←

43–47, 49–52. Lateral view of penis valve and aedeagus (black). Figs. 48, 53. Lateral view of aedeagus (black), penis valve and paramere, volsella omitted. Abbreviations: Ae. = *Aelurus*, An. = *Anthobosca*, Di. = *Dimorphothynnus*, Ei. = *Eirone*, Rh. = *Rhagigaster*.

## Eirone aquilonius Kimsey, new species
(Fig. 46)

*Holotype male.*—Body length 11 mm; forewing length 7 mm. Face with impunctate medial stripe above antennal sockets, punctures shallow and 0–0.5 PD apart, shallower and less distinct on clypeus; clypeus flattened, apical margin broadly truncate; F-I length 2.3× breadth; F-II length 3× breadth; pronotum nearly impunctate, punctures shallow and indistinct, 4–5 PD apart; mesopleural punctures 0.5–1 PD apart, becoming further separated ventrally; scutal punctures nearly contiguous; scutellar punctures large, shallow and 1–2 PD apart; propodeum impunctate with dense fine transverse wrinkles or striae; S-I with short medial ridge; epipygium broadly rounded, apical rim thin and transparent, punctation and sculpturing the same as previous tergum; hypopygium slightly thickened apically, and bilobate, apical margin with a few long setae; paramere short and broadly rectangular, without apical row of flattened setae, instead apex with setae and 3–4 long spines; volsella without distinct basal lobe, dorsal part bilobate, broadest of the two dorsal lobes setose; penis valves with elongate, slender, apically hooked dorsal lobe extending outside of capsule, and elongate bilobate ventral structure extending alongside volsella (Fig. 46); gonocoxa without slender digitate lobe ventromedially. Hindwing anal lobe without enlarged basal lobe. Body black with pale yellow W-shaped mark on clypeus and transverse medially broken pale yellow band on anterior pronotal carina. Wing veins dark brown, membrane clear.

*Type material.*—Holotype male, New Britain, Mosa Palm Oil Plantation, near Hoskins, 25 Jan.-1 Feb. 1969, J. E. Benson (LONDON).

*Etymology.*—This species has one of the most northerly distributions in the genus, thus the name *aquilonius* = northern (L.).

*Discussion.*—This species can be distinguished from other species of *Eirone* by the black body color with few pale whitish markings, simple and apically truncate clypeus, hypopygium apically slightly bilobate, and peculiar genital capsule. The male genitalia in this species is remarkable --the paramere is unusually short and ear-like and the dorsal lobe of the volsella is very slender with an abrupt hook apically. This species appears to be closely related to *valokaensis* on the basis of overall similarity.

## Eirone cheesmanae Kimsey, new species
(Fig. 45)

*Holotype, male.*—Body length 12 mm; forewing length 8 mm; facial punctures external to antennal sockets and lower frons dense and small, nearly contiguous, punctures on upper frons and vertex 2–3 PD apart and highly polished between, rest of head with punctures 0.5–1 PD apart; clypeus broadly trilobate; flagellomere I twice as long as broad; flagellomere II length 2.4× breadth; pronotal punctures 2–3 PD apart; mesopleural punctures contiguous to 1 PD apart, further separated toward venter; scutal and scutellar punctures 1–2 PD apart; propodeum impunctate, and densely and finely shagreened; epipygium unmodified; hypopygium apically broadly rounded with thickened apical rim fringed with an even row of short spines; paramere broadly rhomboid with truncate apex rimmed with elongate flattened setae; volsella with long slender apical lobe and broader subapical one; penis valves with short, slender dorsal lobe and longer ventral apical one (Fig. 45); aedeagus with rounded basal bulb and short linear apical neck. Body black with yellow markings on lower half of clypeus, base of mandible, pronotal lobe and transverse pronotal carina; wing membrane clear, except brown stained in costal, marginal and submarginal cells; veins brown.

*Type material.*—Holotype, male, "Dutch New Guinea", Waigeu Camp Nok., 2500 ft, may 1938, L. E. Cheesman (LONDON)

*Etymology.*—The species is named after the collector, L. E. Cheesman.

*Discussion.*—*Eirone cheesmanae* can be distinguished from other *Eirone* by the flat medially pointed clypeus with an obtusely trilobate apex, broadly rounded and thickened apical rim of the hypopygium, which is margined by a row of stout spines, and principally black body color with few yellow markings. This species does not closely resemble any other.

**Eirone schlingeri Kimsey, new species**
(Fig. 47)

*Holotype, male.*—Body length 10 mm; forewing length 8 mm. Facial punctures 1–2 PD apart, smallest on clypeus, becoming large and shallow on frons and vertex; clypeus flattened, apical margin broadly truncate; F-I length 2.6× breadth; F-II length 3.8× breadth; pronotal punctures 0.5–1 PD apart; mesopleural punctures dorsally contiguous to 0.5 PD apart, becoming 0.5–1 PD apart ventrally; scutal and scutellar punctures 0.5–1 PD apart; propodeum densely transversely scratched or striate, punctures shallow and nearly contiguous; terga finely shagreened with punctures shallow and obscure, 2–4 PD apart; S-I with short medial ridge; epipygium broadly rounded, apical rim thin and transparent, punctation and sculpturing the same as previous tergum; hypopygium apically thickened with narrow subtriangular platform, and apical rim margined with row of short spines; paramere broadly rectangular, apical row of flattened setae, with setae about as long as apical margin; volsella with large narrowly rounded and setose basal part, and bilobate dorsal part, the broader of the two dorsal lobes setose; penis valves bilobate, dorsal lobe slender and strongly bending ventrally, ventral lobe wider and broadly rounded (Fig. 47); gonocoxa without slender digitate lobe ventromedially. Hindwing anal lobe without enlarged basal lobe. Body black with few bright yellow markings: pronotum with transverse yellow band on anterior carina broken medially; legs yellow, except coxae black. Wing veins dark brown, membrane yellow becoming darker in marginal cell.

*Type material.*—Holotype male, Papua New Guinea: Mt Kaindi, 8000 ft., 21 Feb. 1978, E. I. Schlinger (SAN FRANCISCO).

*Etymology.*—This species is named after the collector, Everett I. Schlinger.

*Discussion.*—The coloration of *E. schlingeri* is distinctive. It is the only New Guinean species with yellow legs and entirely black face. Additionally, the hypopygium ends in a thickened and narrowly rounded apex rimmed with short spines, the aedeagus is highly reduced and the penis valve lobes both project dorsally.

**Eirone speciosus Kimsey, new species**
(Fig. 7)

*Holotype, male.*—Body length 13 mm; forewing length 12 mm. Clypeal punctures 1–2 PD apart, densest and becoming nearly contiguous laterad of antennal socket and along posterior eye margin, punctures larger and deeper and much further apart on rest of head; frons and vertex highly polished; medial facial sulcus depressed above antennae; antennal lobes forming transverse platform; clypeus flattened, apicomedially slightly trilobate; F-I length twice breadth; F-II length 2.6× breadth; pronotal punctures 2–3 PD apart; mesopleural punctures contiguous dorsally becoming 2–3 PD apart ventrally; scutellar punctures contiguous to 1 PD apart outside of notauli, between notauli 1–3 PD apart; propodeum highly polished, and nearly impunctate; terga finely shagreened with punctures 1–3 PD apart; S-I with short slightly hooked medial ridge; epipygium broadly rounded, apical rim thin and transparent, punctation and sculpturing the same as previous tergum; hypopygium very broadly and bluntly rounded with apical rim margined with row of short spines; paramere curved, narrowest medially with broadly rounded base and apex, apical row of flattened setae, with setae shorter than apex width;

volsella forming floor of capsule, with short heavily sclerotized basal lobe extending toward midline of capsule, and elongate apically setose lobe protruding from paramere side and protruding from capsule dorsally; gonocoxa with slender digitate lobe ventromedially. Hindwing anal lobe with enlarged basal lobe (Fig. 7). Body black with bright yellow markings: clypeus yellow, with darker margin; frons with broad, transverse yellow band; pronotum with transverse yellow band on anterior carina and around posterolateral lobe; scutum with large posteromedial spot between notauli and along lateral margin; tegula yellow; mesopleuron with large yellow spot below wing fossa; scutellum with large yellow spot medially; metanotum with broad posteromedial spot narrowly separated from lateral one; forefemoral apex yellow, midfemur basally brown, apically yellow, hindfemur and all tibiae and tarsi yellow; propodeum with large transverse medial spot, narrowed medially; T-I-III with broad transverse yellow stripe; T-IV with large lateral yellow spot; T-V with smaller lateral yellow spot; apical tergum grading from black to amber posteriorly; S-II with lateral yellow spot; S-III with small lateral yellow spot; apical sternum yellow, darker basally; paramere amber with bright yellow apical third. Wing veins brown, membrane yellow becoming dark amber in costal and marginal cells.

*Type material.*—Holotype male, Papua New Guinea: East Highlands, Kainantu, Yabunka, Feb. 1975, malaise trap (OTTAWA).

*Etymology.*—The species name refers to the spectacular coloration of the male. No other species of *Eirone* is colored like this one.

*Discussion.*—In the type male the apical four flagellomeres on one side, and seven on the other are lost. Despite this damage this species is described because it represents several remarkable structural departures from other *Eirone* species, including

the hindwing jugal lobe having a large basal lobe, the bright coloration and the aedeagus having an elongate elaborately coiled apical loop. The body is bright black and yellow banded; a very different color pattern than all other species of *Eirone*. There do not appear to be any other described species similar to this one.

**Eirone valokaensis** Kimsey, new species

*Holotype male.*—Body length 7 mm; forewing length 5 mm. Facial punctures around antennal sockets and on clypeus 0–1 PD apart, punctures on frons and vertex widely separated, 1–4 PD apart; clypeus flattened, apical margin broadly truncate; F-I length 1.5 × breadth; F-II length 2.4 × breadth; pronotal and scutellar punctures 2–3 PD apart; mesopleural punctures separated by 0.5–1 PD, becoming slightly further apart ventrally; scutal punctures 0.5–1 PD apart; propodeum densely and finely wrinkled or striate, with dense nearly contiguous punctures between striae and increasing in density laterally; S-I with trace of medial ridge; epipygium broadly rounded, apical rim thin and transparent, punctation and sculpturing the same as previous tergum; hypopygium slightly thickened apically, margined with short spines; paramere short and broadly rectangular, without apical row of flattened setae, instead with setae and three long spines; volsella without distinct basal lobe, dorsal part bilobate, broader of the two dorsal lobes setose; penis valves with elongate, slender, apically hooked dorsal lobe extending outside of capsule, and elongate bilobate ventral structure extending alongside volsella; gonocoxa without slender digitate lobe ventromedially. Hindwing anal lobe without enlarged basal lobe. Body black with cream-colored markings; lower half of clypeus, basal half of mandible and transverse anterior pronotal band cream-colored; legs dark brown; apex of forefemur, external surface of foretibia, base of mid- and hindtibiae and base of hindbas-

itarsus all cream-colored. Wing veins dark brown, membrane clear.

*Type material.*—Holotype male: New Britain, Valoka, 8 Jul. '962, Noona Dan Exp., malaise trap (CANBERRA). Paratype male, same data as holotype.

*Etymology.*—This species of *Eirone* is named after the collection site Valoka, in New Britain.

*Discussion.*—Superficially *valokaensis* resembles the other species described from New Britain, *aquilonius*. Both have the same markings and basic coloration, a simple, apically truncate clypeus, short almost ear-like parameres, and penis valves with a very slender, hooked apical lobe. However, *valokaensis* is smaller, F-I and II are shorter, and the propodeum is coarsely punctate posteriorly, compared to *aquilonius*.

## Rhagigaster Guérin

(Figs. 9, 16, 21, 22, 26, 34–38, 40, 43, 44)

*Rhagigaster* Guérin 1839:213. Type: *Rhagigaster unicolor* Guérin 1839:214. Orig. desig.
*Rhytidogaster* Turner 1907:229. Type: *Rhagigaster aculeatus* Saussure 1867:113. Orig. desig.

*Male.*—Mandible slender and apically bilobate; labrum small and linear, broadly attached; maxillary palpus with 6 articles, labial palpus with 4; occipital carina dorsally obsolescent; frons generally smooth, although some species with transverse carina or welt; pronotum with well-developed transverse carina; mesopleuron evenly rounded, ecarinate, scrobe obsolescent; scutum narrow and linear; metasternum strongly bilobate medially, with lobes somewhat overlapping hindcoxae (Fig. 9); propodeum evenly rounded, ecarinate; tarsal claws dentate; hindcoxal carina strongly angulate; abdominal segments often coarsely punctate, and somewhat constricted subapically; basal abdominal sternum with transverse subbasal ridge joining a short medial carina (Fig. 21); apical sternum with long slender curved unciform prong below at most a

small notch or lip dorsally (Figs. 34–36); apical tergum with narrowed apical lobe (Fig. 26); parameres broad and tapering with interior lobe; volsella broad, covering floor of genital capsule and bending up laterally, with digitate setose dorsal lobe (Fig. 37); basal ring, dorsally elongate and broadly joined to genital capsule; penis valve a simple lobe adjacent to aedeagus (Figs. 43, 44); aedeagus short and blunt with short discrete apical neck (Figs. 43, 44).

*Female.*—Head as broad as long or broader; eyes ovoid, one-third as long as head or less; mouthparts unmodified, maxillary palpus with 6 articles and labial palpus with 4; pronotum subquadrate; mesopleuron flattened medially and angulate ventrally above midcoxa; metasternum with broadly bilobate projection between mid and hindcoxae; propodeum narrowed anteriorly, evenly sloping posteriorly and angulate laterally; terga smooth and ecarinate; tergum II declivous anteriorly; sternum II with small basal tooth, and constricted posteriorly; apical tergum evenly rounded; apical sternum broadly U or V-shaped apically.

*Distribution.*—Members of this genus are known only from Australia.

*Discussion.*—*Rhagigaster* appears to be somewhat intermediate between *Dimorphothynnus* and *Aelurus + Eirone*. Males superficially resemble those of *Dimorphothynnus*, having a heavily sclerotized body, long slender abdomen, unciform apical sternum, and traces of a transverse frontal carina in many species. However, females most closely resemble those of *Aelurus + Eirone*, having the metasternum projecting, although strongly bilobate apically, a long slender head, and sternum II ventrally dentate. There is a tendency toward palpal reduction in *Rhagigaster* females, but not to the extent seen in *Aelurus* and *Eirone*. *Rhagigaster* females can also be distinguished from these genera by the dentate tarsal claws.

*Included species.*—*Rhagigaster aculeatus*

Saussure, *alexius* Turner*, *approximatus* Turner*, *aruensis* Turner*, *auriceps* Turner*, *bidens* Saussure, *breviusculus* (Turner)*, *burnsi* Given, *castaneus* Smith*, *cinerellus* Turner*, *comparatus* Smith*, *connectens* (Smith)*, *corrugatus* Turner*, *crassipunctatus* Turner*, *decembris* Montet, *deductor* Turner*, *demattioi* (Dalla Torre)*, *denticulatus* Turner*, *depraedator* Turner*, *discrepans* Turner*, *emarginatus* (Fabricius)*, *ephippiger* Guérin, *fulvipennis* Turner*, *fuscipennis* Smith*, *hammerlei* (Dalla Torre)*, *heideri* (Dalla Torre), *interstitialis* Turner*, *iracundus* Turner*, *jubilans* Turner, *kiandrensis* Given, *laevigatus* Smith*, *latisculcatus* Turner*, *lecheri* (Dalla Torre)*, *lyelli* Turner, *mammeus* Montet, *mandibularis* Westwood*, *montanus* Given, *neptunus* Turner*, *nigritulus* Turner*, *obtusus* Smith*, *picticollis* Turner*, *pinguiculus* Turner*, *prothoracicus* Turner*, *pugionatus* Saussure, *reflexus* Smith*, *rugifer* Turner*, *rugosus* Smith, *scalae* (Dalla Torre)*, *stradbrokensis* Given, *thymetes* Montet, *unicolor* (Guerin), *wolframi* (Dalla Torre).

## ACKNOWLEDGMENTS

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# Generic Concepts in the Perilampidae (Hymenoptera: Chalcidoidea): An Assessment of Recently Proposed Genera

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*Abstract.*—The 26 new genera of Perilampidae proposed by Argaman (1990, 1991) are evaluated to determine if these concepts improve our understanding of the systematics of the family. It is demonstrated that: 1) many of the proposed genera are polyphyletic assemblages; 2) some of the type species of the genera are based on misidentified specimens and are problematic with respect to the International Code of Zoological Nomenclature; 3) except for eleven monotypic genera, the putatively monophyletic genera are formalizations of species groups recognized by earlier authors; and 4) the generic concepts do not contribute to a comprehensive system for classifying the species of *Perilampus* Latreille—a large number of disparate and unrelated species remain exiled in *Perilampus* Latreille (sensu Argaman). Argaman's generic classification has not been adopted nor should it. Twenty-six **new synonyms** of *Perilampus* Latreille, 1809 are proposed, 1 subjective synonym based on the synonymy of the type species with the type species of *Perilampus, Olarlar* Argaman, 1990, and the following 25 subjective synonyms: *Bagdasar* Argaman, 1990; *Balintos* Argaman, 1990; *Bukbakas* Argaman, 1990; *Dekterek* Argaman, 1990; *Durgadas* Argaman, 1990; *Ecalibur* Argaman, 1990; *Fifirtiz* Argaman, 1990; *Fulaytar* Argaman, 1990; *Goyurfis* Argaman, 1990; *Ihambrek* Argaman, 1990; *Itonayis* Argaman, 1990; *Kekender* Argaman, 1990; *Lufarfar* Argaman, 1991; *Mivarhis* Argaman, 1990; *Naspoyar* Argaman, 1990; *Nilgator* Argaman, 1990; *Pondoros* Argaman, 1991; *Sicatang* Argaman, 1990; *Taltonos* Argaman, 1990; *Tiboras* Argaman, 1990; *Tondolos* Argaman, 1990; *Vadramas* Argaman, 1990; *Vaktaris* Argaman, 1990; *Yertatop* Argaman, 1990; *Zuglavus* Argaman, 1990. The synonymy of *Afroperilampus* Risbec, 1956 with *Perilampus* Latreille, 1809 is reestablished (**revised status**) and **lectotypes** are also designated for 6 species: *Chalcis aenea* Rossi, 1790; *Perilampus chrysonotus* Förster, 1859; *Perilampus igniceps* Cameron, 1909; *Perilampus minutus* Girault, 1912; *Perilampus nigriviridis* Girault, 1912; and *Perilampus tristis* Mayr, 1905. In addition to restoring the nomenclature, many character systems of importance for an improved understanding of the systematics of the Perilampidae are discussed and illustrated, and a proposal is made to continue to recognize informal species groups within the genus *Perilampus.*

## INTRODUCTION

The potential work load of systematists has increased markedly in recent years. Not only are there fewer specialists but their distribution across taxa is ill-matched to species richness and the magnitude of the work remaining (Gaston and May 1992). The "biodiversity crisis", with the need to provide accurate and relevant information for conservation and development initiatives, is placing additional demands on systematists. Nowhere are the problems greater than in entomology. Not only is inventory and descriptive work at a very early stage in entomology but the importance of terrestrial arthropods as indicators of ecosystem health is now more generally appreciated (Wilson 1987). There is now a pressing need for both inventory and monitoring programs of terrestrial arthropods (Kremen *et al.* 1993). However, it must be remembered that systematists are responsible for naming and organizing organic diversity. If classifica-

tions are to have the predictive value of a phylogenetic system (Wheeler 1990)—one that reflects evolutionary history—then constant vigilance must be kept on the taxonomy of all groups of organisms.

Scrutiny is particularly important at the generic level. Because of the requirements for binominal nomenclature, names are the point of entry for information assembled in both the literature and collections. For many groups of insects, generic names summarize important biological information, but only if the classifications are based on sound phylogenetic principles. Failures in this regard, and the taxonomic chaos generated, have elicited concerns about the utility and efficiency of a binominal nomenclature (Mayr 1969), and have also precipitated suggestions to restrict publication of available names to accredited sources or to establish a system of "protected" works (Cornelius 1987).

This paper addresses a generic reclassification of the Perilampidae by Argaman (1990, 1991) that threatens the stability of the nomenclature and the predictability of the classification of the Perilampidae. Unfortunately, the publications under consideration (Argaman 1990, 1991) meet the criteria for availability as set out by the International Commission of Zoological Nomenclature (ICZN). These publications were, however, ignored during the preparation of chapters for the *Hymenoptera of Costa Rica* (1995a) and the *Genera of Nearctic Chalcidoidea* (Darling, in press) but until an assessment of the generic concepts of Argaman (1990, 1991) is published, both the classification and nomenclature of the Perilampidae are compromised (Gibson 1993). Specifically, it will be demonstrated that the taxonomic changes at the generic level proposed by Argaman, which splits the genus *Perilampus* Latreille into 27 genera, are at best retrogressive. The 26 new species described by Argaman will not be dealt with specifically, nor will his idiosyncratic approach to classification and phylogenetics be discussed.

There are two basic requirements for a revised generic classification to advance our understanding. Firstly, all new genera must be arguably monophyletic; character polarity must be determined. This requires that generic studies be as comprehensive as possible at either the subfamily or family level. Secondly, the proposed genera should form a comprehensive system, ideally with all species referred to monophyletic genera. Guidelines such as the "inverse ratio" recommendation (Mayr 1969:92)—that the size of the gap between genera (degree of difference) be in inverse ratio to the number of species in the genus—are useful in preventing the proliferation of monotypic genera but only after the basic conceptual requirement of monophyly is met. It is from this perspective that the genera proposed by Argaman will be discussed and that subjective synonymies are proposed herein.

## SYNOPSIS OF ARGAMAN (1990, 1991)

Argaman's work on the Perilampidae was published in two parts, I (1990) and II (1991), and consists mainly of an illustrated key of 234 couplets to 28 genera and species of *Perilampus* s.l. (1990). Also included is a section describing new taxa (1990; except 1991 for *Pondoros* and *Lufarfar*) and an annotated checklist of species which includes the material examined (1991). The generic treatments consist only of the designation of a type species and a description that is purportedly comparative with *Perilampus* s.s. No differential diagnoses are provided and most of this evaluation of Argaman's generic concepts is based on the morphological information provided in the key.

Argaman's study was based in large part on a collection of perilampids in the Hungarian Natural History Museum, Budapest, which was "gathered together tediously by the late Dr. Lajos Biró" (Argaman 1990:192). Much of the material was collected by Biró, but many of the specimens "were received from other muse-

ums'', perhaps through loans or exchange. Much of this material now resides in Argaman's personal collection. Argaman also apparently based many of his conclusions on Biró's notes and/or unpublished manuscripts (Z. Bouček, *in litt.*). This has contributed to the major shortcoming of the paper—most conclusions are not based on type material or even, as is now apparent, accurately identified specimens. In many cases this is only conjecture because Argaman has only made a few specimens from his personal collection available for study. Argaman acknowledged the above shortcoming (1990:190): "In some instances, no type material was available, and the respective species were treated in the key on the basis of identified material, which may be or may be not consistent with the type of that species." This is critical in cases where type species of new genera are designated. As will be discussed, in several cases the specimens referred by Argaman to the type species were misidentified. In accordance with Article 70 of the ICZN, each of these cases should be referred to the Commission to designate the type species. The Commission could summarily deal with these generic names by designating *Cynips italica* Fabricius as the type species of the Argaman genera. This species is the type species of *Perilampus* Latreille, 1809 (*q.v.*) and the Argaman genera would then become objective synonyms of *Perilampus* (Art. 61(c)(iii)). This would restore accustomed usage and preclude the names, and the uncertainty associated with them, from resurfacing in the future.

Another problem with the approach taken by Argaman was his failure to adequately consider other described genera of Perilampidae. These are currently classified in two subfamilies, Chrysolampinae and Perilampinae (see Bouček, 1988). Perilampinae includes, in addition to *Perilampus*, *Euperilampus* Walker, *Krombeinius* Bouček, *Monacon* Waterston, *Steffanolampus* Peck, and *Burksilampus* Bouček. Each

of these genera is separated from *Perilampus* by a distinct morphological gap and are putatively monophyletic, but they almost certainly render *Perilampus* as a paraphyletic assemblage. As will be demonstrated, the taxonomic changes proposed by Argaman only exacerbate the paraphyly of the Perilampinae.

## METHODS

The genera proposed in Argaman (1990, 1991) are evaluated individually with respect to the criteria for genera discussed above. Of particular importance is the question of monophyly. Argaman stated that *Euperilampus* is the sister-genus of *Perilampus* (*s.l.*), but provided no justification for this claim. Darling (1983) presented morphological data that, when analyzed from a cladistic perspective, suggests that the recognition of *Euperilampus* (and *Krombeinius* and probably *Burksilampus*) renders *Perilampus* paraphyletic; *Euperilampus* is therefore an inappropriate outgroup. I will base my outgroup comparisons on *Steffanolampus*, which is regarded as the most plesiomorphic genus of Perilampinae (Darling 1988), and *Chrysolampus* Spinola (Chrysolampinae).

Evaluating generic concepts is predicated on the study of the type species but this is problematic if the specimens used to designate the type species were misidentified at the time of typification. The ICZN instructs that correct identification be assumed unless there is compelling evidence to the contrary. In the absence of conclusive evidence to the contrary, this assumption was made for each of Argaman's genera. So typified, it will be shown that these genera do not advance our understanding of the systematics of Perilampidae. In some cases it has been possible to demonstrate that the type species was based on a misidentified specimen. The use of these names would lead to nomenclatural instability and would require that a separate case be submitted to the Commission for each genus (ICZN, Art. 70).

The synonymies proposed and the use of informal species groups *Perilampus* would obviate formal petitions to the Commission.

The genera proposed by Argaman are discussed in the context of the informal species groups of *Perilampus* (s.l.) that have been recognized by previous authors. To facilitate locating the treatments of a particular genus, an alphabetical index has been provided in Appendix 1. The material examined sections list only those specimens studied during this reanalysis and includes both specimens examined by Argaman and determined or type material that was not available to him. In the generic accounts, the only included species listed are those mentioned in the text or species which have been previously referred to species groups. Figures referred to as fig. x are found in Argaman 1990 unless credited otherwise; those cited as Fig. x are contained herein. Museum acronyms are as follows: ANIC, Australian National Insect Collection, Canberra; BMNH, British Museum (Natural History), London; CNC, Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa; HNHM, Hungarian Natural History Museum, Budapest; MCSN, Museo Civico di Storia Naturale "G. Doria", Genoa; MNHN, Museum National D'Histoire Naturelle, Paris; NMV, Naturhistorisches Museum Wien, Vienna; ROM, Royal Ontario Museum, Toronto; UA, University of Arkansas, Lafayette; USNM, National Museum of Natural History, Washington, D.C.

## MORPHOLOGICAL FEATURES USED BY ARGAMAN (1990, 1991)

Many of the genera proposed by Argaman are a result of elevating provisional species groups proposed by other workers (*e.g.*, Smulyan 1936; Bouček 1956; Darling 1983). However, many of the defining features of these species groups are subject to convergence and reversals and species groups are both an effective and conservative approach under these circumstances. Argaman further complicates the issue by "redefining" some of the diagnostic features of these species groups. Consider, for example, "head carinated". Argaman (1990:200) expanded this from the traditional definition of a sharp carina from the anterior ocellus to the antennal torulus (his "carina very often sharp with outer side sulcate", fig. 14, 21, 26) to include simply "a sharp edge of the depression", fig. 5) and even a "concealed" carina (fig. 67, 70)! Notwithstanding this complicated and confused morphology, Argaman used this "character" as a major subdivision in the genus *Perilampus* and, as is discussed below, closely related species were referred to different genera because he considered the species to have different states of the frontal carina. Other workers have realized that the frontal carina is difficult to characterize unequivocally, particularly if the vertex and inner orbits have longitudinal costae (Fig. 3) or if the frons meets the vertex at a sharp keel (Fig. 5), but have restricted the term to include only a sharply raised carina that is extended from behind the anterior ocellus ventrad on each side of the scrobal cavity to the level of the antennal toruli (Fig. 1, 2). This definition of the frontal carina is equivalent to the carina with the "outer side sulcate" sensu Argaman (Figs. 1, 2). Fortunately there is another morphological feature, finger-like axillula (Fig. 8 cf. Fig. 7), which is unequivocal in its manifestation, and is also found in all of the truly carinate New World species. This latter feature allows the assessment of variability in the development of the frontal carina in a demonstrably monophyletic group, the clade containing the *Perilampus hyalinus* + *Perilampus platigaster* species groups. Unless carefully defined, a frontal carina can even be variable within a species (see discussion of *Kekender*).

Other morphological features used by Argaman to support his generic reclassification include: the size and shape of the

prepectus relative to the lateral pronotal panel; the presence of tubercles or scales on the mesoscutum and scutellum; and sculptural features such as fine punctures on the second metasomal tergite (T2), cross-arcuate costae or rugae on the mesoscutum, oblique costae on the malar region of the head, and the presence or absence of various carinae on the propodeum. Even a cursory look at other monophyletic groups within the Perilampinae, for example the species currently referred to *Euperilampus* and *Krombeinius* (Darling 1983, 1988, 1995), documents homoplasy in many of these character states, which argues against monothetic generic concepts based on these states. In some cases, species that I regard as closely related are referred to different genera by Argaman simply because they differ in a single very labile feature. For example, Argaman placed great importance on the sculpture of the vertex and the relative length of the malar sulcus. He separated two pairs of genera on the basis of a long *versus* short malar sulcus (relative to front margin of malar cavity), one pair of genera having the vertex smooth, devoid of sculpture (*Vadramas* and *Sicatang*), and the other pair with the vertex sculptured (*Perilampus* s.s. and *Mivarhis*). If the sculpture of the vertex is subject to homoplasy (see below) then the number of genera is reduced by two. Moreover, if the length of the malar sulcus is evolutionarily labile (see below) then all four generic names would be regarded as synonyms.

Argaman did introduce some new morphological character systems for consideration, but the phylogenetic significance of many of these are compromised by his errors in basic morphology and phylogenetic interpretation. Perhaps the most interesting novel character state is the bicarinulate posterior margin of the pronotum (Fig. 18 cf. Fig. 17). But Argaman used both the absence and the presence of a bicarinulate pronotum as the sole justification for the establishment of genera. The

New World genus *Goyurfis* is distinguished from *Taltonos* by the absence of this character state whereas the presence of a bicarinulate pronotum distinguishes the Old World genus *Tiboras* from *Fulaytar*. It is clear, however, from outgroup comparison with both *Steffanolampus* and *Chrysolampus* that the presence of a bicarinulate pronotum is apomorphic in the Perilampinae. The bicarinulate pronotum is also subject to homoplasy even within clearly defined clades. For example, the bicarinulate pronotum is present in most species of *Krombeinius* (Darling 1995b) but only in some species of *Euperilampus* (e.g., present in *E. tanyglossa* Darling, Darling 1983, fig. 33, apparently reduced in most species of the *E. triangularis* group, Darling, 1983, figs. 13–15, and absent from *E. scutellatus* (Girault) and *E. mediterraneus* Bouček). A further complication is that some of the species Argaman characterized as having a bicarinulate pronotum do not, based on an examination of type material (see discussion of *Tiboras*).

## THE GENERA RECOGNIZED BY ARGAMAN (1990, 1991)

The structure of the head, in particular the degree of development of frontal carina or ridges, has figured prominently in virtually all previous attempts to both identify and organize the species of *Perilampus* (s.l.). The first couplet of Argaman's key is also based on the structure of the head and purports to separate species with a frontal carina, the "carinate" species from the "acarinate species", those lacking a frontal carina. This assessment of the 28 genera recognized by Argaman is organized in two sections, the carinate and the acarinate genera (*sensu* Argaman, based on couplet 1). Within each of these two groups the "genera" are arranged by other morphological features, by previously recognized species groups, or by the types of problems encountered (e.g., monotypic genera, polyphyletic assemblages).

## A. The Carinate Genera of Argaman

Eleven genera were proposed for putatively carinate species, seven of which are monotypic. Three of the monotypic genera do not have a frontal carina on the head and are almost certainly more closely related to acarinate species of *Perilampus* (s.l.). Two other monotypic genera were based on autapomorphic features but are clearly related to other carinate genera. Four of the remaining genera were based either on misinterpretations of morphology or on character states that are variable in other genera of Perilampinae. Of the two remaining genera, one was based on a plesiomorphy and the other might be a highly variable single species, *P. hyalinus* Say.

(1) Genera Lacking a True Frontal Carina

Three monotypic genera were erected by Argaman for species that actually lack a frontal carina. One is a highly apomorphic species of uncertain affinities which is known only from the male, and both of the two genera are based on species that are closely related to species that lack a frontal carina on the head.

**Kekender** Argaman, 1990:233. Type species: *Kekender bouceki* Argaman, 1990, by original designation. Monotypic.

*Material Examined.*—Holotype ♂, "[Kenya] Muto-Berg, Kenia"; Argaman collection. Also examined: ♂, "[Zimbabwe] Bulawayo S. Rhodesia 9.11.1924 Rhodesia Museum"; ♂, "N. Nigeria: Zaria 12.x.1971 J.C. Deeming"; ♀, "[Namibia?] Kranzberg III-1932 G. v. Son", "Transvaal Museum"; all temporarily BMNH.

Argaman based this genus on a single male from Kenya. Three additional males were examined by me, through the kindness of Dr. Zdenek Bouček, who has known of the existence of these remarkable wasps for many years and planned to describe the species in the context of a revision of the African species of *Perilampus* (pers. comm.). I regard all four specimens

as conspecific. As Argaman noted, in the holotype the first funicular segment is twice as long as wide and almost as long as the following two segments combined. This distinctive configuration of the antenna is also found in the other three males. Argaman treated *Kekender* as a carinate species based on an abruptly margined scrobal depression (fig. 5). A distinct frontal carina is not present in the holotype of *K. bouceki* but there is variability in the structure of the head in this species. The specimen from Kranzberg has a short carina which, however, is restricted to the region of the ocellar triangle.

The most remarkable feature of *K. bouceki* is the configuration of the scutellum. In lateral view the scutellum is doubly convex, with two very distinct promontories along the midline (fig. 4). However, there is considerable variability in the degree of development of the doubly convex scutellum. All three specimens examined are virtually the same size, approx. 4 mm; the variable development of the scutellum is not the result of simple allometry. The specimen from Nigeria has the scutellum almost normal in configuration and the specimen from Namibia has the most extreme development of the scutellum; Argaman's holotype (fig. 4) and the specimen from Zimbabwe are intermediate. Otherwise, the four specimens are virtually identical. Until the female is discovered it will not be possible to determine if the development of the scutellum is sexually dimorphic; if so, then sexual selection might be responsible for the peculiar and variable nature of the scutellum.

Argaman did note some other peculiarities of *K. bouceki*: the malar space is long and lacks a distinct sulcus; the legs are rather long and narrow; and the structure of the propodeum is rather distinctive, i.e., the discal areas are sculptured as opposed to glabrous. However, I am at a loss to explain the first feature mentioned in his key couplet 3 (a ventrally directed tubercle on the propleuron, mesosternum and pro-
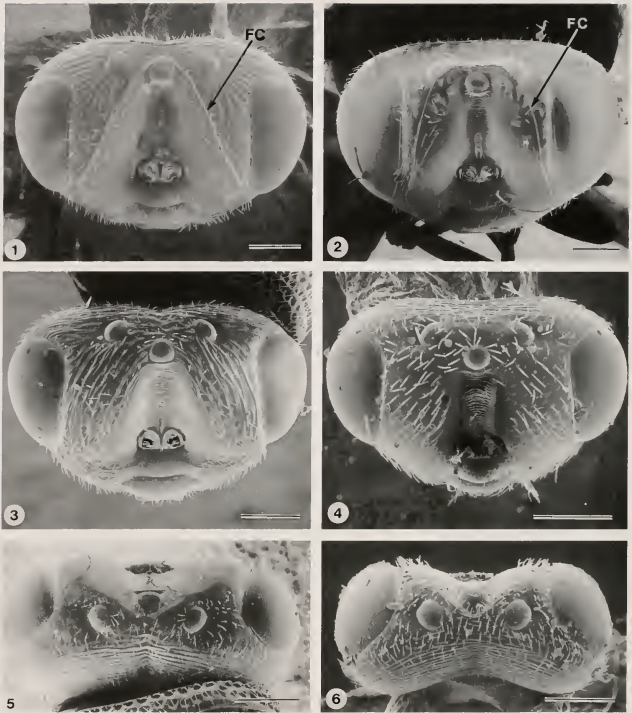
Figs. 1–6. Heads of *Perilampus* species, 1–4 oblique frontal view, 5 and 6 dorsal view. 1. *P. hyalinus*. 2. *P. platigaster*. 3. *P. emersoni*. 4. *P. anomocerus*. 5. *P. tristis*. 6. *P. fulvicornis*. FC, frontal carina. Scale lines, 0.25 mm.

podeum), and his description and illustration of the prepectus (fig. 4) do not agree with the specimens I have examined (Fig. 23). Argaman was so impressed by the apomorphies that he stated that there were "no close relatives of this species within Perilampidae" and that "I regard this genus as the most transient perilampid toward that family [Eucharitidae]" (Argaman 1990:234). Interestingly, he failed to mention (although he illustrated, fig. 5) perhaps the most significant feature of this species from a phylogenetic perspective. The mandibles are falcate, much

narrower than in most species of *Perilampus*, which could be used to support his hypothesis of a close relationship with Eucharitidae (see Heraty 1994).

There is no question that this is a very different perilampine. However, the apomorphic character states mentioned above do not unequivocally confer generic status, at least not until the female is associated and described, and until affinities of *K. bouceki* with other species of *Perilampus* (s.l.) are investigated in more detail. It is almost certain that generic status for this species would only increase paraphyly in the classification of the Perilampinae. I therefore regard *Kekender* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (NEW SYNONYMY).

**Balintos** Argaman, 1990:241. Type species: *Perilampus parvus* Howard, 1897, by original designation. Monotypic.

*Material Examined.*—Holotype ♂: "Mount Gay Est. (Leeward side) Grenada, W.I., H.H. Smith", "Type No. 69560 U.S.N.M." [red, printed]; USNM.

*Perilampus parvus* was described from a single specimen that agrees with the label data given above; this specimen was labelled by me as holotype. The specimen agrees with Howard's brief description, except that the sex was stated as female. This species is a rather typical member of the *Perilampus fulvicornis* group; all members of this species group lack a frontal carina and the frons and vertex lack costae (as in Fig. 6). *Perilampus parvus* also has a lateral patch of setae on the second metasomal tergite (as in Fig. 20), which is found in many species of *Perilampus fulvicornis* group (*q.v.*). Howard (1897), in the original description, noted that this species was similar to *Perilampus politifrons* Howard, which Argaman referred to the acarinate genus *Pondoros* (q.v.).

Argaman incorrectly considered *Perilampus parvus* in the key and in fig. 36 as a carinate species with the inner orbits costate ("vertical carinules"). Argaman

did not study the holotype of *P. parvus* and based his concept of this species on a specimen, apparently identified by him and deposited in his personal collection, from Haiti; attempts to borrow this specimen were unsuccessful. It is almost certain that *Balintos* is based on a misidentified specimen, most likely on a species of the *Perilampus platygaster* group based on the black body color and fig. 36. I therefore regard *Balintos* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (NEW SYNONYMY).

**Yertatop** Argaman, 1991:242. Type species: *Perilampus emersoni* Girault, 1930, by original designation. Monotypic.

*Material Examined.*—♀, "Australia Biró 1900", "N.S. Wales Mt. Victoria [verso] VI, 15"; det Argaman; HNHM. ♀, "[Australia, western New South Wales] 60 W Wilcannia 22 Nov 49 E F Riek", det Riek and included in Riek, 1966: 1224; ANIC.

The specimens listed above are regarded as conspecific. This is, however, not a carinate species, although the frons and inner orbits have very strong longitudinal costae (Fig. 3). Argaman described this monotypic genus because he regarded *P. emersoni* as the only carinate species with an extremely narrow prepectus. This form of prepectus is noteworthy only if this species is compared to carinate species, all of which have a large prepectus (as in Fig. 8). *Perilampus emersoni* is a rather typical acarinate species, referable to the *Perilampus laevifrons* group (*Mivarhis* sensu Argaman). The third metasomal tergite (T3) is not punctate and the prepectus is very narrow. There is no justification for a monotypic genus based on *Perilampus emersoni* and I therefore regard *Yertatop* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (NEW SYNONYMY).

## (2) Carinate Genera with Triangular Axillula

Argaman recognized five genera for Old World species with a distinct frontal

carina on the head (as in Figs. 1, 2). Three, possibly all four of these genera are monotypic.

**Nilgator** Argaman, 1990:242. Type species: *Perilampus mirabeaui* Girault, 1930, by original designation. Monotypic.

*Material Examined.*—♀, "N. Guinea Biró [18]96, Krima Astrolabe B[ay]", det. Argaman; HNHM. ♀, [Australia] Queensland Mt. Tamb.[ourine] 20.2.1911; specimen discussed in Riek, 1966; also two specimens seen from Papua New Guinea, 1 ♀ discussed in Riek, 1966; ♂ "PAPUA NEW GUINEA: Kairiru Is., Wewak Br. O. William Borrell", "Nest No. (see 1/59) Borrell Notes, Hymenoptera Section, ANIC, August 1974"; both ANIC. Note: No host data is provided in the Borrell field notes, but the specimen was almost certainly reared from a mud-nesting aculeate wasp (Ian Naumann, *in litt.*).

Argaman did not examine the holotype of this species but I regard his exemplar as conspecific with *Perilampus mirabeaui.* This a very distinctive Australian species with a striking, raised scale-like tubercle on the scutellum (fig. 35). Riek (1966) revised the Australian species of *Perilampus* and saw no reason to regard this species as anything other than a *Perilampus* and I concur. Similar protuberances occur on the mesoscutum of *Perilampus auratus* (Panzer) and these structures may function in escaping from the cocoon, pupa, or puparium of the host. *Perilampus mirabeaui* has distinct punctures on the third metasomal tergite (T3) and in this and other regards is similar to species I regard as forming the *Perilampus punctiventris* group (see also discussions of *Tondolos* and *Fulaytar*). The character states used by Argaman do not warrant recognition of a monotypic genus. I therefore regard *Nil-*
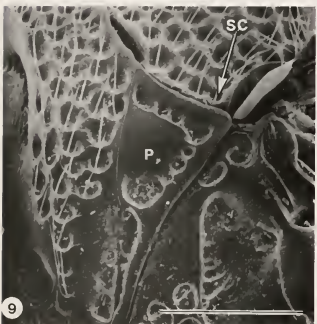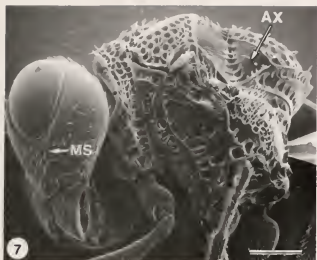
*gator* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

**Tondolos** Argaman, 1990:243. Type species: *Perilampus tasmanicus* Cameron, 1916, by original designation. Two species included by Argaman, also *P. cairnsensis* Girault, 1913 which is "very probably the same species as *tasmanicus*" (Bouček 1988:507).

*Material Examined.*—♀, "AUSTRALIA: Sydney: Cabramatta Georges R. valley. 7.11.1959", "N. Nikitin B.M. 1960–203". Compared with Lectotype *P. tasmanicus,* BM 5–400; ROM. ♂, "Canberra ACT coll 8 Aug 1961 P B Carne", "Hyperparasites ex Paropsis reticulata [Coleoptera: Chrysomelidae]", det Riek; ANIC. ♀, "[Australia] Mackay 4.[19]00", det. Argaman; HNHM.

I regard the exemplar examined by Argaman as conspecific with the two specimens identified by Riek. Argaman recognized three genera for species with parallel costae on the frons and vertex: *Yertatop, Nilgator,* and *Tondolos. Tondolos* was recognized for two nominal species without the defining features of each of the other two genera, i.e, without the tubercle on the scutellum of *Nilgator* and without the narrow prepectus of *Yertatop.* As discussed above, the type species of *Yertatop* is acarinate and most likely related to the *Perilampus laevifrons* group, all species of which have a very narrow prepectus. The distinctiveness of *P. tasmanicus* noted by Argaman is a result of the plesiomorphic absence of one feature, the tubercle on the scutellum, and a comparison with a distantly related species. I regard *P. tasmanicus* as a typical member of the *Perilampus punctiventris* group. There are no apomorphies that warrant the recognition of this genus. I therefore regard *Tondolos* Arga-

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Figs. 7–12. Mesosomata of *Perilampus* species. 7. *P. chrysopae,* axillula (AX) triangular. 8. *P. hyalinus,* axillula (AX) finger-like. 9–12 detail of prepectus and lateral pronotal panel. 9. *P. tristis.* 10. *P. anomocerus.* 11. *P. stygicus.* 12. *P. fulvicornis.* MS, malar sulcus; P, prepectus; SC, scapula. Scale lines, 0.25 mm.

man as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

**Tiboras** Argaman, 1990:243. Type species: *Perilampus maurus* Walker, by original designation. Monotypic.

*Material Examined.*—Lectotype ♀, "[South Africa] Port Natal [verso] 49 29", "B.M. Type HYM 5.1684", "Perilampus maurus Walk.", "Lectotype ♀, G. J. Kerrich 1955"; BMNH. ♀, "S. AFRICA Richmond XI.1938 P. Regnard ACC. 256 Ex: Adapsilia latipennis ?"; ROM. Note: apparently reared from a Pyrgotidae (Diptera); see Evenhuis 1989:498. ♀, "Port-Natal Sud. Africa", "Ex Mus. Walker", det. Argaman; Argaman collection.

*Tiboras* was based on a single African specimen with a bicarinulate pronotum, identified by Argaman as *P. maurus*. He did not examine the lectotype of the type species and I do not regard his exemplar as conspecific with *P. maurus*. Argaman's exemplar does have a bicarinulate pronotum but the lectotype of *P. maurus* does not. In addition, the prepectus (Fig. 22) is very different in these two species (Note: Argaman's representation of the prepectus (fig. 106) is very inaccurate) and the second metasomal tergite is devoid of sculpture in the lectotype *versus* finely punctured in Argaman's exemplar. I regard Argaman's exemplar as an undescribed species of the *P. punctiventris* group, the only known species in that group with a bicarinulate pronotum (see discussion of *Fulaytar*). Notwithstanding the misidentification of the type species, this single feature does not justify generic status, especially when it is noted that closely related carinate species are variable in this character and that a bicarinulate pronotum may be plesiomorphic (see discussion of *Durgadas*). I therefore regard *Tiboras* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

**Fulaytar** Argaman, 1990:243. Type species: *Perilampus singaporensis* Rohwer, 1923, by original designation. Monotypic.

*Material Examined.*—Holotype ♀: "Singapore Coll. Baker", "Type No. 24974 U.S.N.M." [red, printed], "Perilampus singaporensis TYPE ♀. Roh." [handwritten]; USNM. Also examined: "Pusa Coll. 21", "Pusa 10.xii.12 G.R.D.", "from nest of *Sceliphron coromandelicum* (Hyperparasite)"; USNM. Note: There is no locality data associated with this specimen but the host is recorded from India, Sri Lanka, and Burma (Bohart and Menke 1976). ♀, "[Indonesia] SUMATRA Pangherang-Pisang X.[18]90 e III.[18]91. E. Modigliani", det. Argaman; MCSN.

Argaman based his genus on a single specimen from Sumatra. However, I do not regard his exemplar as conspecific with the holotype of *P. singaporensis*, although both are referable to the *P. punctiventris* group. *Perilampus singaporensis* is very closely related to *P. mirabeaui* and both species share an unequivocal apomorphic character state, a raised scale-like tubercle on the scutellum. This structure is much more distinct in *P. mirabeaui* but is clearly evident in the holotype of *P. singaporensis*, and is completely absent from Argaman's exemplar. I regard *P. mirabeaui* and *P. singaporensis* as part of a monophyletic species group, the *Perilampus punctiventris* group, that also includes in addition to *P. punctiventris* Crawford, *P. orientalis* Rohwer, *P. luxonensis* Crawford, and Argaman's exemplar. Argaman's exemplar is not conspecific with *P. singaporensis*, the type species of *Fulaytar*, and the diagnostic feature of the genus used in the key, the absence of a bicarinulate pronotum is plesiomorphic and identical to the form of the pronotum found in the type species of *Tiboras* (see also discussion of *Tiboras*). I therefore regard *Fulaytar* as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

**Afroperilampus** Risbec, 1956. Type species: *Af-*

*roperilampus meloui* Risbec, by original designation. Eight included species.

*Material Examined.*—Holotype ♀ "MUSEUM, PARIS COTE D'IVOIRE, Singerville. G. Melou 1914'', "Perilampus Meloui Risbec'', handwritten; MNHN.

Neither the holotype nor even an identified specimen of the type species of *Afroperilampus* was examined by Argaman; he apparently based his species concept on Risbec (1956), which, unfortunately, has inaccurate caricatures for illustrations. *Afroperilampus* was described by Risbec for a single species and based on wing venation, i.e., the postmarginal vein was stated in the key to genera as longer than the marginal vein. This is not true in either Risbec's illustration (unnumbered) or in the holotype.

*Afroperilampus* was regarded as a synonym of *Perilampus* by Bouček (1972). Argaman resurrected this genus for a subset of species with a triangular axillula that lack parallel costae on the face; the lateral pronotal panel is stated by Argaman (1990:209) as having "two rows of moderately large punctures opposite to prepectal triangle''. The sculpture of the third metasomal tergite is stated as variable, but there are no punctures in the holotype of the type species. In his discussion of this genus, Argaman as much as stated that this is an artificial assemblage; he actually suggested that yet another new genus is required for an aggregate of the included species! In addition to concerns over monophyly, the type species does not have the configuration of the prepectus that is used in the key to differentiate *Afroperilampus* (Fig. 26) from *Tiboras* (Fig. 24) and *Fulaytar* (Fig. 25). The lateral pronotal panel is virtually identical in the type species of these three genera. I therefore concur with Bouček (1972) and regard *Afroperilampus* Risbec as a junior subjective synonym of *Perilampus* Latreille, 1809 (**REVISED STATUS**).

**(3) Carinate Genera with a Finger-like Axillula**

Three genera were described by Argaman for an exclusively New World group of species. The combination of a frontal carina on the head (Figs. 1, 2) and finger-like axillula (Fig. 8) distinguishes these species (Smulyan 1936). These species almost certainly form a monophyletic group but recognizing this clade at the generic level renders *Perilampus* paraphyletic (see Darling 1983 for a cladogram with synapomorphies of these species and *Euperilampus* + *Krombeinius*). It is in this species group where Argaman has wrecked the most havoc on the nomenclature. Eighteen described species of *Perilampus* were referred to either *Goyurfis* or *Taltonos*, and eight new species were described on the basis of inadequate material. A monotypic genus, *Durgadas*, was also proposed.

**Taltonos** Argaman, 1990:234. Type species: *Perilampus hyalinus* Say, by original designation. Sixteen included species, the *Perilampus hyalinus* group (sensu Smulyan 1936).

*Material Examined.*—*Perilampus hyalinus* group species are the most commonly collected perilampids in the New World and are distributed from Canada to Argentina and Chile. I have examined thousands of specimens in this species group from all of the major museums in North America, including: the material that formed the basis for Smulyan's (1936) revision of *Perilampus* [mainly USNM]; specimens reared as primary parasitoids of *Neodiprion* sawflies [ROM, CNC]; and specimens reared as parasitoids of Ichneumonidae, Braconidae, and Tachinidae (hyperparasitoids) attacking *Hyphantria cunea* (Drury) (Lepidoptera, Arctiidae), the fall webworm [ROM, UA].

The type material of Say's species is generally regarded as lost (Peck 1963). This is acknowledged in Argaman's checklist (1991:9) but label data are also provided for a specimen, now in his personal collection, that agrees with all of the
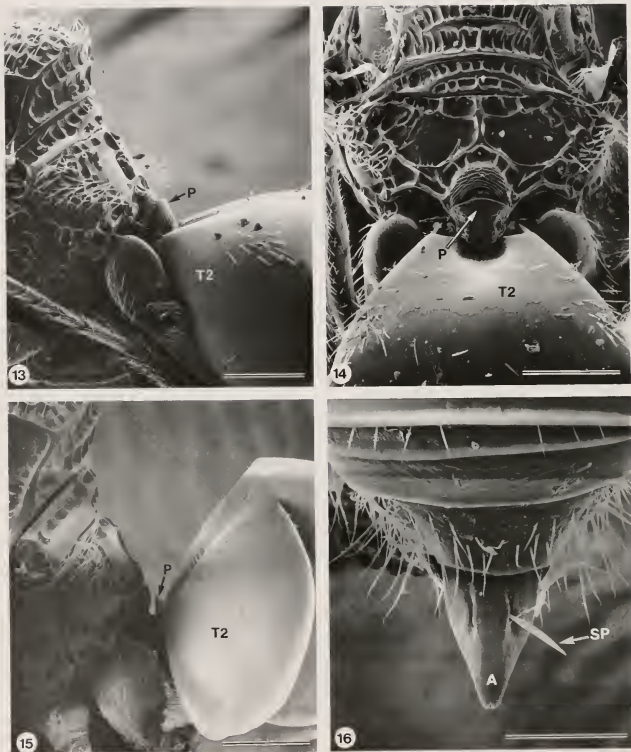
Figs. 13–16. 13–15, Petioles (P) and second metasomal tergites (T2) of *Perilampus* species. 13. *P. anomocerus*, lateral view. 14. *P. anomocerus*, dorsal view. 15. *P. tristis*, lateral view. 16. Aedeagus (A), dorsal view, *P. tristis*, showing laterally directed spine (SP). Scale lines, 13–15, 0.25 mm., 16, 0.10 mm.

particulars of the type material! It must be noted that the statement "Type" red label" in Argaman's checklist cannot be regarded as indicating type material; Argaman used this notation throughout his checklist when type material is extant and deposited in other institutions (e.g., *P. maurus*). He probably regards the so labelled specimens as his exemplars of the species, but my requests for clarification of

this issue have gone unanswered. As discussed, but not clarified by Argaman, the taxonomy of *P. hyalinus* is confused by diverse host associations and modes of parasitism. The situation is still best summarized by Burks (1979:771), "This may be a species complex, rather than a single species; careful rearings have produced specimens, at present indistinguishable, that are either primary or secondary parasites."

Fortunately, this species group is very distinctive and Argaman's generic concept of *Taltonos* is concordant with the accepted concept of the *Perilampus hyalinus* group (Smulyan 1936, Darling 1983) and the question of generic status can be dealt with expediently. The same cannot be said for the problems that Argaman has created at the species level. Unless Argaman acquired Say's type material, a neotype will need to be designated for *P. hyalinus* in the context of a thorough revision. This should be a reared specimen to fix the host association and mode of parasitism of *P. hyalinus* (primary or hyperparasitoid). Argaman's types of *Taltonos* species will then need to be evaluated both with respect to the neotype and to the full range of variation in this species group. Fortunately, the types of all six of Argaman's new species of *Taltonos* are in Budapest (HNHM), not in his personal collection, and are available for study.

The *Perilampus hyalinus* group is characterized by oblique costae transversing the malar region and completely obliterating the malar sulcus (Darling 1995, figs. 11.135, 11.145). A distinct malar sulcus is present in virtually all other species of *Perilampus* (as in Fig. 7), including the species referred to *Goyurfis* and *Durgadas* by Argaman. All species are iridescent blue or green in general body color, never black, and all species examined by me have a bicarinulate pronotum (Fig. 18), as pointed out by Argaman. Oblique costae on the malar region and iridescent color are both apomorphic based on outgroup compari-

son, but are shared also with species of *Euperilampus* and *Krombeinius*. Paraphyly of *Perilampus* is a problem, as discussed in Darling (1983), but generic status for the *Perilampus hyalinus* group does not improve the situation, it only clutters the nomenclature. Moreover, as discussed below, *Durgadas pappi* further complicates the issue. I therefore regard *Taltonos* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

**Goyurfis** Argaman, 1990:242. Type species: *Perilampus platigaster* Say, by original designation. Seven included species, the *Perilampus platigaster* group (sensu Smulyan 1936).

*Material Examined.*—*Perilampus platigaster* group species are also commonly collected perilampids in the New World and I have examined hundreds of specimens from all of the major museums in North America including: the material that formed the basis for Smulyan's (1936) revision of *Perilampus* [mainly USNM]. There is almost no detailed host information for any included species, but specimens have been reared from pupae of Lepidoptera, most likely as secondary parasites (hyperparasitoids).

The situation regarding Say's type material of *P. platigaster* is identical to that of *P. hyalinus*. Although generally regarded as lost, Argaman lists what could be type material in his personal collection! Again, a neotype may be required to stabilize the concept of this species, but there is no doubt that Argaman's *Goyurfis* is but a formalization of Smulyan's (1936) *Perilampus platigaster* group. It should be noted that *P. mexicanus* Cameron, referred by Argaman to *Goyurfis*, actually belongs to the *Perilampus hyalinus* group; the type material of this species is in the BMNH and the type listed in Argaman's checklist is spurious.

The *Perilampus platigaster* group is presently characterized by plesiomorphic states of characters when compared with

the *Perilampus hyalinus* group; the malar
sulcus is distinct and all species are black.
As noted by Argaman, the pronotum is
not bicarinulate (Fig. 17). In order to main-
tain a consistent ranking with the *Perilam-
pus hyalinus* group and in recognition of
the lack of synapomorphies, I regard *Go-
yurfis* Argaman as a junior subjective syn-
onym of *Perilampus* Latreille, 1809 (**NEW
SYNONYMY**).

**Durgadas** Argaman, 1990:239. Type species:
    *Durgadas pappi* Argaman, by original desig-
    nation. Monotypic.

*Material Examined.*—Holotype ♀, "[Bra-
sil] Para, Rio Acara, E. Horvath, 1930/
VII.25"; HNHM. ♀♀, ♂♂, "Akuriman
Bol. VENEZ[uela] X 1940 P.J. Anduze;
USNM, ROM.

*Durgadas* was distinguished by the fol-
lowing two features, both of which are
found in carinate New World species of
*Perilampus*: bicarinulate pronotum (apo-
morphic and shared with the *Perilampus
hyalinus* group) and the presence of a dis-
tinct malar sulcus (plesiomorphic and
shared with the *Perilampus platigaster*
group). The type species of *Durgadas* is
black in color, as are all species of the *P.
platigaster* group, and were it not for the
bicarinulate pronotum, this species would
readily be referred to the *Perilampus plati-
gaster* species group. As noted above, a bi-
carinulate pronotum is also found in *Eu-
perilampus* and *Krombeinius*, and in some
acarinate species of *Perilampus* (cf. *Tiboras*).
The sculpture of the mesoscutum is also
unusual for *Perilampus*, cross-arcuate cos-
tae are present (fig. 28 is a fairly accurate
depiction of this sculpture). This type of
sculpture was regarded as a synapomor-
phy of *Euperilampus* + *Krombeinius* (Dar-
ling 1983). The type species of *Durgadas*
therefore exhibits features not only of two
distinctive species groups of *Perilampus*,
but also of related genera and the polarity
of these character states is uncertain. A
monotypic genus does nothing to clarify
the situation. I therefore regard *Durgadas*

Argaman as a junior subjective synonym
of *Perilampus* Latreille, 1809 (**NEW SYN-
ONYMY**).

## B. The Acarinate Genera of Argaman

Seventeen genera were recognized by
Argaman for species of *Perilampus* (s.l.)
which he considered not having a frontal
carina on the head. Four of these are
monotypic and five have only two includ-
ed species and by far the largest number
of species (45) are referred by Argaman to
*Perilampus* (s.s.), mostly by default. *Peri-
lampus* sensu Argaman is not defined by
synapomorphies but includes all species
that either do not fit easily in the other
acarinate genera or that were not available
to him for study! As such, his generic clas-
sification is suspect even if the segregated
genera were putatively monophyletic. As
will be discussed below, most are either
monotypic and therefore monophyletic by
default, or are artificial assemblages of
species. More importantly, many of these
genera cut across arguably monophyletic
species groups, which are based on better
substantiated morphological features than
those advanced by Argaman.

### (1) Synonym Based on Synonymy of Type
Species

**Olarlar** Argaman, 1990:252. Type species: *Chal-
cis aenea* Rossi, 1790, subsequent designation,
herein. Four included species.

Argaman inadvertently listed two nom-
inal species as the type species of *Olarlar*,
*Perilampus aeneus* (Rossi) (Argaman 1990:
199) and *Olarlar cocegus* Argaman (1990:
252). As First Reviser (ICZN, Article 24), I
designate *Chalcis aenea* Rossi as the type
species of *Olarlar* Argaman (**PRESENT
DESIGNATION**). This typification is con-
sistent with Recommendation 69A of the
Code; *Perilampus aeneus* is one of the most
common and distinctive species of *Peri-
lampus* in the Palaearctic region. On the
other hand, *Olarlar cocegus* is known only
from the holotype which is deposited in
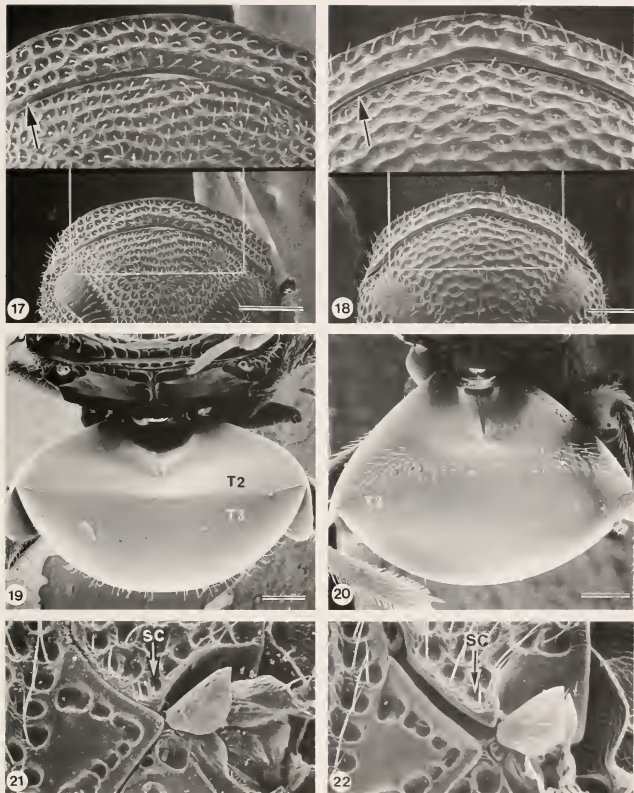
Figs. 17–22. 17 and 18, Pronotum and mesonotum, oblique dorsal view, detail above. 17. *P. platigaster*, posterior margin of pronotum not bicarinulate. 18. *P. hyalinus*, posterior margin of pronotum bicarinulate. 19–20, Second and third metasomal tergites (T2 and T3), dorsal view. 19. *P. platigaster*. 20. *P. fulvicornis*. 21 and 22, Scapula (SC), dorsolateral view. 21. *P. stygicus*, normal configuration of the scapula. 22. *P. prothoracicus*, reflexed lobe-like scapula. Scale lines, 0.25 mm.

Argaman's personal collection. Based on this typification, *Olarlar* Argaman, 1990 is a subjective junior synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)** because the type species of *Perilampus* (*Cynips italica* Fabricius, 1793) is a junior synonym of *Chalcis aenea* Rossi, 1790 (synonymy by Illiger 1807, confirmed by Steffan 1952, and accepted by Bouček 1956). More recently, Z. Bouček has studied two specimens of *Diplolepis italica* Fabricius that Rossi sent to Illiger and that formed the basis for Illiger's synonymy. Bouček has labelled a male specimen (examined, "Italien Rossi, I.", "Type", "13494", "Chalcis aenea Rossi", "Zool. Mus. Berlin", "LECTOTYPUS ♂ Chalcis aenea Rossi, 1790 det. Bouček, 1971" "♂ Perilampus aeneus (Rossius) Z. Bouček, 1972") as the lectotype of *Chalcis aenea* Rossi **(PRESENT DESIGNATION)**. This specimen agrees with accepted usage of *Perilampus aeneus* and is deposited in the Zoological Museum, Humboldt University, Berlin.

(2) Polyphyletic Assemblages

**Vadramas** Argaman, 1990:255. Type species: *Perilampus nigriviridis* Girault, 1912, original designation. Seven included species, including *P. maceki* Bouček, *P. cephalotes* Bouček, *P. polypori* Bouček, *P. saleius* Walker, *P. levifacies* Girault & Dodd, and *Vadramas tetar* Argaman.

*Material Examined.*—*Perilampus nigriviridis*: Lectotype ♂, **PRESENT DESIGNATION**, "Paraguay San Bernardino K. Fiebrig S.V. 30.6", "6352", "Ex Coll Girault", "Perilampus nigriviridis ♀", "TYPE [red]", "31948", "Zool. Mus. Berlin", "Lectotype ♂ Perilampus nigriviridis Gir. D. C. Darling"; Zoological Museum, Humboldt University, Berlin. ♂, ♀, "[Brazil] Sao Paulo. 1928. Bury J. György", det. Argaman; HNHM. ♀, "Costa-Rica Surrubres", det. Argaman; HNHM. *Vadramas tetar*: Holotype ♂, "[Nicaraguo] Sierra di Managua, A. Solari [18]98"; MCSN.

Argaman (1990:256) described *Vadramas* with the caveat, "This genus is another

heterogenous one, and surely not natural". In fact, this genus is considerably more heterogenous than even Argaman imagined; the type species of the genus is in fact a carinate species with finger-like axillula, i.e., a typical member of the *Perilampus hyalinus* group (*Taltonos* sensu Argaman)! However, until the status of the type material of *Perilampus hyalinus* is clarified and the range of variation attributed to species of this species group is better documented, it is not possible to determine if *P. nigriviridis* is a valid species. Most likely it will fall as a synonym of *P. hyalinus* and *Vadramas* would be a secondary synonym of *Taltonos*.

This is yet another case where the type species is based on a misidentification; Argaman did not examine the type material of this species and his exemplar is not conspecific with the lectotype designated above. Notwithstanding the question of typification, there is little to unite the remaining included species. Three are European species perhaps related to *Perilampus micans* Dalman (Bouček 1971), and three are described Australian species. The only new species described by Argaman in this genus, *Vadramas tetar*, is a Central American species that violates the only character that Argaman used to separate this "genus" from *Sicatang*, i.e., the relative length of the malar sulcus! He stated (1990:257), "The expanded scape, narrow mesosternum and short malar sulcus places this species into the genus *Mivarhis*; but the smooth upper front, . . . into the genus *Vadramas*". There is no basis for the recognition of this genus and I therefore regard *Vadramas* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

**Fifirtiz** Argaman, 1990:259. Type species: *Perilampus noemi* Nikol'skaya, 1952, by original designation. Eight included species, including *P. minutalis* Steffan, *P. neglectus* Bouček, and *P. glabrifrons* Riek.

*Material Examined.*—Syntypes 2 ♀ ♀, Ta-

jikistan, Kondara; BMNH. ♂, "Kapa, O. Turkest" and ♀, "[Russia] Dzungarischer Ala-Tau", both det. Argaman; Argaman Collection.

Argaman did not examine type material but I regard his exemplars as conspecific with the syntypes mentioned above. This genus was described for species with a very narrow head (in dorsal view) and with a blunt ridge starting at the anterior ocellus and converging on the inner orbits just below the top of the eye (fig. 127). Bouček (1983) studied the syntypes of *P. noemi* (no lectotype has been selected) and stated that "the head seen dorsally is 2.2–2.35 times as broad as long (stout)". The blunt ridge on the head described by Argaman is not present in either the syntypes of *P. noemi* or the specimens examined by Argaman! In fact, the head of the type species in frontal view is unremarkable (fig. 15 in Bouček 1983 is an accurate representation of the head of *P. noemi*, cf. Argaman's fig. 127). Furthermore, the species included by Argaman in *Fifirtiz* are a diverse polyphyletic assemblage. For example, *P. neglectus* is regarded as a member of the *Perilampus tristis* group (Bouček 1956); and *P. minutalis* (Steffan 1952) and *P. glabifrons* (Riek 1966) are closely related to *P. laevifrons*, which Argaman designated as the type species of *Mivarhis* (q.v.). There is no justification for this generic concept and I therefore regard *Fifirtiz* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (NEW SYNONYMY).

**Sicatang** Argaman, 1990:257. Type species: *Sicatang catilus* Argaman, 1990, by original designation. Note: This species is referred to as *Sicatang catilius* [*lapsus calami*] in Argaman (1991). Two species, also *S. picpus* Argaman.

*Material Examined.*—*Sictang catilus,* Holotype ♂, "[Turkey] Tschukur-hissar, Anatol."; Argaman Collection. *Sicatang picpus,* Holotype ♀, "KOREA, Prov. Gangvon district On-dzong, Kum-gang san, along Ok-ru dong, 300–600m", "No. 317,

5 August 1975 leg. J. Papp et A. Vojnits", "Hym. Type 6563 Mus. Budapest"; HNHM.

Argaman described *Sicatang* for two new species that he apparently could not accommodate in his existing genera because of the combination of a short malar sulcus and a smooth vertex. A short malar sulcus is characteristic of the *Perilampus laevifrons* group (*Mivarhis* sensu Argaman), which Argaman restricts to species with a "wrinkled" or sculptured vertex. Argaman experienced the same difficulty with the specimens he described as *Vadramas tetar* (see discussion of *Vadramas*), but he resisted the temptation to describe yet another new genus for *V. tetar*. Not so in the case of *Sicatang*. I regard the sculpture of the vertex as variable in the *Perilampus laevifrons* group and I would refer *Sicatang catilus* to this species group based primarily on the size and shape of the prepectus (Fig. 27). However, *Sicatang picpus* is not a member of the *Perilampus laevifrons* group; the prepectus does not have a narrow dorsal lobe (Fig. 28). This genus is almost certainly an artificial assemblage and I therefore regard *Sicatang* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (NEW SYNONYMY).

**Vaktaris** Argaman, 1990:248. Type species: *Perilampus auratus* Panzer, 1798, original designation. Four species, including *P. igniceps* Cameron; *P. brisbanensis* Girault is provisionally included.

*Material Examined.*—*Perilampus auratus:* ♂, "[Italy] Calabria Aspromonte Paganetti", det Argaman; HNHM. ♀, "Bulgaria, 1928. Madara. Biró [verso] VII 20", det. Argaman; HNHM. ♀, "[Italy] Voltaggio, App. Genovesa 20.VII a 30.VIII. F. Solari", det. Argaman; MCSN. ♂, ♀, "[Italy] N. S. dalla Vittoria Apenmino di Genova, G. Mantero VI-1936", det Argaman; MCSN. ♂, "Germany, Darmstadt coll. Meyer 10.6.27"; ♀, "[Russia] CRIM"; both det. S. Novitzky; ROM. *Perilampus igniceps:* Lectotype ♀, **PRESENT DESIGNATION**, "[Argentina]
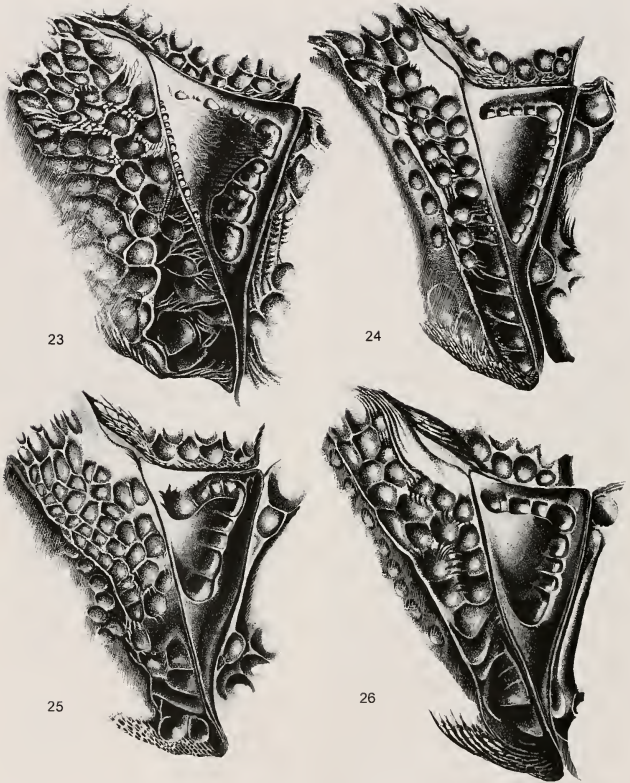
Figs. 23–26.  Prepectus and lateral pronotal panel of *Perilampus* species. 23. *P. bouceki*, Holotype. 24. *P. maurus*. 25. *P. singaporensis*. 26. *P. meloui*, Holotype.

Mendosa", "P. Cameron Coll. 1914–110", " Perilampus igniceps Cam. Type", "BM Type Hym 5.405", "*Perilampus* This species is near *auratus* Panzer G.J. Kerrich det.

1959"; BMNH. *Perilampus brisbanensis*: 2 ♀♀, "[Australia] Illawarra N.S. Wales H. Petersen", ANIC; "[Australia] Brisbane: H. Hacker 27.10.14", USNM.

Argaman's concept of *P. auratus* agrees with other authors, which is not too surprising since this is one of the most distinctive species of *Perilampus*. Argaman defined *Vaktaris* on the basis of a single morphological feature, a scale-like protuberance on the mesoscutum. Argaman (1990:248) noted that, except for this feature, *Vaktaris* "is the most heterogenous genus among the others treated herein". He goes on to explain morphological variability in a number of features that elsewhere he uses to confer generic status, e.g., shape of the prepectus and size of prepectus relative to the lateral pronotal panel. In addition, *P. brisbanensis*, one of two additional species "that probably belong here" (1990:249), has a distinct frontal carina! There are many undescribed species in the New World with a tubercle on the mesoscutum, which will further extend the range of variation of such a monothetic "genus". Argaman's suggestion is to "subdivide this taxa [sic] into more homogenous units" (1990:249). My conclusion is that a tubercle on the scutellum has evolved independently a number of times and is not a good indicator of phylogenetic affinities; it may well be a functional structure related to emergence of the adult from the host pupa, puparium, or cocoon. As presently defined, the genus is not demonstrably monophyletic, and is most likely polyphyletic. I therefore regard *Vaktaris* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

(3) Monotypic Genera

**Itonayis** Argaman, 1990:248. Type species: *Perilampus micans* Dalman, 1820, by original designation. Monotypic.

*Material Examined.*— ♀, "[Hungary] Simontornya. Hung. occ. 1912 VI.18-K'', det Argaman; HNHM. ♀, "[England] Bred from oak in B.M. June. 1928 F. Laing", "ex. larvae Lyctus linearis", "♀ *Perilampus micans*, Dalm. J. Waterston det.''; BMNH;

this specimen was reared from the same host as listed in the original description.

Argaman did not examine the holotype of *P. micans* but I regard his exemplar as conspecific and in agreement with accepted usage. As noted by Argaman, this species does have a "frenal crest" on the scutellum (frenum present) and the prepectus is large, forming an equilateral triangle with coarse punctures on all three sides. There are, however, additional species that share these features and a number of other attributes with *P. micans* (the *Perilampus micans* group of Bouček 1971); e.g., *P. polypori* Bouček (which Argaman places in *Vadranes*). Bouček (1956, 1971) noted that species of the *Perilampus micans* group also have a distinct uncus on the stigma. Possibly related to this species group according to Bouček (1971) are *P. aeneus* and *P. ruschkai* Hellén, which Argaman refer to *Olarlar* and *Burksilampus* (!), respectively. *Steffanolampus salicetum* (Steffan) also has these morphological features and both *S. salicetum* and *P. micans* are regarded as primary parasitoids of xylophagous beetles. As discussed above, I regard *Steffanolampus* as an outgroup, possibly the sister group of *Perilampus* (s.l.), suggesting that the morphological features used by Argaman to define *Itonayis* are plesiomorphies. All of these considerations suggest that a monotypic genus for *Perilampus micans* is inappropriate, or at least premature. I therefore regard *Itonayis* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

**Bagdasar** Argaman, 1990:250. Type species: *Bagdasar amnonius* Argaman, 1990, by original designation. Monotypic.

*Material Examined.*—Holotype ♀, "SOUTH AFRICA Natal Pietermaritzburg", "Ashburton 3.X.83 A. Freidberg"; Argaman Collection.

This is another previously undescribed species with a raised scale or tubercle on the dorsum of the scutellum (fig. 99). The scale is in a similar location on the scutel-

lum as that of *P. mirabeaui* (*Nilgator* sensu Argaman), but Argaman's species is not closely related to this species and does not belong to the *P. punctiventris* group; the head is acarinate and the third metasomal tergite is not punctate. The prepectus is much broader than the adjacent pronotal panel and the metasoma is flat and elongate, not strongly arched, similar in these regards to *P. ruficornis* and *P. auratus*. If, in fact, *B. amnonius* is closely related to these two species, the raised scale on the scutellum is not remarkable; *P. auratus* has a raised scale on the mesoscutum and low protuberances on the scutellum, and protuberances are completely absent from *P. ruficornis*. Argaman, perhaps realizing the weakness of the scale on the scutellum as a generic character (although he used this feature to define *Nilgator*, q.v.), supported his generic concept by stating that the anellus is "unusually" long. In fact, his illustration of the antenna (fig. 115) is very inaccurate, e.g. an 8-segmented funicle and a quadrate anellus are represented. In fact, the antenna of the holotype is rather typical in structure to most other species of Perilampinae. A monotypic genus does nothing to improve the classification, particularly if this species forms a monophyletic group with *P. ruficornis* and *P. auratus*. I therefore regard *Bagdasar* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809, **(NEW SYNONYMY)**.

(4) Segregates of the *Perilampus fulvicornis* Group

Smulyan (1936) recognized the *Perilampus fulvicornis* group for seven small, black, acarinate species found in America north of Mexico. The defining features, discussed only in the key, were that the first tergite of the metasoma is petiolate and that the petiole does not have a raised flange or scale on the anterior margin (cf. *P. anomocerus* group, Figs. 13–15) and the sculpture of the petiole is rugose (Figs. 20, 30–32). These species appear to be unrelated to small black species of *Perilampus*

from other regions of the world, most of which do not have a distinct petiole. *Burksilampus* was described for a New World species with a very long petiole (Fig. 33), suggesting that this species could be regarded as a member of the *Perilampus fulvicornis* group. However, there are significant differences in both the sculpture of the petiole (alveolate or coriaceous *versus* rugose) and the malar region of the head (malar sulcus absent *versus* present) between the type species of *Burksilampus* (*Chrysolampus anobii* Burks) and species of the *P. fulvicornis* group (Darling, 1995a). The length of the petiole is variable across species and sexes, and is usually much longer in males (Figs. 30, 31). The *Perilampus fulvicornis* group may be the most speciose species group in the New World, where there are many undescribed species. Argaman described the following three genera for species of the *Perilampus fulvicornis* group.

**Naspoyar** Argaman, 1990:261. Type species: *Perilampus fulvicornis* Ashmead, 1886, by original designation. Five included species: *P. philembia* Burks, *P. muesebecki* Smulyan, *P. similis* Crawford, *P. minutus* Girault.

*Material Examined.*—*Perilampus fulvicornis*: Holotype ♂, "E. Fla. Ashmead", "♂", "Type No. 22886 USNM", "Perilampus fulvicornis Ashm."; USNM. *Perilampus minutus*: Lectotype ♀, **PRESENT DESIGNATION**, "Paraguay (San Bernardino) K. Fiebrig S.V.", "4506", "Ex Coll Girault", "minutus", "TYPE [red]", "31947", "Zool. Mus. Berlin", "Lectotype ♀ *Perilampus minutus* Gir. D. C. Darling"; Zoological Museum, Humboldt University, Berlin. *Perilampus philembia*: Paratype ♀, ♂ Peru: Tingo Maria; see Burks, 1969 for details; USNM.

There is considerable uncertainty surrounding the identity of *P. fulvicornis* in North America; there are numerous host records and morphologically distinctive forms are currently referred to this species both in collections and in the literature.

Argaman apparently based his concept of *P. fulvicornis* on the single male specimen in his personal collection, which may or may not be conspecific with the holotype. Argaman noted that species of *Naspoyar* have a dense patch of setae laterad on the second metasomal tergite, T2 (Fig. 20). However, this is only true for three of the five species included by Argaman in *Naspoyar* (absent from *P. minutus*, *P. philembia*) and there are also many species not studied by Argaman (and therefore left in *Perilampus*) that are petiolate with a distinct patch of setae laterad on T2 (e.g., *P. gahani* Smulyan, *P. parvus* Howard, and *P. politifrons* Howard). Both *P. minutus* and *P. philembia* do not have the patch of setae on T2 and are more closely related to *P. prothoracicus* Smulyan (cf. *Zuglavas*). The question of generic status for the *Perilampus fulvicornis* group of Smulyan, and including at least *P. robertsoni* (*Ecalibur*, q.v.), and perhaps *P. prothoracicus* and *P. stygicus* Provancher (*Zuglavas*, q.v.), is complicated and will require a comprehensive study of the New World species of *Perilampus*. For example, the patch of setae on T2 is also found in species of the *Perilampus anomocerus* group (Figs. 13, 14) and may be plesiomorphic at the level of the *Perilampus fulvicornis* group. Clearly, it is inappropriate to burden the nomenclature with an additional generic name at this time. I therefore regard *Naspoyar* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

**Zuglavas** Argaman, 1990:251. Type species: *Perilampus stygicus* Provancher, 1888, by original designation. Two species, also *P. prothoracicus* Smulyan.

*Material Examined.*—*Perilampus stygicus*: Lectotype ♀: [Canada, Quebec, Cap Rouge] "1599" [yellow], "Perilampus stygicus Prov."; Laval University, Sainte-Foy, Québec. Designated by Gahan and Rohwer, 1918. Lectotype labels of Comeau 1947, Gahan and Rohwer 1915, and Barron 1971. ♀,♂ "[USA] NY: Tompkins Co.

White Church IX-11-1981 M. Sharkey"; ROM. ♀,♂ "U.S.A.: Michigan Ann Arbor ix-x 1975, Fitton"; BMNH. *Perilampus prothoracicus*: Holotype, ♀: "[USA] Loui[siana] 2568", "Collection CF Baker", "Type No 49785 USNM", "Perilampus fulvicornis var. prothoracicus Type Smul."; USNM. ♀,♂ "[Canada] Ludlow N.B. [various dates] D.P. Pielou Ex: Polyporum betulinus"; CNC, ROM. ♀, "[USA, NY] Amer. sept. Horv. 1907", "Adirondak Long Lake", det. *Zuglavas stygicus* by Argaman; HNHM. Note: Argaman did not examine the type material of these two species, and, as discussed below, confused these two species.

*Perilampus stygicus* is one of the most distinctive species of *Perilampus* in North America; both males and females have a distinct infuscate band on the forewing below the marginal vein and the lateral pronotal panel is rounded (Fig. 11). As Argaman noted, this species is closely related to *P. prothoracicus*. These are the only two species referred by Smulyan (1936) to the *Perilampus fulvicornis* group that lack a distinct patch of setae on the lateral margin of T2. Until Argaman's study, *P. stygicus* was most easily separated from *P. prothoracicus* by the coloration of the forewing; *P. prothoracicus* does not have a distinct infuscate region on the forewing, the wing is either hyaline or has a very faint darkened region below the marginal vein. Argaman has discovered another important morphological feature to distinguish these two species, the shape of the scapula. Argaman stated (1990:212) that in *P. stygicus*, the lateral lobe of the scapula is "deeply emarginate anterad to tegula, producing an acute, backward directed peg-like structure" (fig. 104). However, he misinterpreted the distribution of this character because of a misidentified specimen(s). This reflexed lobe-like configuration of the scapula is *not* present in *P. stygicus* (Figs. 11, 21), but is present in *P. prothoracicus* (Fig. 22). The scapula of *P. stygicus* (Fig. 11) is virtually

identical to that of *P. tristis* Mayr (Fig. 9) and *P. fulvicornis* (Fig. 12). The apomorphic configuration of the scapula is therefore found in only one of the two species included by Argaman in *Zuglavas* and not in the type species (*P. stygicus*)! A monotypic genus based on this apomorphic configuration of the scapula (for *P. prothoracicus*) is inconsistent with the close relationship of this species and *P. stygicus*. I therefore regard *Zuglavas* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

**Ecalibur** Argaman, 1990:260. Type species: *Perilampus robertsoni* Crawford, 1914, by original designation. Monotypic.

*Material Examined.*—Holotype ♀ "[USA] [No.] 9729", "Robertson S. Illinois", "♀", "Type No. 18299 U.S.N.M.", "Perilampus granulosus Type ♀"; USNM.

Argaman based his concept of *P. robertsoni* on a single male in his personal collection. My attempts to borrow this specimen have not been successful. From a study of Argaman's key it is apparent that generic status was awarded to this species based on the following features (190:227): "Head with residual scrobal carina primitively retained"(!) and T2 with a "not very dense patch a pale pubescence". There is no diagnosis of *Ecalibur* and the key separates the type species from *Naspoyar* on the basis of the features listed above and on features of the surface sculpture. Smulyan (1936) remarked that the head has a well developed keel "sometimes with a semblance of a carina", but appreciated the natural affinities of this species even without apparently realizing the importance of the patch of setae on T2. Argaman, on the other hand, realized that this species has a patch of setae on T2, but still erected a monotypic genus because of the structure of the head. *Perilampus robertsoni* is clearly a member of the *Perilampus fulvicornis* group. I therefore regard *Ecalibur* as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

## (5) Segregates of the *Perilampus anomocerus* Group

Smulyan (1936) recognized the *Perilampus anomocerus* group for two acarinate species found in America north of Mexico, *P. anomocerus* Crawford and *P. granulosus* Crawford. The distinguishing feature of this species group, discussed only in the key, is that the anterior margin of the first metasomal tergite (petiole) is strongly elevated as a flange or scale that can completely cover the neck or nucha of the propodeum (Figs. 13, 14). Both of these species also have a distinct lateral patch of very long setae on T2 (Fig. 14) and also share numerous other morphological features. Argaman described a genus for each of these species.

**Ihambrek** Argaman, 1990:252. Type species: *Perilampus chrysonotus* Förster, 1859, by original designation. Two species, also *Perilampus anomocerus* Crawford.

*Material Examined.*—*Perilampus chrysonotus*: Lectotype ♀, **PRESENT DESIGNATION**, [Germany] "[Germany] Bopp[ar]d.", "Collect. G. Mayr", "P. chrysonotus Förster, Type", "Lectotype ♀ *Perilampus chrysonotus* Förster D. C. Darling", Paralectotypes 1♂,1♀, same collector and type labels; NMV. ♀,♂ [Central Europe], det. S. Novitzky; BMNH. *Perilampus anomocerus*: Holotype ♀, "[USA] Colo[rado] [No.] 1584", "Collection CF Baker", "♀", "Type No. 18302 U.S.N.M.", "Perilampus anomocerus Cwfd Type ♀"; USNM.

Specimens identified as *P. chrysonotus* by Argaman were not available for study. This is one of the most distinctive Palaearctic species and it is likely that Argaman's exemplar is conspecific with the lectotype. Argaman (1990:213) distinguished *Ihambrek* in the key on the basis of the configuration of the mesosomal sclerites, i.e., "Spiracle between pro- and mesonotum indistinct, covered, the notal sclerites not emarginate there as usual" and "Upper border of prepectus meeting directly and perpendicularly the prono-
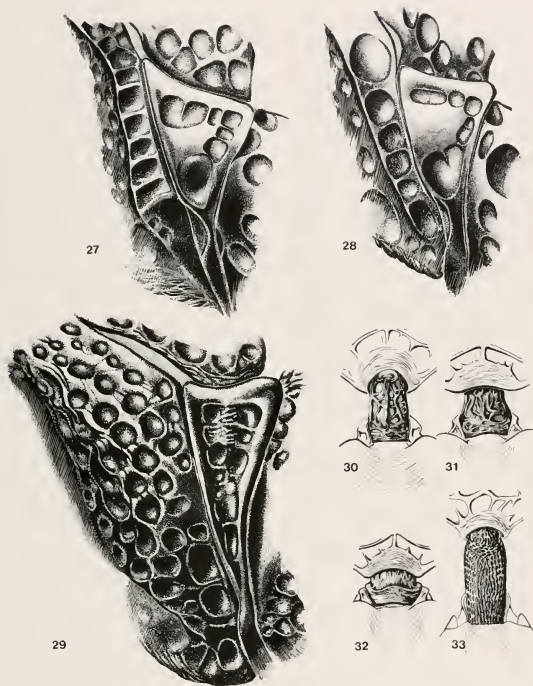
Figs. 27–33. 27–29. Prepectus and lateral pronotal panel of *Perilampus* species. 27. *P. catilus*, Holotype. 28. *P. picpus*, Holotype. 29. *P. chrysonotus*. 30–32. Petiole of *Perilampus* species, dorsal view. 30. *P. stygicus* ♂. 31. *P. stygicus* ♀. 32. *P. fulvicornis* ♀. 33. Petiole of *Burksilampus anobii* ♀, dorsal view.

tum.'' These statements are inaccurate based on the material I have examined. However, in both *P. chrysonotus* (Fig. 29) and *P. anomocerus* (Fig. 10), the mesonotum is emarginate, and the upper border of the prepectus is horizontal only in *P. chrysonotus* (Fig. 29, cf. Fig. 10, *P. anomocerus*). What is interesting is that both species have a scale-like petiole (Figs. 13, 14), a character apparently missed by Argaman although discussed by Smulyan (1936). The petiole is virtually identical in these two species, and the scale-like petiole is found only in these two species, in *P. granulosus,* and in undescribed species of the *P. anomocerus* group. Significantly, *P.*

*chrysonotus* does not have a patch of setae laterad on T2; these setae are restricted to New World species of the *Perilampus anomocerus* and *P. fulvicornis* groups. Also, the structure of the prepectus and lateral pronotal panel is different in the Old World and New World species; in *P. chrysonotus* there is a distinct and continuous suture between these sclerites (Fig. 29), which is absent from *P. anomocerus* (Fig. 10). In conclusion, not only is the diagnostic feature of *Ihambrek* not present in the type species, but the two included species almost certainly do not form a monophyletic group. I therefore regard *Ihambrek* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

**Dekterek** Argaman, 1990:262. Type species: *Perilampus granulosus* Crawford, 1914, by original designation. Two species, also *Perilampus kaszabi* Bouček.

*Material Examined.*—*Perilampus granulosus*: Holotype ♀, "[USA] Alab[ama] [No.] 1967","Collection CF Baker", "Type No. 18305 U.S.N.M", "Perilampus granulosus Type ♀"; USNM. *Perilampus kaszabi*: Paratype ♀, Mongolia; see Bouček 1983 for details; BMNH.

Argaman studied a single female of *P. granulosus*, which is apparently now deposited in his personal collection. He based his generic concept on the structure of the prepectus and mesepisternum; however, the prepectus of the holotype is virtually identical to *P. anomocerus* and bears little resemblance to Argaman's illustration (fig. 69, cf. Fig. 10). It is likely that Argaman's exemplar was misidentified; he did not mention the granulose sculpture laterad on the scutellum that is diagnostic for this species (Crawford 1914, Smulyan 1936). Furthermore, he stated that T2 is glabrous, but a distinct patch of setae is present in the holotype (as in *P. anomocerus*, Figs. 13, 14). *Perilampus granulosus* is unquestionably closely related to *P. anomocerus* (Smulyan 1936) and I therefore regard *Dekterek* Argaman as a ju-

nior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**).

(6) Segregates of the *Perilampus tristis* Group

This informal species group has been used by European authors (Bouček 1956, Steffan 1952) for small black species that have the prepectus very closely associated with the lateral pronotal panel. There is a distinct suture along the pronotum dorsad, but ventrad the suture is obliterated by vertical rows of alveolae on both the pronotal panel and prepectus (Fig. 9). The first metasomal tergite (petiole) is transverse with a raised scale (Fig. 15); the scale is narrower and less heavily sculptured than in *P. chrysonotus* and *P. anomocerus* (Figs. 13, 14). Argaman used "fusion" of the prepectus to separate a group of 6 genera, three of which were discussed above as segregates of the *Perilampus fulvicornis* group and three of which are discussed here as segregates of the *Perilampus tristis* group.

**Pondoros** Argaman, 1991:1. Type species: *Perilampus tristis* Mayr, 1905, by original designation. Nine included species.

*Material Examined.*—*Perilampus tristis*: Lectotype ♂, **PRESENT DESIGNATION**, "[Germany] Först.", "Collect. G. Mayr", "Peril. tristis G. Mayr, Type", "TYPUS" [red, printed], "Lectotype ♂ *Perilampus tristis* Mayr D. C. Darling", Paralectotypes 2♂♂,3♀♀ [Germany, all labelled with red type label]; NMV. Note: The syntype series in Vienna also contains 5♂♂ and 2♀♀ (on 6 pins) that are not conspecific with the Lectotype, det. *P. minutalis* Steffan, D. C. Darling. ♀, "[Germany?] Mödling Schmidt", det. Argaman; HNHM. ♂, ♀ "Switzerland: H. L. Parker 1957 hyper. Ryacionia buoliana"; ROM.

*Perilampus tristis* is a very distinctive species that is rather common in European collections. The most striking characteristic of this species is the long, paired, laterally-directed spines on the aedeagus (Fig. 16). These spines are clearly visible

on the lectotype and in male specimens that were introduced into North America. This species is a common hyperparasitoid of the codling moth and was apparently inadvertently introduced into North America, where the species was described as *P. capitatus* by Smulyan (1936) and later synonymized by Steffan (1952). The name *P. tristis* has been applied uncritically to many small black species of *Perilampus* in European collections and this lectotype designation will stabilize the nomenclature for this species. It should be noted that Argaman's lectotype designation for *P. tristis* (1991:16) is invalid; the specimen designated is from his personal collection and not one of the syntypes!

Argaman based his concept of *Pondoros* on a correctly identified specimen of *P. tristis*, although his illustration of the prepectus is very inaccurate (fig. 111, cf. Fig. 9). He distinguished *Pondoros* from other "genera" with a "fused" prepectus by the presence of a plical carina on the propodeum and the postmarginal vein longer than the radial vein. Both of these features are widely distributed in *Perilampus* and are most likely plesiomorphic. The *Perilampus tristis* group remains rather poorly defined. The close association of the prepectus and pronotum ventrad (Fig. 9), and a low scale on the petiole (Fig. 15) is all that delimits this species group. A similar form of prepectus is found in the *Perilampus fulvicornis* group (*Naspoyar* sensu Argaman) (Figs. 11, 12), but the form of the petiole differs (Figs. 30–32). Until the affinities of *P. tristis* are better understood, it is premature to recognize separate genera or a monotypic genus for *P. tristis*. I therefore regard *Pondoros* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1990 (**NEW SYNONYMY**).

**Lufarfar** Argaman, 1991:3. Type species: *Lufarfar rainerius* Argaman, 1991, by original designation. Two included species.

*Material Examined.*—*Lufarfar rainerius*: Holotype ♀, "[Egypt] Coll. A. Mochi VII.6.1935 Gebel Asfar Egitto"; MCSN. Paratype ♀, "[Egypt] Coll. A. Mochi 6.VII.1936 Gebel Asfar Egitto"; MCSN.

Argaman distinguished *Lufarfar* from *Pondoros* by three attributes: absence of a plical carina on the propodeum, postmarginal vein shorter than stigmal vein (his radial vein), and absence of a malar sulcus. However, the malar sulcus is present in the paratype that I examined and the postmarginal vein is shorter than the stigmal vein; his figure 78 is an accurate depiction of the relative lengths of these veins. The absence of a plical carina was regarded by Argaman as a result of further reduction of sculpture laterally on the propodeum, a characteristic of *P. tristis*. In *P. tristis* there is a large glabrous area, without any sculpture, ventrally on the propodeal callus (Fig. 15). The type species of *Lufarfar* also has a smooth area that extends mesally to obliterate the plical carina (fig. 77). In my opinion, these characters do not merit generic distinction, at least not until the full range of variation is assessed in the *Perilampus tristis* group. I therefore regard *Lufarfar* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 (**NEW SYNONYMY**), based on the synonymy of *Pondoros* with *Perilampus* discussed above.

**Bukbakas** Argaman, 1990:261. Type species: *Perilampus microgastris* Ferrière, 1930, by original designation. Four included species.

*Material Examined.*—*Perilampus microgastris*: Paralectotype ♀, "[India] Rahatgaon, Hoshangabad, C.P., S. N. Chatterjee 23.IX.1926", "Parasite on Apanteles machaeralis Wilk.", ROM. ♂, ♀ "KOREA, Prov. South Pyongan, Nampo, Wauto", "22.IX.1979, leg. Dr. H. Steinmann et Dr. T. Vásárhelyi, No. 563", det. Argaman; HNHM.

Argaman based his concept of *P. microgastris* on a single female from Korea which I regard as conspecific with the paralectotype. However, he stated that both *Pondoros* and *Lufarfar* have a deep longitudinal furrow on the vertex, which is ab-

sent from *P. microgastris*. This character is the main reason for separating *Pondoros* and *Lufarfar* from *Bukbakas* in the key and is therefore critical in evaluating the status of *Bukbakas*. I can see no major differences in the vertex of the type species of these three genera. I agree that the vertex is smooth in *P. microgastris*, but a distinct furrow is not present in *P. tristis* (*Pondoros* sensu Argaman) (Fig. 5) or in *P. rainerius* (*Lufarfar* sensu Argaman). Argaman distinguished *Bukbakas* from the *Perilampus fulvicornis* group (*Naspoyar* sensu Argaman) by the profile of the mesosoma (fig. 136). Not only does his illustration of *Bukbakas* not agree with the material I have examined, but the profile of the mesosoma in *P. microgastris* falls within the range of variation found in the *Perilampus fulvicornis* group. There is nothing remarkable about *P. microgastris*, and earlier authors (Ferrière 1930, Bouček 1983) have suggested that this species is closely related to *P. tristis*. On the basis of both a lack of morphological criteria and possible affinities with *P. tristis*, I regard *Bukbakas* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

## (7) The *Perilampus laevifrons/chrysopae* Group

The *Perilampus* species that are primary parasitoids of lacewings (Neuroptera: Chrysopidae) have been regarded as belonging to the *P. chrysopae* group in the New World (Smulyan 1936) and the *P. laevifrons* aggregate or group in the Old World (Kerrich 1958, Bouček 1983). These species all have a very narrow prepectus that appears distinctly separate from the lateral pronotum (Fig. 7) and a short malar sulcus (Fig. 7), but as discussed by Bouček (1956) and Kerrich (1958), the most remarkable feature of these species is the strongly expanded scape of the males, which has resulted in modifications to the lower face in certain species. There still remains uncertainty about the possibility of Holarctic species in this group. Argaman

referred most of these species to the genus *Mivarhis*, which he separates from *Perilampus* (s.s.) by a single character, i.e., malar sulcus half as long as front margin of malar cavity *versus* as long as front margin of malar cavity. As diagnosed in the key, species referred to both of these genera have the face sculptured; the ocular-ocellar region has "irregularities, coarse rugulae, wrinkles, or costulae" and the face between the malar sulcus and the clypeus has "wrinkles or rugulae, occasionally only in its extreme inner corner" (1990:215). And as discussed below and in the previous treatments of *Sicatang*, *Vadramas*, and *Fifirtiz* (q.v.), there are species with smooth vertices that agree in most other regards with the *Perilampus laevifrons/chrysopae* group.

**Mivarhis** Argaman, 1990:255. Type species: *Perilampus laevifrons* Dalman, 1822, by original designation. Eleven species, including *P. chrysopae* Crawford, *P. aureoviridis* Stephens in Walker, and *P. masculinus* Bouček.

*Material Examined.*—*Perilampus laevifrons*: ♀, "Yugoslavia Dubrovnik", "1967. VIII. 10–11 leg. Zombori", det. Argaman; HNHM. ♂, ♀ "[Sweden] G. Sandon A. Jansson", Det. G. J. Kerrich 1958; ROM. ♂, "S. ENGLAND. Buck. Loadwater, Bouček 6.VII.75", det. Z. Bouček 1982; ROM. *Perilampus chrysopae*: ♀, USA, California Ex: *Chrysopa californica*; ROM. *Perilampus aureoviridis*: ♂, ♀ Mongolia, det. P. lacunosus Bouček, 1982; ROM. *P. masculinus*: Paratype ♀, Czech Republic; ROM.

For European species, Argaman's concept of *Mivarhis* is identical with the *Perilampus laevifrons* group sensu Bouček (1983). Also included by Argaman as *P. chrysopae*, a North American species closely related to Old World *P. laevifrons* and *P. aureoviridis*. Excluded by Argaman was the Nearctic species *P. rohweri*, which was placed in the *P. chrysopae* group by Smulyan (1936); this species has a smooth vertex, which precludes placement in *Mivarhis* as defined by Argaman. Species in other Argaman genera (e.g., *Vadramas*, *Sica-*

*tang, Fifirtiz*) also have a smooth vertex but agree in most other regards with the *Perilampus laevifrons/chrysopae* group. Furthermore, this genus is separated from *Perilampus* by a single character, the relative length of the malar sulcus, a highly variable character that Argaman himself uses many times in his key to distinguish genera. As presently defined, recognition of the genus *Mivarhis* does not improve our understanding of the phylogenetic relationships of the Perilampinae. I therefore regard *Mivarhis* Argaman as a junior subjective synonym of *Perilampus* Latreille, 1809 **(NEW SYNONYMY)**.

(8) The Core Genus, *Perilampus*

**Perilampus** Latreille, 1809. Type species: *Cynips italica* Fabricius, 1793:103, subsequent designation by Westwood (1840); = *Perilampus aeneus* (Rossi), 1790, synonymy by Illiger 1807, confirmed by Steffan 1952, and accepted by Bouček 1956.

**Cinipsillum** Lamarck, 1817:156. Type species: *Chalcis violacea* Panzer, 1804 [auct. 1805]: 88 (fig. 15), subsequent designation by Gahan and Fagan (1923); = *Perilampus ruficornis* (Fabricius), 1793, synonymy by Bouček (1956).

**Cynipsillum** Lamarck; Agassiz, 1845:325. Incorrect subsequent spelling. Note: Although *Cynipsillum* was probably intended as an emendation of *Cinipsillum* (Agassiz cited Lamarck) the action does not comply with the requirements of Article 33 of the Code and therefore *Cynipsillum* is properly regarded as an incorrect subsequent spelling and is not an available name. The type species designation for *Cynipsillum* by Gahan and Fagan (1923) should be applied to *Cinipsillum*. Gahan and Fagan provided a citation of Lamarck's genus, but with the orthography of Agassiz. In typifying Lamarck's genus they were trying to effect an objective synonymy with *Perilampus*, which they considered (incorrectly) was also typified by *Chalcis violacea* Panzer, 1804.

**Afroperilampus** Risbec, 1956:184. Type species: *Afroperilampus meloui* Risbec, 1956, by original designation. Synonymy by Bouček (1972).

*Material Examined.*—*Perilampus aeneus*: ♀, "AUSTRIA: Wien 25.8.60 S. Novitzky",

det. Bouček 1982; ROM. ♂, "Austria: Vienna dist.: Mödling Novitzky 12.9.52", det. DC Darling; ROM. 2♀♀, 2♂♂, "[Hungary] Ex: larvis Athaliae colibri", det. Szelényi (*P. italicus* Panzer); ROM. 2♀♀ "[Italy] Rosignano, (Piemonte) 15-IX-1883", "Collezione Gribodo" and "Rosignano, (Piemonte) 10-IX-1881", "Collezione Gribodo", both det. Argaman; MCSN.

As discovered by Z. Bouček in 1981 (*in litt.*), the type species of *Perilampus* has been incorrectly regarded as *Diplolepis violacea* Fabricius, 1804, designated by Latreille, 1809 (e.g., Burks 1979, Bouček 1988, Argaman 1990:253). There are two problems with this typification. Fabricius (1804) did not describe *Diplolepis violacea*, he only transferred Panzer's species from *Chalcis* to *Diplolepis*; Fabricius clearly cited "*Chalcis violacea* Panz. Fn. Germ. 88. tab. 15." Secondly, Latreille (1809) is not a valid type species designation for the genus. Two species were listed, "Périlampe. *Diplolepis violacea*, Fab.; ejusd. *D. ruficornis*." and, therefore, ICZN Direction 4 (Hemming 1954) excludes this typification. It does not matter that these are presently regarded as subjective synonyms; more than one nominal species is involved in Latreille's discussion of *Perilampus*. The typification then becomes Westwood (1840:67): "*P. italicus* Fab". The original combination is actually *Cynips italica* Fabricius. This species was also regarded as the type species of *Perilampus* by Ashmead (1904:266).

This new information was made available to Argaman prior to his publications and he discussed the implications of this typification for his generic classification, albeit with the mistaken notion that the ICZN will need to validate *Cynips italica* Fabricius as the type species of *Perilampus* (Argaman 1990:254). It should also be noted that his designations of type species for *Cinipsillum* and *Cynipsillum* are unnecessary and without merit; Agassiz was correcting Lamarck's name and therefore the typification of Gahan and Fagan should

apply to *Cinipsillum*. This typification has been accepted since first published in 1923 and should not be changed.

*Perilampus* sensu Argaman is a heterogeneous assemblage comprised of species that Argaman did not see or did not care to deal with. He treated only twelve species in his key, but refers 45 species to *Perilampus* in his checklist. It is clear that species remained in *Perilampus* if they could not be referred to other genera; *Perilampus* sensu Argaman contains even less information than *Perilampus* (*auctorum*), which is itself demonstrably paraphyletic (Darling 1983). As a result of the synonymies proposed herein, all species of Perilampinae will return to *Perilampus* unless classified in *Euperilampus* Say, *Monacon* Waterston, *Krombeinius* Bouček, *Burksilampus* Bouček, or *Steffanolampus* Bouček; a key to the genera is provided in Bouček (1978).

## DISCUSSION

The net result of the synonymies proposed herein is a return to the status quo. It should be noted that all of the synonomies are subjective; hence, considerable detail has been provided to point out the problems inherent in each of Argaman's generic concepts and the shortcomings of the reclassification as a comprehensive system for the species traditionally referred to *Perilampus*. It is not my intention, nor would it be possible, to suppress Argaman's work. Most of his generic names will remain as available names and some would undoubtedly become valid names if *Perilampus* were subdivided at some later date. The problematic cases from the standpoint of nomenclature are the genera with type species based on misidentified specimens. A number of these cases have been documented and additional cases can only be confirmed by studying Argaman's collection and by assembling all the material that formed the basis for his treatment of particular type species. If nomenclatural instability arises for particular genera, submissions will need to be pre-pared asking the Commission to typify these genera, ideally resulting in objective synonymy with *Perilampus*. The nomenclature of the Perilampidae needs to be stabilized, but does not necessarily need to involve the Commission, which is a time-consuming process. My purpose in providing a rather lengthy discussion of the inadvisability of incorporating the Argaman genera into the nomenclature is to obviate formal action by the Commission.

In the context of evaluating the genera proposed by Argaman, I have tried to indicate some morphological characters that may define monophyletic species groups of *Perilampus*. All of these character systems (e.g., size and shape of T1, shape of prepectus, setae on T2, sculpture on T3), need much more detailed analysis, both in terms of homology and level of generality. Comprehensive phylogenetic studies may eventually support a revised generic classification, but for the present, a system of informal species groups, some of which have been discussed above, will serve both as mnemonic devices and as more inclusive names. Following the suggestion of Smulyan (1936), species group names could be based on the first described species, but other systems are certainly possible. The beauty of such a system is its flexibility and independence from the strictures of zoological nomenclature; and errors, oversights, omissions, and idiosyncracies can be dealt with expediently. Species groups are a lexicon for communication rather than a vehicle for self-aggrandizement.

## ACKNOWLEDGEMENTS

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## APPENDIX 1

Alphabetical index to the primary treatments of the genera recognized by Argaman (1990, 1991).

# Taxonomic Characterization of Some Live-stem Inhabiting *Azteca* (Hymenoptera: Formicidae) in Costa Rica, with Special Reference to the Ants of *Cordia* (Boraginaceae) and *Triplaris* (Polygonaceae)

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*Abstract.*—In the morphological space defined by queen head length and head width, seven Costa Rican species or species complexes in the ant genus *Azteca* have relatively narrow, subrectangular heads (head length ≥ 1.3 times head width), and all of them share characteristic nesting behavior in live stems. These species and species complexes are taxonomically characterized, and queen and worker-based identification guides are provided. A subset of these species are common inhabitants of the specialized ant plants *Cordia alliodora* (Boraginaceae) and *Triplaris melaenodendron* (Polygonaceae). *Azteca longiceps* is an obligate inhabitant of *T. melaenodendron*, but is known only from two mid-elevation Pacific slope sites. In the lowlands *T. melaenodendron* is usually inhabited by either *A. beltii* or *Pseudomyrmex viduus*, two species that are not obligate inhabitants of particular ant plants, but instead may be found in a variety of different ant plant species. The *Azteca pittieri* complex contains the common obligate inhabitants of *Cordia alliodora*. A general description of ant community composition in *Cordia* and *Triplaris* ant plants, and discussion of 1) the adaptive significance of queen characters in *Azteca*, 2) problems of species definitions as revealed by this study, 3) possible mechanisms generating complex character distributions in the *A. pittieri* complex, and 4) the contrasting roles of regional faunas and global revisions are provided. Taxonomic changes are: *Azteca beltii* Emery 1893, **new stat.** [= *laeta* Wheeler 1942 **new syn.**, = *stolli* Forel 1912 **new syn.**]; *Azteca cordincola* Forel 1920, **new stat.**; *Azteca juruensis* Forel 1904, **new stat.**; *Azteca nigricans* Forel 1899, **new stat.**; *Azteca patruelis* Forel 1908, **new stat.**; *Azteca pittieri* Forel 1899 [= *emarginatisquamis* Forel 1920 **new syn.**]; *Azteca sapii* Forel 1912, **new stat.**

## INTRODUCTION

Specialized ant-plant associations are a conspicuous feature of the tropics, and they have been a frequent subject of study in ecology and evolutionary biology (Beattie 1985, Davidson & McKey 1993, Hölldobler & Wilson 1990). Most of the conspicuous ant-plant associations involve communities of interacting species (Longino 1989a, 1991a, Ward 1991, Fiala *et al.* 1991, Davidson *et al.* 1991, Davidson & Fisher 1991, McKey 1991). Studies of these communities are hampered by a lack of basic taxonomy and natural history of the organisms involved. Lack of names and/or a confused state of names impedes effective communication of results. An inability to distinguish among species can lead to mis-

interpretation of field results and/or an underestimation of diversity in ant plant associations. Two ant-plant associations that have received little attention involve the plant genera *Cordia* and *Triplaris*. The last review of these associations was by Wheeler (1942), which contains a wealth of taxonomic and natural history data.

The genus *Cordia* occurs throughout the Neotropics, and two species, *C. nodosa* and *C. alliodora*, are specialized ant-plants (Wheeler 1942). Both species have pyriform cauline swellings at nodes where whorls of branches arise. These domatia are hollow and are usually inhabited by ants. *Cordia nodosa* is South American. *Cordia alliodora* is widespread in South America and also extends through Central

America to southern Mexico. In Costa Rica, *C. alliodora* is the only myrmecophytic *Cordia*. It is a very common tree in anthropogenic habitats, occurring along roadsides and in pastures. On the dry Pacific side, the trees are usually small and bushy, with crooked trunks. On the wet Atlantic side, the trees are tall and straight. It has the common name "laurel" and is considered a valuable timber tree (Opler & Janzen 1983).

Wheeler (1942) considered the following to be obligate inhabitants of *Cordia alliodora*: "*Azteca longiceps* and its subspecies, *A. pittieri* and its var. *emarginatisquamis*, *Pseudomyrma sericea* and its varieties *ita* and *cordiae*, and *Ps. alliodorae*." Wheeler misidentified the material he called *Pseudomyrmex ita* (Forel). True *ita* is a generalist inhabitant of dead twigs, and is occasionally found in *Acacia* thorns (Ward 1993). The material Wheeler identified as "*ita*" is close to or the same as *P. cordiae* (Forel) (Ward, pers. comm.), and is probably an obligate *Cordia* ant. *Pseudomyrmex alliodorae*, described by Wheeler from his study of *Cordia*, is a junior synonym of *P. elongatus* (Mayr), a common and generalized inhabitant of plant cavities (Ward 1989). In the Canal Zone of Panama, Wheeler encountered what he interpreted to be two species of *Azteca* that were specialized inhabitants of *Cordia*. He identified them as *A. longiceps* and *A. pittieri*. *Azteca longiceps* was the most abundant, occurring in 85% of the domatia. The species was previously known only from the type queen, collected in Costa Rica with no biological data, and he redescribed it based on abundant material from *C. alliodora*. His results have influenced subsequent identifications of *Cordia* ants as *A. longiceps* (e.g. Opler & Janzen 1993). As reported below, true *A. longiceps* is a *Triplaris melaenodendron* specialist known from two sites in Costa Rica, and Wheeler's two *C. alliodora* ants should be interpreted as members of the *A. pittieri* complex.

*Triplaris* contains at least 17 species throughout the Neotropics, all of which have hollow stems that are inhabited by ants (Brandbyge 1986, Wheeler 1942). The hollow stems are much like *Cecropia* or bamboo, with short cylindrical internodes separated by solid septa. In many parts of South America, *Triplaris* trees are dominated by the *Pseudomyrmex triplarinus* complex, a set of at least four species of obligate *Triplaris* ants (Ward 1991). *Triplaris melaenodendron* subsp. *melaenodendron* (*sensu* Brandbyge 1986; often identified as *T. americana* in earlier literature; referred to as *T. melaenodendron* in this paper) occurs from Mexico to southern Costa Rica, and is the only *Triplaris* species in Costa Rica. *Triplaris melaenodendron* is moderately abundant on the Pacific side of Costa Rica, where it most often occurs along streams in dry forest areas (pers. obs.).

Wheeler (1942) examined numerous specimens of what he called *Triplaris americana* in Panama, which I assume to be *T. cumingiana* based on Brandbyge's (1986) revision. Wheeler found two ant species he considered to be obligates: *Azteca menceps* and "*Pseudomyrma loewensohni*". *Azteca menceps* is not known from Costa Rica (pers. obs.). The material Wheeler identified as "*loewensohni*" (an unavailable name; Ward 1989) is *symbioticus*, an obligate *Triplaris* ant in the *P. triplarinus* complex, and known from Panama and northern South America (Ward, pers. comm.). As reported below, Costa Rican *T. melaenodendron* is inhabited by a somewhat less specialized community of ants, without close affinities to the specialist *Triplaris* ants from South America.

Ants in the dolichoderine genus *Azteca* are major elements of neotropical forest ant communities (Forel 1899). All are arboreal. The numerous species exhibit a variety of nesting habits, inhabiting external carton nests, dead branches, dead cores of living trees, and live branches. A number of species are obligate inhabitants of specialized ant plants (reviewed in Davidson & McKey 1993). Forel (1878) established

the genus, and his definition remains essentially unchanged. Shattuck (1992) recognized the genus as a monophyletic lineage within the Tapinomini. Emery (1893) provided the first and as yet only revision of *Azteca*, recognizing 25 valid names, but there are now over 150 available names (Shattuck 1994) due to subsequent disconnected descriptions. Longino (1989b, 1991b) has recently reviewed the taxonomy of the species that are obligate inhabitants of *Cecropia* trees.

My studies of the Costa Rican ant fauna have revealed at least 20 species of *Azteca* in the country. Seven of these species nest in live plant stems and have queens with relatively long, narrow heads (head length greater than or equal to 1.3 times head width). This report addresses the taxonomy and natural history of these seven species. The species treated here include the obligate inhabitants of *C. alliodora* and *T. melaenodendron*, as well as other less specialized inhabitants of a variety of plant species. The remaining known Costa Rican *Azteca*, including the five obligate *Cecropia* ants (Longino 1989b, 1991b), have queens with relatively broader heads (head length less than 1.3 times head width).

This is an intentionally regional work. Differentiating species within Costa Rica has proven difficult. Distinguishing continuous geographic variability from discontinuous character change is difficult even in an area the size of Costa Rica, and challenges species concepts. Thus, formal taxonomic changes are restricted to "nomenclatural housecleaning" for a few obvious cases. Species that are insufficiently well-known, primarily due to inadequate knowledge of character variation within and outside of Costa Rica, are given taxonomically unavailable code names. These code names are developed by the author and are unique within the genus *Azteca*. In the future, if numbered taxa are named or associated with existing available names, the numbers will be retired and not reused.

The term "complex" is used for clusters of phenetically similar organisms for which 1) the range of character variation is greater than that typically observed in single species, 2) character variation is at least partially discontinuous, suggesting multiple species, and 3) either the discontinuity is geographically unstable (e.g. *Azteca pittieri* complex) or there is insufficient material to evaluate its stability (e.g. *Azteca nigricans* complex).

A provisional taxonomy is provided, along with keys to queens and workers. The taxonomic results are based on queens because they show greater differentiation between species than workers or males (Longino 1991b, Wheeler and Bequaert 1929). Distinguishing species from workers alone is problematic, because workers exhibit continuous size polymorphism, and colonies of the same species vary greatly in the size of the largest workers. Following the species accounts are a summary of *Cordia* and *Triplaris* ant community composition in Costa Rica, and discussions of 1) the adaptive significance of queen characters, 2) problems of species definitions as revealed by this study, 3) possible mechanisms generating complex character distributions in the *A. pittieri* complex, and 4) the contrasting roles of regional faunas and global revisions.

## LIVE-STEM NESTING *AZTECA*

All members of the group described here nest in live stems. When in *Cordia*, *Triplaris*, or *Cecropia* they inhabit pre-formed cavities in the stems. When in plant species without pre-formed cavities, they occupy irregular chambers throughout the stems, apparently excavated by the workers themselves. Only young stems are occupied; older parts of the plant are gradually abandoned. Colonies are usually polydomous, with all or large parts of a plant crown being inhabited. Brood, often including sexual brood or alate adults, is dispersed throughout the colony space. No cases of polygyny are known, and workers must transport brood among nests in a polydomous colony. Carton construction is common, usu-

ally in the form of small platforms and baffles inside the stems, but sometimes extending outside of the stems to form runways along the stem surfaces. The insides of the stems are usually packed with Homoptera (Coccoidea: mealy bugs and scales), and when carton galleries extend outside of the chambers, abundant Homoptera are often found underneath. Workers do not appear to forage off their host plant, and conspicuous patrolling or foraging outside of the stems is rarely observed. Thus, colonies of these species are relatively inconspicuous. Workers are often somewhat timid, emerging and biting only when the nest space is violently disturbed or actually broken open. A completely different ant fauna may occupy the outer surfaces of the host plant.

## METHODS

Measurements were taken at 50× magnification, using a Nikon micrometer stage with an orthogonal pair of Boeckler rotary micrometers, wired to a dual-axis digital readout. The output of the measuring device was in 0.0001mm increments, and the raw data were recorded as such, but 10 replicate measurements of head length of one specimen had a standard deviation of 0.0025mm. Thus, the 95% confidence interval for measurements spans 0.003mm. Measurement definitions are in figure captions.

The following abbreviations of research collections are used:

IBCR:   Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

LACM:  Los Angeles County Museum of Natural History, Los Angeles, CA, USA.

MCSN:  Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy.

MCZC:  Museum of Comparative Zoology, Cambridge, MA, USA.

MHNG:  Muséum d'Histoire Naturelle, Geneve, Switzerland.

The specimens examined in this work

were mainly from my research collection. These specimens will be deposited in research museums (primarily LACM and IBCR).

## CHARACTERS

Species definitions are based on the following character set:

### Queens

- Head shape (Fig. 1).
- Plot of head width vs. head length (Fig. 2, 3; measurement definitions provided in figure caption).
- Mandible sculpture and pilosity (Fig. 4).
- Pilosity of the propodeum (Fig. 5).
- Shape of the petiole in lateral view (Fig. 6).
- Color
- Plot of head width vs. scape length (Fig. 7).

### Workers

- Head shape of largest workers (Fig. 8).
- Plot of head width vs. head length (Fig. 9).
- Plot of head width vs. scape length (Fig. 10).
- Pilosity of the mesosomal dorsum (Fig. 11).

Each character (except color) is illustrated, with a discussion in the caption of character variation. The figures and keys provide diagnostic information, so it is not repeated in species accounts. Species accounts contain taxonomic changes, taxonomic comments, distribution data, and biological data. Costa Rican place names are used commonly in the species accounts (Fig. 12).

## TAXONOMIC SYNOPSIS

*Azteca beltii* Emery 1893, **new stat.**; Honduras to Panama; ant-plant generalist
   = *fasciata* subsp. *laeta* Wheeler 1942, **new syn.**
   = *stolli* Forel 1912, **new syn.**

*Azteca cordincola* Forel 1920, **new stat.**, Bolivia; *Cordia* specialist?

*Azteca* JTL-003, unavailable code name; Costa Rica; *Cordia* specialist

*Azteca* JTL-007, unavailable code name; Costa Rica; *Ocotea* specialist?

*Azteca juruensis* Forel 1904, **new stat.**, Brazil; in *Swartzia* stems (Fabaceae)

*Azteca longiceps* Emery 1893; Costa Rica; *Triplaris* specialist

*Azteca nigricans* Forel 1899, **new stat.**; Panama

*Azteca (nigricans* complex) JTL-001, unavailable code name; Costa Rica; live-stem generalist

*Azteca (nigricans* complex) JTL-002, unavailable code name; Costa Rica; live-stem generalist

*Azteca patruelis* Forel 1908, **new stat.**, Mexico (*pittieri* complex); *Cordia* specialist?

*Azteca pittieri* Forel 1899; Costa Rica; *Cordia* specialist

= *pittieri* var. *emarginatisquamis* Forel 1920, **new syn.**

*Azteca sapii* Forel 1912, **new stat.**, Brazil; in *Sapium* stems (Euphorbiaceae)

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## KEY TO QUEENS

Key to *Azteca* queens that: 1) are known to occur in Costa Rica, and 2) have subrectangular heads, with head length ≥ 1.3 times head width. Species definitions in this treatment strongly rely on length and width of the queen head capsule, and the key should be used in conjunction with Figures 2 and 3.

1.a. Color largely orange; head width > 1.2mm (Fig. 2) ............................................*beltii*
1.b. Color largely or entirely black; head width < 1.2mm ......................................... 2
2.a. Mandible with even covering of coarse, piligerous puncta (Fig. 4A); mandible surface appearing bristly (*nigricans* complex) ......................................................... 3
2.b. Mandible always with row of piligerous puncta along masticatory margin, but large puncta sparse to absent on mandible surface proximal to this row, and with at most four puncta bearing setae (Fig. 4B-F) ................................................................. 4
3.a. Petiolar node low and blunt, ventral lobe deep (Fig. 6D); scape relatively short (Fig. 7) ...................................................................................................**JTL-001**
3.b. Petiolar node sharp; ventral lobe shallow (Fig. 6E); scape relatively long (Fig. 7) ...**JTL-002**
4.a. Head strongly rectangular, with flat sides and lateral margin of vertex relatively sharp (Fig. 1, *longiceps* and JTL-003); head length > 0.275 + 1.3(head width) (above line in Fig. 2) ........................................................................................................ 5
4.b. Head less rectangular, with sides slightly convex, and lateral margin of vertex more broadly rounded (Fig. 1, remaining species); head length < 0.275 + 1.3(head width) (below line in Fig. 2) ......................................................................................... 6
5.a. Petiolar node low, anterior face of petiole flat (Fig. 6C); propodeum with sparse short setae concentrated posterior to spiracle (Fig. 5C); mandible lacking large puncta proximal to masticatory margin (Fig. 4E) ..................................................................**JTL-003**
5.b. Petiolar node higher, anterior face somewhat concave (Fig. 6B); propodeum with setae sparse or abundant (Fig. 5); mandible with about 5 large puncta proximal to masticatory margin (Fig. 4F) ..................................................................................*longiceps*
6.a. Mandible with about 5 large puncta proximal to masticatory margin, about 3 of these bearing setae (Fig. 4C); propodeum sparsely setose (Fig. 5C) .....................**JTL-007**
6.b. Mandible with about 3 large puncta proximal to masticatory margin, these not bearing setae (Fig. 4D); propodeum densely setose over most of surface (Pacific slope; Fig. 5A) or sparsely setose (Atlantic slope, Fig. 5B) ...........................*pittieri* complex

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## KEY TO WORKERS

This key is a corroborative device when one also has queens and/or host plant data.

1.a. Promesonotum with sparse pilosity (Fig. 11A); setae present on propodeum; head width of largest workers often, but not always, > 1mm (Fig. 9) ............................ 2
1.b. Promesonotum with abundant pilosity (Fig. 11B-E); propodeum with or without pilosity; head width of largest workers often, but not always, < 1mm (Fig. 9) ................ 3

## SPECIES ACCOUNTS

### *Azteca beltii* Emery new stat.
#### (Figs 1–11)

*Azteca bicolor* race *beltii* Emery, 1893:142. Holotype worker, Costa Rica (Alfaro) [MCSN] (examined).

*Azteca fasciata* subsp. *laeta* Wheeler, 1942:227. Holotype (unique syntype) queen: Panama, Canal Zone, Barro Colorado Island, 9 July 1924 (Wheeler #637), from a domatium of *Cordia alliodora* [MCZC] (examined). **new syn.**

*Azteca stolli* Forel, 1912:54. Syntype workers: Guatemala, Retaluleu (Stoll) [MHNG] (examined). **new syn.**

Under *beltii* Emery (1893) described a major worker from one collection and two small workers from a different collection. In the publication he designated the single major worker as the type (considered the holotype here), and conjectured that the smaller workers might represent a distinct taxon. The major worker, collected by Alfaro and simply labeled "Costa Rica," matches material commonly collected from *Triplaris* and other trees in the Pacific lowlands of Costa Rica. The smaller workers, also examined, are from "Jimenez," a lowland Atlantic site, and are workers of *Azteca alfari*. The *stolli* syntype workers clearly come from a single nest series, and appear identical to queen associated material of *beltii* from Costa Rica and Honduras.

Large size, orange head, and sparse dorsal pilosity make workers of this species relatively distinctive. *Azteca beltii* is known to occur from Guatemala to Panama. In Costa Rica it is common at Santa Rosa, Palo Verde, and along the road to Monteverde. It is one of the more common inhabitants of *Triplaris melaenodendron*, but has also been collected from *Cordia nodosa, Cecropia peltata, Cochlospermum vitifolium* (Janzen, pers. comm.), and *Pithecellobium saman*. Colonies can be large, filling the crown of large *Pithecellobium* trees. The nest space is entirely within live stems at branch tips, and workers are rarely seen foraging outside of the stems. This species is much more common than museum collections might suggest, because of its cryptic habits.

An observation of queen founding behavior is described below under *A. longiceps*.

I have examined scattered material from southern South America that is either the same species, a close relative, or a highly convergent species. These include the type queens of Emery's *fasciata* and *mayri*, former syntype workers of *bicolor* (workers excluded from types and *bicolor* synonymized with *alfari* in Longino 1991b), and recent Bolivian collections by P. S. Ward. If the South American material is *beltii*, then the biology and distribution of *beltii* is strikingly similar to that of *Pseudomyr-*
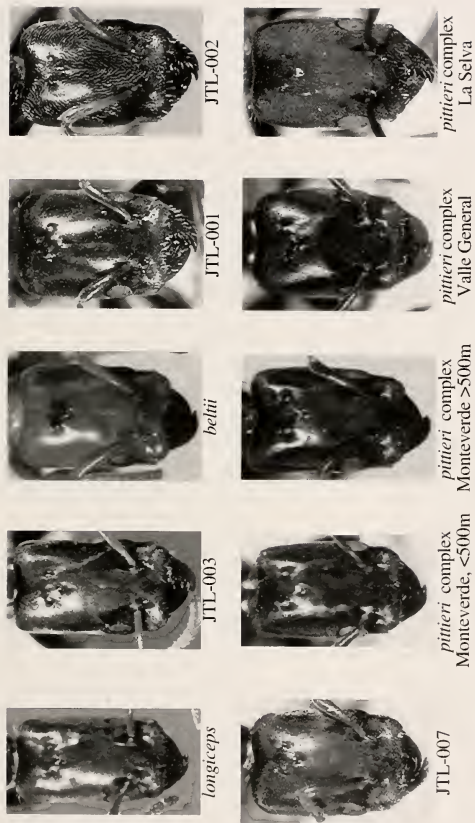
Fig. 1. Queen head shape. Image scales are adjusted to equalize head size in figure. For relative size data, see Figure 2.

*mex viduus* (Ward 1991). Both show catholicity with respect to which ant-plants they will inhabit, and both are present in both Central America and southern South America.

### Azteca cordincola Forel new stat.

*Azteca longiceps* subsp. *cordincola* Forel, 1920: 203. Holotype (unique syntype) worker: Bolivia (Bang, n.1178) in cauline swellings of *Cordia* [MHNG] (examined).

The single small worker (head width 0.59mm) is nondescript and I cannot distinguish it from most *Azteca* species. Wheeler (1942:232) described the queen and redescribed the worker based on Mann collections from cauline swellings of *Cordia alliodora* in Ivon, Beni, and Huachi Beni, Bolivia. Wheeler also listed "Cochabamba" as the type locality for *cordincola*, although this does not appear in the original description nor on the type specimen label. The queen that Wheeler described has head length 2× head width, and so may be part of the *pittieri* complex, but Mann's collections cannot be assumed conspecific with the type.

### Azteca JTL-003
### (Figs 1–11)

This species is known only from between 400–500m on the road to Monteverde, from six different *Cordia alliodora* trees. It has been collected in two different clusters of trees along the road, and is sympatric with *A. beltii*, *A. longiceps*, and two forms of the *A. pittieri* complex.

### Azteca JTL-007
### (Figs 1–11)

This species is known from one collection from Carara Biological Reserve. *Ocotea nicaraguensis* is an understory lauraceous tree at Carara. It is part of a group of understory Lauraceae whose stems are always occupied by ants (Stout 1979, Hammel 1986, Burger & van der Werff 1990). The ants are usually obligate inhabitants in the genus *Myrmelachista*, but

*Pseudomyrmex viduus* and *Azteca* may also be found. During a brief examination of *O. nicaraguensis* plants at Carara, I observed that plants in shaded understory were small and all inhabited by *Myrmelachista*, while plants in more sunny areas along stream banks were larger and inhabited by *Azteca*. However, only one voucher collection of the *Azteca* was taken, from a vigorous colony with alate queens in the stems.

### Azteca juruensis Forel new stat.

*Azteca longiceps* var. *juruensis* Forel, 1904:699. Syntype workers, females, male(s): Brazil, Amazonas, Jurua, Jurua Mirim, Aug 1901 (Ule), in branches of *Schwartzia* [MHNG] (examined).

A syntype queen has head length 1.24mm, head width 0.77mm. In general habitus *juruensis* looks like a *pittieri* complex species, including the same lateral profile of the petiole. The size is considerably smaller than any Costa Rican material. It is very similar and possibly conspecific with *sapii* (see below). I cannot distinguish the two, but I defer synonymy for lack of data on character variation in Amazonian stem-nesting *Azteca*.

### Azteca longiceps Emery 1893
### (Figs 1–11)

*Azteca longiceps* Emery, 1893:344. Holotype (unique syntype) queen: Costa Rica, Alajuela (Alfaro) [MCSN] (examined).

The species is now known from the type queen, collected in Alajuela before the turn of the century, and seven collections, all from between 700 and 900m elevation in the Guacimal river valley below Monteverde. The type has no biological data. The seven new collections are all from live stems of *Triplaris melaenodendron*. Some collections are from mature colonies, and others are founding queens from stump sprouts. Extensive collections in the area have not revealed *longiceps* using any oth-
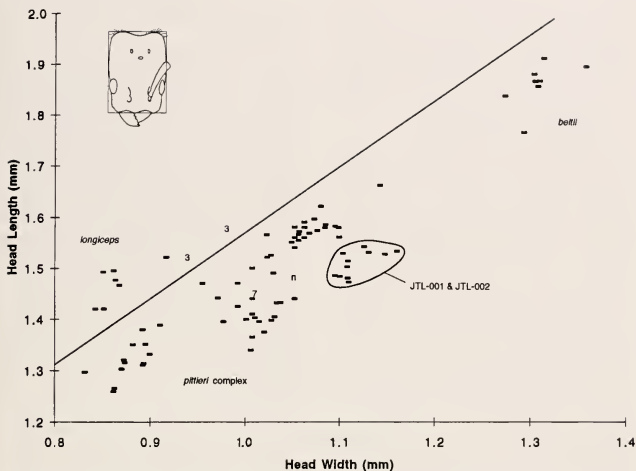
Fig. 2. Queen head width vs head length. Head width is the greatest width of the head in full-face view. Head length is measured along the median axis, from the anterior border of the clypeus to a line tangent to the posteriormost extent of the vertex lobes. Line: Head Length = 0.275 + 1.3(Head Width). "n" = *nigricans* type; "3" = JTL-003; "7" = JTL-007.

er plant species, and so *longiceps* is probably a host specialist in *T. melaenodendron*.

The discovery of *longiceps* as a *Triplaris* ant was unexpected. Subsequent to the naming of *longiceps*, Forel named a number of *longiceps* subspecies based on ants from *Cordia* and other plants (*cordincola, patruelis, juruensis,* and *sapii*). Wheeler (1942) encountered two species of *Azteca* regularly inhabiting *Cordia alliodora* in Panama (Canal Zone). He identified the more common one as *longiceps*, and thoroughly described the worker, queen, and male based on his new material. Myself and other contemporary workers have continued to identify the common *Cordia* ants as *longiceps* or cf. *longiceps*. Examination of the type revealed that *longiceps* was not one of the common *Cordia* ants. Short-

ly after examination of the type, the Monteverde population of *longiceps* was discovered in *Triplaris* trees. As interpreted here, *longiceps* is a narrowly circumscribed *Triplaris* ant, with the queen head relatively narrower than most *Cordia* ants. The *Cordia* ants examined by Wheeler are interpreted here as more closely related to *pittieri*. In order to dissociate the infraspecific taxa *cordincola, patruelis, juruensis,* and *sapii* from *longiceps*, all are raised to species elsewhere in this paper.

The following observations, derived from field notes, describe the nesting habits of *A. longiceps*:

5 July 1991, Longino #2956: I climbed a *Triplaris* tree and cut out 3 small branches that all contained parts of a colony. No workers appeared as I climbed the tree,

nor after I cut branches. A few workers emerged from cut branch bases. Only as I began to split stems did large numbers of workers swarm out. Abundant Homoptera were inside stems, and a few males and a few alate queens. There was abundant worker brood throughout.

I examined a 24cm long section in detail. The internodes contained "knöllen," discrete mounds of sticky bran-like material filled with nematodes, tiny dipteran larvae, and what appeared to be abundant stylets of Homoptera. (Knöllen are also found in nests of Cecropia ants (Müller 1880–1881, Longino 1991a), and are probably common to many or all stem-nesting Azteca.) There were pink coccids in the occupied internodes: 5, 7, 32, 31, 8, 7, 4 coccids in the 7 occupied internodes. There was a single pseudococcid in these 7 internodes. Many of the exit holes were originally large enough to accommodate a queen, but had been reduced to worker size with resinous carton. Some of the internodal septa were perforated, others not. There were perforated partitions made of resinous carton, which formed artificial septa. Some were found in the middle of internodes, others were partially closing chewed-out internodal septa.

There was one unoccupied internode in the middle of the branch, with solid septa on both sides. The sclerenchyma was thicker on the occupied side than the unoccupied side of the septa, as though the sclerenchyma were a secondary response to ant presence. The walls of ant-occupied internodes were black. The walls of unoccupied internodes were covered with flaky red brown material. Inner diameters of occupied internodes were greater than inner diameters of unoccupied internodes, but the sclerenchyma layer was thicker in the former, again suggesting that the sclerenchyma layer was a response to the ants.

The ant entrance holes were irregularly scattered, not in any predictable location. The terminal internodes, near the unoccupied apical shoot area, were the most recently entered.

5 July 1991, Longino #2972: I climbed a 4m tall Triplaris tree. It contained a populous colony, and workers emerged onto trunk when I climbed tree. The largest branch segments I examined from this tree were 3cm dia., and still contained hollow internodes with ants. A large basal section contained relatively few workers and scattered pseudococcids, with no coccids. Exit holes were still maintained through 1cm of wood. I dissected 180cm of occupied branch. There were abundant brood, workers, carton partitions, and exit holes, much like #2956. There were scattered alate queens, and at least one male. Unlike #2956, there was no trace of pink coccids, and pseudococcids were widespread and common.

5 July 1991, Longino #2969-s: I cut one branch from a Triplaris tree. The terminal 20–40cm, the leafy part, was unoccupied. Lower in the branch, 2 founding queens of Azteca longiceps and beltii occupied adjacent cavities. The cavities of the two queens formerly were continuous through a perforated septum, but a plug of particulate matter separated the two. The plug was asymmetrical, as though built from the beltii side (Fig. 13).

## Azteca nigricans complex

The queens of this complex have the mandibles with an even cover of large piligerous puncta, so that the mandibles are bristly. Azteca nigricans s.s. is known only from the type queen from Panama, JTL-001 occurs in the Pacific lowlands of Costa Rica, and JTL-002 occurs in the Atlantic lowlands. The three "species" recognized here differ in queen head size and relative scape length. However, samples are available from few localities, and knowledge of geographic variation in these characters is inadequate to confidently establish species boundaries.
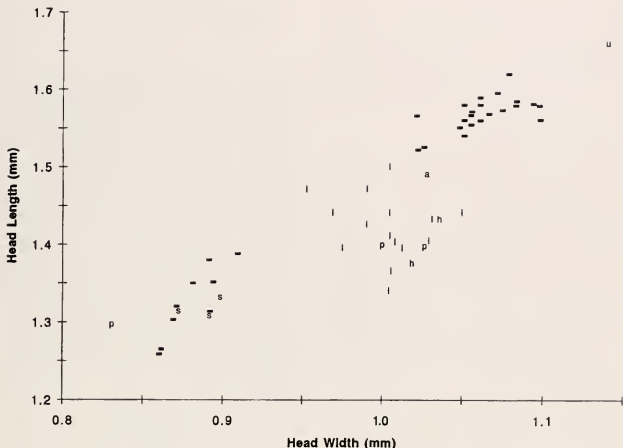
Fig. 3. Queen head width vs head length for *Azteca pittieri* complex. Dashes = road from PanAmerican Highway to Monteverde; "a" = Nuevo Arenal, on north side of Lake Arenal; "h" = Hone Creek, south of Limón; "l" = La Selva; "p" = 4–10km east of Palmar Norte, along the Río Grande de Térraba; "s" = Santa Rosa National Park and vicinity; "u" = Santiago de Puriscal.

**Azteca nigricans** Forel, new stat.

*Azteca fasciata* var. *nigricans* Forel, 1899:122. Unique syntype queen: Panama, Bugaba, Volcan de Chiriqui (Champion) [MHNG] (examined).

**Azteca (nigricans complex) JTL-001**
(Figs 1–11)

This species is known from a number of nest collections from lowland rainforest in southwestern Costa Rica, and two alate queens in collections: one from Golfito, and one from Cerro el Hacha near Santa Rosa.

The following observations, derived from field notes, describe the nesting habits of this species:

28 Aug 1982, Longino #28Aug82/1500: In the uppermost crown area of a large *Licania* tree (Chrysobalanaceae), a colony occupied chambers in the center of nearly every branch tip I could reach. The chambers looked chewed out by ants, and were not a natural feature of the plant. The chambers had many pink coccids on the walls, and some chambers had brood. The branches showed a history of synchronous new growth flushes. Chambers in the latest flush were most active; chambers in older or dead stems were abandoned or had few workers. The chambers in sequential shoots were usually not connected. All the chambers were connected externally by an extensive system of galleries, made of a black, very crusty carton, filled with tiny, circular holes.

3 Sep 1982, Longino #3Sep82/1100: In the same canopy *Licania*, I observed a queen investigating a small hole in a living shoot. The hole was too small for her to enter.

25 Mar 1990, Longino #2651: A colony occurred in live stems of a small *Grias* tree (Lecythidaceae). Branch surfaces were covered with black, crusty carton, with a high density of small, circular entrance holes. Irregular cavities in stems contained abundant Homoptera.

28 Sep 1982 (Longino): Founding queens were in separate chambers at the tips of living branches, 10m high in a tree (Moraceae). The stems of this tree frequently had small, pre-formed internal chambers, some with dead *Azteca* remains.

Leeanne Tennant studied the ant-plant *Tetrathylacium costaricensis* (Flacourtiaceae) in Corcovado National Park, during July 1987. She found JTL-001 to be one of the most common inhabitants. This ant-plant has pre-formed chambers that split, allowing entrance of ants without excavation.

### Azteca (nigricans complex) JTL-002

This species is known from numerous recent collections from La Selva Biological Station, and one old (1926) collection from Parismina, on the Atlantic coast. Like JTL-001, it appears to be a generalist, nesting in live stems of a variety of plant species. At La Selva, workers were encountered in two of 18 canopy fogging samples, from crowns of *Carapa guianensis* (Meliaceae) and *Tapirira guianensis* (Anacardiaceae). Nests have also been sampled from scattered small chambers in live stems of *Dendropanax arboreus* (Araliaceae), *Pentaclethra macroloba* (Leguminosae), *Inga* sp. (Leguminosae), *Erythrina peoppigiana* (an introduced species, Leguminosae), and *Phoebe chavarriana* (Lauraceae). Wetterer collected a founding queen in an internode of a *Cecropia insignis* sapling. Although inconspicuous, *Azteca* JTL-002 is one of the most common *Azteca* species in the canopy at La Selva.

### Azteca patruelis Forel, new stat.

*Azteca longiceps* subsp. *patruelis* Forel, 1908:392. Syntype workers, queen: Mexico, near Coli-

ma (Townsend), in *Cordia alliodora* [MHNG] (examined).

A syntype queen of *patruelis* has head length 1.62mm, head width 1.10mm. In most characters, including head shape, it closely matches *pittieri* complex specimens from upper elevation collections near Monteverde (see below). Although not examined on the type, a queen from near the type locality (Mexico, Jalisco: Estación Biológica Chamela, 19°30'N, 105°02'W, 100m (Ward #9253), ex *Cordia alliodora*) differs slightly in the pilosity of the ventral surface of the petiole. On Costa Rican specimens, the setae on the anteroventral margin are longer and more appressed. Pending additional data on character variation between Costa Rica and Mexico, *patruelis* is retained as a valid species (see Discussion below).

### Azteca pittieri complex
### (Figs 1–11)

Ants in the *Azteca pittieri* complex are the primary obligate inhabitants of *C. alliodora* throughout Costa Rica. In some areas character variation is discontinuous, suggesting discrete, parapatric species, but these differences are not stable geographically. In a plot of queen head length vs. head width (Fig. 3), specimens from the Pacific lowlands form one cluster, specimens from above 500m near Monteverde form a second cluster, and specimens from the Atlantic lowlands and the Valle General form a third cluster somewhat intermediate between the first two. One queen from Santiago de Puriscal (swept from vegetation, and thus not known with certainty to be a *C. alliodora* ant) is discontinuously larger than all other queens examined.

Collections along an elevational transect (400–900m along the road from the Pan American Highway to Monteverde) revealed two phenotypes that could be interpreted locally as two species. One form has relatively small queens (Fig. 3), and
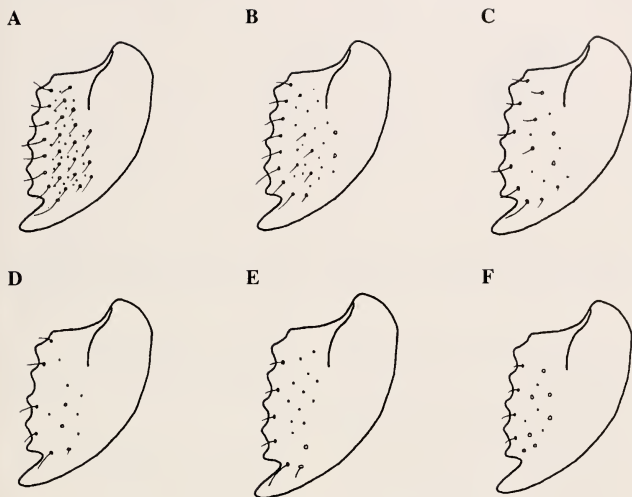
Fig. 4. Queen mandible sculpture and pilosity. A. *nigricans*, JTL-001, JTL-002; B. *beltii*; C. JTL-007; D. *pittieri* complex; E. JTL-003; F. *longiceps*.

workers with the margin of the vertex shallowly excavated and the sides of the head nearly flat (Fig. 8). The other form has relatively large queens, and workers with the margin of the vertex more deeply excavated and the sides of the head more convex. The two forms have a sharply parapatric distribution, with small-queen colonies occurring from 400–500m, and large-queen colonies occurring from 500–900m. In the narrow zone of sympatry both forms were found in adjacent trees, and founding queens of both forms were found in different nodes of the same small stump sprout or sapling. A similar pattern may occur on the more southern Pacific slopes, where one small and two large queens were collected near Palmar Norte (Fig. 3).

Variation in queen propodeal pilosity is discordant with head shape. Queens from the Pacific side of Costa Rica, regardless of queen head shape, have dense pilosity on the propodeum (Fig. 5A). Queens from La Selva on the Atlantic slope have sparser propodeal pilosity, and it varies from a uniform covering to a discontinuous covering, with a few setae near the mesopropodeal suture, a gap with no setae, and a cluster of setae posterior to the spiracle (Fig. 5B). La Selva queens with the relatively shortest heads are indistinguishable from two queens collected from Hone Creek south of Limón, and these relatively small queens exhibit the extreme of propodeal pilosity reduction. Relatively larger queens tend to have more uniform propodeal pilosity.

Fig. 5. Queen propodeum pilosity. A. Pacific slope *pittieri* complex. B. Atlantic slope *pittieri* complex. C. JTL-003, JTL-007, JTL-001, and JTL-002. *beltii* and *longiceps* are variable, with sparse setae that are either clustered posterior to the spiracle, as in **B**, or more uniformly distributed over the propodeum, but never dense as in **A**.

## Azteca pittieri Forel

*Azteca pittieri* Forel, 1899:120. Syntype workers: Costa Rica, Buenos Aires (Pittier) [MHNG] (examined).

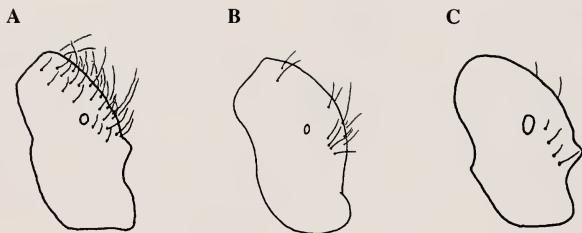*Azteca pittieri* var. *emarginatisquamis* Forel, 1920: 204. Syntype workers: Costa Rica (Pittier, n.6701), found by Chodat in cauline swellings of *Cordia gerascanthus* [MHNG] (examined). **New syn.**

I examined an herbarium sheet at the National Museum of Costa Rica. It was part of the Pittier collection, and had the label "Cordia gerascanthus, arbre, Plaine du Rio Ceibo à Buenos Aires, Alt: 300m, Dat: I 1892, Legit: Tonduz," and it had Tonduz collection number 6701. It had a 1984 J. S. Miller determination label as *Cordia alliodora*. This collection was no doubt the source of the syntypes of *emarginatisquamis*, which Chodat probably found in a duplicate specimen in Europe. Thus *pittieri* and *emarginatisquamis* have the same type locality, and the types are possibly from the same colony. Pittier apparently distributed Tonduz collections under his own name (L. D. Gomez, pers. comm.), and thus the types of *pittieri* s.s. could have been from the same collection, sent to Forel by Pittier.

## Azteca sapii Forel new stat.

*Azteca longiceps* race *sapii* Forel, 1912:56. Syntype workers, queens: Brazil, Amazonas, St. Antonio de Iça (Ducke), in stems *Sapium glandulosum* [MHNG] (examined).

A syntype queen has head length 1.20mm, head width 0.73mm. I cannot distinguish this species from *juruensis* (see above).

## COMMUNITY COMPOSITION AND DISTRIBUTION

### Cordia alliodora

Individual *Cordia* trees usually harbor a number of ant species. In small saplings or stump sprouts, many species of founding queens may be found dispersed in the available nodes. In mature trees, live nodes typically house species distinct from those housed in dead nodes. Most often a dominant colony occupies most but not all of the live nodes, with smaller colonies of other species occupying the remaining nodes. Alternatively, a single dominant colony may not be recognizable. Instead, the tree may contain a mosaic of numerous colonies, or many nodes may be unoccupied.

The species of ants in individual trees are a subset of the surrounding community of available ant species. As with insect herbivores, those species exhibit a broad range of host specificity. A large number of species of generalist inhabitants of dead stems may be available to
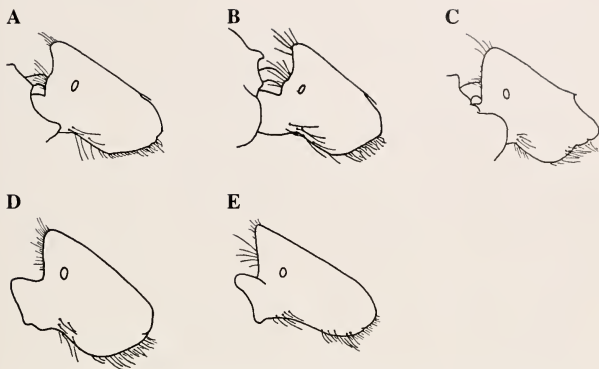
Fig. 6. Queen petiole shape and pilosity. Drawing scales are adjusted to equalize petiole size in figure. A. *beltii*. B. *pittieri* complex (JTL-007 and *longiceps* are the same). C. JTL-003. D. JTL-001. E. JTL-002.

occupy dead nodes of a *C. alliodora* tree. In the Neotropics these include members of the genera *Crematogaster*, *Dolichoderus*, *Tapinoma*, *Camponotus*, *Leptothorax*, *Pseudomyrmex*, *Brachymyrmex*, *Zacryptocerus*, *Paratrechina*, and others. A smaller number of generalist inhabitants of live stems may be available to occupy live nodes, and part or all of a crown may be inhabited by one or more colonies of these generalists. These include some species of *Crematogaster*, *Pseudomyrmex*, *Zacryptocerus*, and *Azteca*. These live stem generalists may have small colonies in one or a few nodes, or they may form large, dominant colonies that occupy much of the tree. Generalist inhabitants of *C. alliodora* show no obvious specialization for use of the plant. They are often scavengers and omnivores, and forage both on and off the plant. Species that form large, dominant colonies are not necessarily restricted to a single tree. Their large, polydomous colonies may extend into the surrounding vegetation.

In contrast to these generalists, a smaller

pool of available colonists make specialized use of *C. alliodora*. They usually form large, dominant colonies, occupying most or all of a live crown, and they are typically the most common inhabitants in an area. Their nest space is entirely within a single tree (or tight cluster of trees if from stump sprouts), and they do not forage off the tree. In spite of their local abundance in *C. alliodora* trees, they are never found nesting elsewhere, which suggests that they are obligate host specialists. The *Azteca pittieri* complex and, at least locally, *Azteca* JTL-003 appear to be the dominant or primary host specialists in Costa Rica.

Not all host specialists are dominant ants. The most ubiquitous inhabitant of *C. alliodora* is *Zacryptocerus setulifer* (Emery). This myrmicine ant has phragmotic soldiers which plug the entrance to the nest with their perfectly circular heads. They are inconspicuous and timid ants. They are capable of coexisting in the same tree with any of the above dominant ants, and they can live in trees without a dominant ant colony. They appear to be an obligate
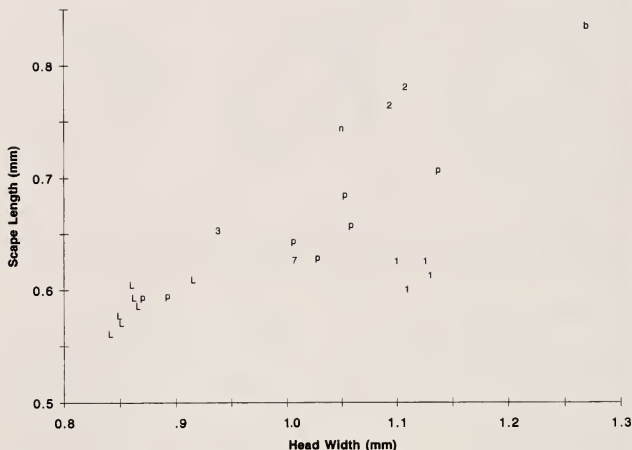
Fig. 7. Queen head width vs. scape length. "b" = *beltii*; "L" = *longiceps*; "n" = *nigricans* type; "p" = *pittieri* complex; "1" = JTL-001; "2" = JTL-002; "3" = JTL-003; "7" = JTL-007.

inhabitant of *C. alliodora*; I have never encountered them anywhere else. Nearly every *C. alliodora* population I have examined in Costa Rica has had *Z. setulifer* in some of the nodes.

Two ant species, *Pseudomyrmex viduus* (Fr. Smith) and *Azteca beltii*, show a combination of traits of host specialists and host generalists. They exhibit the behavior of a specialized plant-ant: they confine their nesting and foraging territory to the host tree itself, and, in the case of *P. viduus*, they may aggressively defend their host tree. However, they are generalists with respect to which species of host plant they inhabit. Both species can be found in different genera of well-known ant-plants (*e.g.*, *Cecropia*, *Triplaris*, and *Cordia*), and *A. beltii* has also been found in other species of non-ant-plants.

Most trees in populations of *C. alliodora*

are occupied by members of the *A. pittieri* complex, with *Zacryptocerus setulifer*, *Azteca beltii*, and *Pseudomyrmex viduus* as less common background elements. This is well-illustrated with data from an elevational transect. The road from the Pan-American Highway to Monteverde passes through an elevational gradient from 200m to 1400m, all of which is in pastures and second growth vegetation. *Cordia alliodora* trees are common in patches along the roadside, starting at 400m around Guacimal, and extending to about 900m, along 10km of road. In 1984 and in 1991, I sampled ants from *C. alliodora* trees along this road. *Azteca beltii* occurred occasionally throughout the transect. *Pseudomyrmex viduus* occupied patches of trees near 500m. I found *Azteca* JTL-003 in two patches of trees around 500m, and collected the only known samples of this species. Mem-

bers of the *A. pittieri* complex occupied the great majority of trees. As described earlier, there appeared to be two different biological species in the *A. pittieri* complex along this transect, with a lowland form changing to an upland form around 500m elevation.

It is unknown what impact parasitoids may have on community dynamics and structure. Founding *A. pittieri* complex queens are often attacked by parasitoid larvae inside *Cordia* nodes. They are probably larvae of *Conoaxima* (Eurytomidae); they are similar to larvae of *Conoaxima* I have observed attacking *Azteca* queens in *Cecropia* (Longino 1991b). At La Selva Biological Station I have observed larvae feeding externally on dead queens, and in two cases parasitoid pupae were on the walls with dead queen remains in the bottom.

### *Triplaris melaenodendron*

Similar to *C. alliodora*, individual *T. melaenodendron* trees usually host a community of ants, and the same general observations regarding host generalists and host specialists apply. Dead branches and some live branches may be occupied by generalist arboreal ants, while the bulk of the live crown may be occupied by a dominant ant.

In contrast to the situation for *C. alliodora*, *T. melaenodendron* does not have a dominant host specialist ant in all parts of its range in Costa Rica. *Pseudomyrmex viduus* is the most common occupant in the Pacific lowlands, followed by *Azteca beltii*.

A dominant host specialist occurs near Monteverde. Along the road to Monteverde, between 700 and 900m elevation, *T. melaenodendron* occurs in a few spots along the road where there are seeps or stream crossings. *T. melaenodendron* trees also occur along the margins of the Río Guacimal (just below Monteverde on the Pacific slope), between 800 and 1000m. In 1991, I examined these trees, both along the road and along the Río Guacimal. In contrast to the lowlands, the most common inhabi-

tant was the specialist *A. longiceps,* followed in frequency by *A. beltii*. I found no *Pseudomyrmex viduus* at this elevation.

## DISCUSSION

### Adaptive Significance of Queen Characters

The species of live-stem inhabiting *Azteca* treated in this paper are often distinguishable by head size and shape, and by mandible sculpture and pilosity. Why should these characters vary between species, and have relatively low variance within species? And why are queens more differentiable among species than workers?

Alate queens of arboreal ant species must disperse and find suitable nest sites in vegetation. Ant queens are typically filled with flight muscles and reproductive organs, and thus are favored prey for birds, rodents, and other ants. While searching for nest sites, queens are highly conspicuous and vulnerable. There must be strong selection on queens to reduce this vulnerable period to a minimum. Selection should act to make queens extremely efficient at finding a particular kind of nest site, and quickly gaining access. Characters that influence nest site selection are concentrated in the head. Head size will influence the muscle mass available to power the mandibles, and thus will influence both the hardness of substrates that can be cut and the speed of cutting. Mandible sculpture and pilosity will also influence the performance of the mandibles on different substrates. Head size and shape will determine the size of stems that can be entered. Within species, selection may tailor head characteristics to optimally match a highly canalized behavioral (visual or chemical) search image for particular nest sites. Intense selection for specialization during colony founding may be driving diversification in *Azteca,* and this diversification is manifested in high interspecific diversity of queen head shape.
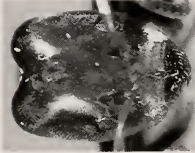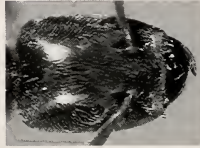
Fig. 8. Worker head shape. Image scales are adjusted to equalize head size in figure. For relative size data, see Figure 9.

The long, narrow heads of the species addressed in this paper may simultaneously provide great mandible strength and reduced head cross-section for entry into plant cavities in narrow stems.

Worker morphology may be much less constrained by nest site characters, and similarity between workers and queens may be the result of developmental constraints rather than strong selection on the workers. Strong selective factors acting on worker morphology are more likely to involve foraging and colony defense. These factors may vary little across *Azteca* species, and be independent of or only weakly influenced by nest site characters. Thus, there may be little selection for divergence in worker morphology between species.

Variation in queen mandible pilosity may also be strongly related to colony founding. The pilose mandibles of the *A. nigricans* complex are in striking contrast to the nearly hairless mandibles of the obligate *Cordia* and *Triplaris*-inhabiting species. Mandibles of *beltii* and JTL-007 exhibit intermediate degrees of pilosity. Differences in mandibular pilosity are not due to differential wear. Alate queens of *Cordia* and *Triplaris* ants that have yet to leave their natal nest have largely hairless mandibles, and the large puncta from which hairs arise would not be effaced by wear. *Azteca longiceps, pittieri* complex, and JTL-003 all appear to be primary occupants of specialized ant-plants. To found their colonies, they have to cut rapidly through plant tissue into a domatium. The smooth, hairless mandibles may be an adaptation for rapid cutting. *Azteca beltii* and JTL-007 have been found in ant-plants that have other primary occupants. Although there are no direct observations of founding behavior, the one observation of the close proximity of founding *longiceps* and *beltii* queens (Fig. 13) hints at the possibility that *beltii* and JTL-007 are secondary occupants of ant-plants. They may rely on the primary occupants to excavate entrances, entering subsequently and either

fighting or walling off the primary occupant.

The stiff setae on the mandibles of ants in the *A. nigricans* complex appear as though they would impede cutting into plant stems. In the case of *Tetrathylacium costaricensis*, it is clear that the queens do not have to excavate an entrance hole to enter the stems; on maturation the stems split down the side, allowing ant entry. Perhaps ants in the *A. nigricans* complex, rather than being specialized to excavate entrances in a particular kind of hostplant, are instead specialized to find preexisting entrance holes into plant cavities, regardless of plant species. Strongly pilose mandibles may be an adaptation for efficient and rapid construction of carton nest material, which would be necessary to close large and/or irregular preexisting entrances.

These speculations regarding the functional aspects of queen head morphology deserve greater study. Direct and close observations of early nest establishment behavior by *Azteca* queens are needed.

### Problems of Species Definitions

The *A. pittieri* complex exhibits at least one area where two morphologically diagnosable groups of organisms are parapatric, with the zone of sympatry being less than 5km wide. However, the characters that are diagnostic in this area are not stable in other parts of the range. Taxonomists routinely face this level of knowledge about patterns of organismal diversity, and the frequency of encountering patterns such as this can only increase with the current emphasis on intensive biodiversity inventories at the national or more local scale (Janzen 1991, Longino 1994, Stork 1994). How taxonomists treat this situation nomenclaturally underlies the conflict that often occurs between the local field collector's and the museum taxonomist's definitions of species (Gentry 1990).

Parapatric boundaries between diagnos-
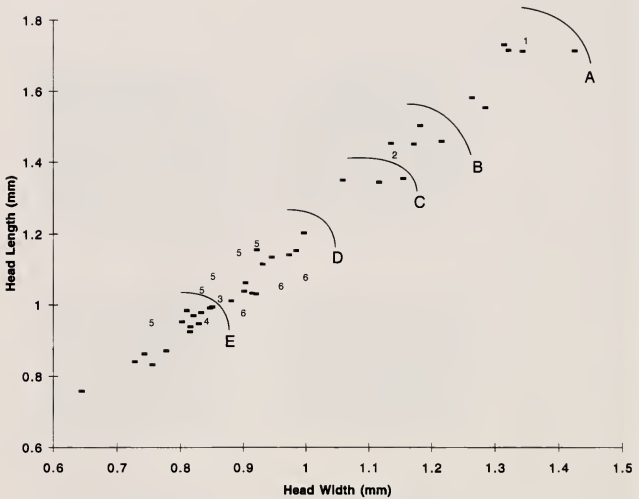
Fig. 9. Worker head width vs. head length. For definitions of measurements see Figure 2. Each measurement is from a different colony, from among the largest workers in the collection. Most are from queen-associated collections, and so identification is relatively secure. Because of worker polymorphism, and inter-colony variation in the size of largest workers, the spread of points within species is large, and species generally converge in the lower left region of the plot. The curved lines delimit the maximum sizes observed for species or sets of species. A) *beltii*; B) JTL-003; C) JTL-002; D) *pittieri* complex; E) JTL-007. Numbers refer to measurements of individual workers. 1) *beltii* type; 2) *stolli* type; 3) *pittieri* type; 4) *emarginatisquamis* type; 5) *longiceps*; 6) JTL-001. Note that *longiceps* workers tend to have relatively narrower heads, and JTL-001 workers tend to have relatively wider heads.

able groups are commonplace, and are the subject of extensive study on hybrid zones and clines (e.g. Endler 1977, Harrison & Rand 1989). In many cases they have been demonstrated to be genetically leaky boundaries, maintained by opposing forces of dispersal and selection or a number of other mechanisms (Hewitt 1989). It is common to treat such cases as intraspecific genetic structuring of a single "polytypic" species, partly due to the biological species concept and its emphasis on reproductive isolation (Cracraft 1989). Cracraft

criticizes this approach on the grounds that it obscures or ignores data on differentiation, and that such differentiation data can be used to support hypotheses about the phylogenetic history of the group. Cracraft defines a phylogenetic species as "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." In some well-sampled and well-studied groups, this approach has led to a greater understanding of biological diver-
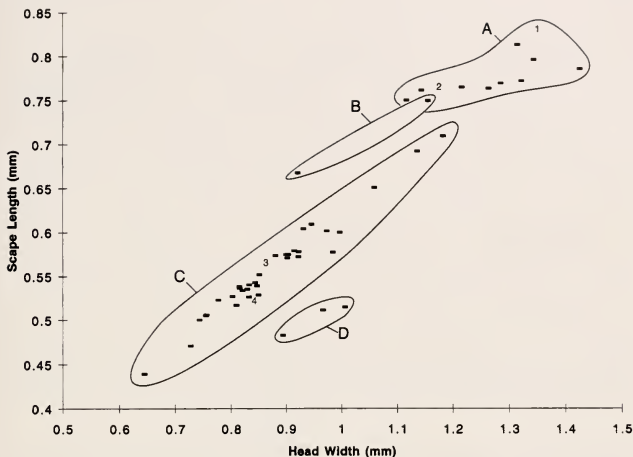
Fig. 10. Worker head width vs. scape length. Letters refer to clusters of measurements. Numbers refer to measurements of individual workers. A) *beltii*; B) JTL-002; C) *longiceps, pittieri* complex, JTL-003, JTL-007; D) JTL-001; 1) *beltii* type; 2) *stolli* type; 3) *pittieri* type; 4) *emarginatisquamis* type.

sity and an improved species-level no-
menclature (e.g. Hillis 1988 for the *Rana
pipiens* complex, Ward 1993 for the *Pseu-
domyrmex ferrugineus* complex).

However, applying a phylogenetic spe-
cies concept is premature in situations like
the *A. pittieri* complex, where there are
data on differentiation, but they are insuf-
ficient to identify monophyletic groups.
The phylogenetic species concept may not
even be appropriate if the character dis-
continuity is a purely local phenomenon
generated by strong selection or other con-
temporary mechanisms, in which case the
differentiation is not due to a history of
lineage splitting and subsequent diver-
gence. To address this level of uncertainty
regarding species boundaries, I have re-
ferred to species complexes rather than
polytypic species. The observed character

discontinuities are not "captured" in any
official nomenclature, but use of the term
"complex" will alert a user to the presence
of complex character patterns within the
group, and the possibility of future reso-
lution into multiple phylogenetic species.

A phylogenetic species concept requires
autapomorphies for species. Adherence to
this approach should result in greater cau-
tion being applied to the naming of new
species and the matching of local species
to types from distant localities. In the case
of Costa Rican *Azteca*, local species are de-
fined phenetically, as clouds of points in a
metric character space. Queens from sur-
rounding countries are often very similar
to one of the Costa Rican species, but not
exactly the same. As additional queens
from other areas are measured and added
to figure 2, the plot gradually fills in. The
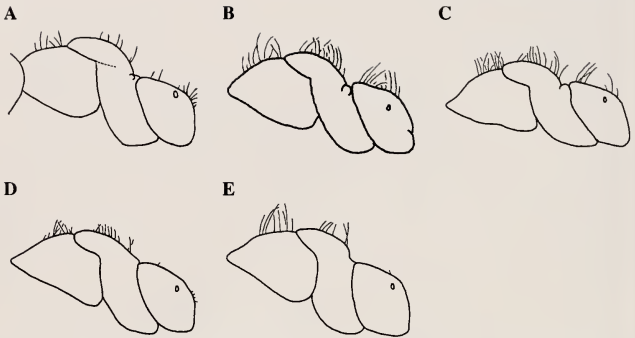
Fig. 11. Worker lateral mesosoma, showing dorsal pilosity. *beltii* (drawn from type. JTL-003 is similar). B. *pittieri* complex from Pacific slope near Monteverde (*longiceps* and JTL-007 are similar). C. *pittieri* complex from La Selva. D. JTL-002. E. JTL-001.

phenetic clouds of points drift around geographically. When a queen from a distant locality falls within one of the Costa Rican phenetic clouds, it is uncertain whether this is due to shared ancestry or convergence on that morphometric point. For example, *A. pittieri* complex queens from above 500m near Monteverde are very similar to the type of *A. patruelis* from Mexico. However, the ventral setae on the petiole are not exactly the same. Perhaps molecular markers or newly discovered morphological traits will reveal that the Monteverde population of *A. pittieri* and Mexican *A. patruelis* form a monophyletic group. However, I think it just as likely that there is a complex mosaic of species between Costa Rica and Mexico, and the similarity is purely coincidental (or parallel response to similar selection). In other words, even though Monteverde *A. pittieri* and Mexican *A. patruelis* are phenetically very similar, there are no well-supported synapomorphies uniting them. For these reasons, I have often relied on unavailable code names for locally-defined species,

pending larger character sets and placement in a global context.

Further understanding of Costa Rican *Azteca* will require population samples from additional localities within the country. To understand the stem-nesting *Azteca* at a global level will require similarly thorough sampling throughout the Neotropics. The lack of similar specimen coverage from other parts of the Neotropics is a severe impediment to global definitions of species.

## Possible Determinants of Character Distribution in *A. pittieri* Complex

What mechanisms might produce the patterns of character variation seen in the *A. pittieri* complex? Possibilities include contemporary selection pressures and secondary contact following anthropogenic landscape changes.

Stabilizing selection may vary geographically, producing geographic variation in the presence of gene flow (Endler 1977). Selection may be strong, for the reasons noted above, increasing the likeli-

Fig. 12. Map of Costa Rica, showing localities appearing in text. Dotted line is approximate divide between Atlantic and Pacific drainages. Atlantic lowlands and southern Pacific lowlands are evergreen wet habitats with dominant South American affinities; northern Pacific lowlands are seasonal dry habitats, with dominant Mesoamerican affinities. C = Carara. P = Palmar Norte on the Río Grande de Térraba. S = Santiago de Puriscal. Buenos Aires is in the Valle del General. Bar below Monteverde is location of elevational transect.

hood that queen morphology would close-ly track geographic variation in selection regime. Selection gradients can produce discontinuous character variation such as that seen below Monteverde (Endler 1977). There may be a selective trade-off affecting queen size. Smaller queens would be less costly in terms of resources and could disperse farther. Larger queens with greater muscle mass in the head would have larger and more powerful mandibles for chewing into *C. alliodora*

nodes. Montane plants subject to cool, windy conditions often have thick, gnarled stems, reflecting a greater invest-ment in structure (Lawton 1984). *Cordia al-liodora* at higher elevations may thus have relatively thicker-walled nodes than at lower elevations, which would tip the se-lection balance in favor of relatively larger queens.

An alternative explanation is secondary contact and intergradation of previously isolated forms. Rapidly changing land use
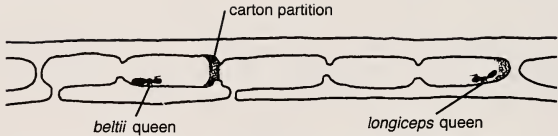
Fig. 13. Sagittal section of *Triplaris melaenodendron* branch multiply occupied by queens of *Azteca beltii* and *longiceps*. Note that the two queens occupied chambers that were formerly continuous across perforated septa, but were subsequently separated by an asymmetrical plug of carton, with concave shaped side facing *beltii*.

in Costa Rica may be causing dramatic changes in distribution and dispersal of *C. alliodora* ants (and possibly also creating new and shifting selective regimes). In recent decades the Atlantic lowlands have gone from nearly unbroken rainforest to a largely agricultural landscape. It is unknown what the prehistoric distribution of *C. alliodora* was, but currently it is a very common pasture tree. It is a candidate species for plantation forestry, and there are several plots of various ages at La Selva. The La Selva *A. pittieri* exhibit high variance, ranging from relatively small queens with reduced propodeal pilosity to relatively larger queens with greater propodeal pilosity. A few queens examined from south of Limón exhibit the former condition. At La Selva, we may be witnessing a dynamic invasion and/or hybridization process as formerly Pacific slope forms spread with agricultural development and come into contact with Atlantic lowland rainforest forms. Prior to extensive land clearing, there may have been allopatric populations of *C. alliodora* containing morphologically differentiated populations of the *A. pittieri* complex. *Cordia alliodora* requires bare ground and high insolation to establish (J. Haggar, pers. comm.). On the Atlantic slope, trees may have been restricted to highly dynamic river margins where rivers meandered across the coastal plane. Queens with relatively short, wide heads and reduced propodeal pilosity may represent the original Atlantic lowland form, and thus

should be widespread and associated with large areas of primary forest. The mid-elevation Pacific slope form with larger head and greater propodeal pilosity may have dispersed eastward with land-clearing, or been transported with nursery stock, and may occur as pockets of invasion or else closely associated with extensive land-clearing.

## The Role of Local Faunas

The above discussion illustrates some of the differences between locally and globally defined species. Sorting local species can often be done simply and quickly, using highly accessible characters. The task of global revisions is a much greater challenge, requiring large specimen bases and the use of different character systems, often those requiring dissection or molecular analysis. Ideally, large effort should go to the immediate production of global revisions, from which the clarification of local faunas will be a by product. However, publication of local faunas prior to a global understanding of taxa serves several purposes. For the systematist, local faunas provide clues to characters that differentiate locally sympatric species, and these characters may be useful in global studies. Local faunas give the field collector an idea of what to expect in local communities, and the kind of sampling effort required to adequately sample a region. They also provide identification tools, which may inspire non-systematists to use the group for study, which in turn may

increase the importance of systematic study of the group. For the non-systematist, regional faunas provide a realistic assessment of diversity, and one hopes prevent the conflation of species that is so common in ecological studies of arthropods. Finally, conservation efforts in particular regions require immediate taxonomic knowledge of the fauna, and cannot wait for the painstaking global revision of groups.

## ACKNOWLEDGMENTS

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# Synonymy of the Genus *Occipitalia* Richards, 1978, with *Clypearia* de Saussure, 1854 (Hymenoptera: Vespidae; Polistinae, Epiponini)

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*Abstract.*—The genera *Occipitalia* and *Clypearia* are synonymized. The single species included in *Occipitalia*, *sulcata* (de Saussure), is the sister-group of *Clypearia*, based on morphological and behavioral characters. This species is intermediate in the morphological and nest architectural characters defining *Clypearia*. There is thus no useful reason to separate these genera.

In December of 1990, JMC and JWW collected six colonies and numerous individuals of the paper wasp *Occipitalia sulcata* (de Saussure) along the Amazon and Napo Rivers in Loreto, Peru. The collection included the hitherto undescribed male and larva of this species. The nests represent a larger sample than any previously available, and detailed study of nest architecture, along with adult and larval morphology, lead us to the conclusion that the genus *Occipitalia* Richards should be synonymized with *Clypearia* de Saussure.

## TAXONOMIC HISTORY

*Clypearia* de Saussure, 1854, was described as a subgenus of *Polybia* Lepeletier for the single species *apicipennis* (Spinola, 1851). Duke (1904: fig. 4) first described the nest of this species, noting its similarity to that of the genus *Synoeca* de Saussure. The nests of these taxa are what is now termed astelocyttarus: with combs lacking pedicels, built directly on the substrate, and covered with an envelope. Duke (1905a) first raised *Clypearia* to genus (Richards 1978: 191, cited Duke 1905b), in part because of its nest architecture, on which basis he grouped *Clypearia*

with *Synoeca* and *Metapolybia* Ducke rather than *Polybia*. The nests of *Polybia* are termed phragmocyttarus: with a series of stacked combs, each having an envelope and built on the envelope of the preceding comb. Ducke (1906) described another species of *Clypearia*, *angustior*, and Araujo (1951) illustrated its nest and described the male. As noted by Richards (1978: 192), *Clypearia* is a "genus whose species are rather rare in collections," and received little further attention in the literature until Richards' monograph, in which he described five new species. Since then, Jeanne (1979) figured the nest of *weyrauchi* Richards, Jeanne (1980) described meconium extraction in *apicipennis*, Jeanne *et al.* (1983) described sternal glands in this species, and Snelling (1983) and Sarmiento (1994) provided range extension records for *naumanni* Richards. The genus was discussed in the chapters by Carpenter, Jeanne, Wenzel, and Downing in the recent book, *The Social Biology of Wasps* (Ross and Matthews 1991).

In his monograph, Richards (1978) described the genus *Occipitalia* to include two species formerly placed in *Polybia*. These were *sulcata*, the type species, and *traili* Cameron. Richards justified the new

genus as follows (p. 198): "It has always been noted that *P. sulcata* and *P. traili* (*P. ujhelyi*) were very unusual species of *Polybia* but they were rare and nothing was known about their biology. Dr W. D. Hamilton found them in some numbers on the Amazon and discovered that the nests are astelocyttarus, quite unlike any species of *Polybia* (all phragmocyttarus). I think therefore it is appropriate that they should be generically separated since they also lack the pronotal fovea found in all other *Polybia*."

Richards' phylogenetic tree for the genera of Polistinae (his fig. 40) showed *Occipitalia* as most closely related to *Clypearia*, with both genera sharing the state of larval mandibles "rather long, two teeth" (9a in his table 1; the origin of this state is not unique on Richards' tree, but as discussed by Carpenter (1991), that diagram is not based on a parsimonious mapping of the characters presented by Richards. Note also that Richards described the larva of *Occipitalia* on p. 198 as "with one long apical tooth," contradicting both his tree and key to larvae). Richards grouped *Occipitalia* + *Clypearia* in a clade including *Synoeca* and *Metapolybia*, based on absence of the pronotal fovea, secondary spiracular entrance raised and narrow, and nests astelocyttarus.

Snelling (1981) treated *Occipitalia* as a synonym of *Polybia*, stating only (p. 374) that he did not consider it "sufficiently distinct from *Polybia*." That action was certainly unjustified. But then Raw (1985) split *Occipitalia*, describing the new genus *Asteloeca* for *traili*. Raw stated (p. 185): "Morphologically, the two species are quite different so I compared them with related genera. The genus is not monophyletic, but neither of the two species is sufficiently close to any recognized genus to justify a transfer." Raw considered that *Occipitalia* and *Asteloeca* formed "a natural group" with *Synoeca*, *Metapolybia* and *Clypearia*, and compared 11 characters among these five genera. He did not discuss states

in other genera, but concluded (p. 187) that "*Asteloeca* lies closer phylogenetically to *Metapolybia* than to *Occipitalia*." About the relationships of *Occipitalia* he came to no conclusions, although his table 1 showed it differing from *Clypearia* in only three characters, fewer than the four differentiating *Asteloeca* and *Metapolybia*.

Carpenter's (1991) analysis of generic relationships in Polistinae established a monophyletic group comprising *Occipitalia sensu stricto*, *Asteloeca*, *Clypearia* and *Metapolybia*, based on the raised pronotal prominence (= anterior pronotal carina; see Carpenter 1989), but did not resolve their interrelationships. The sister-group of these four genera is *Synoeca*, based on loss of the pronotal carina and astelocyttarus nests. These five genera are a lineage within Epiponini, a tribe that comprises all of the neotropical polistines that found new colonies by swarms (Carpenter 1993). Wenzel's (1993) detailed analysis of nest architecture likewise recognized a lineage comprising these five genera; he did not detail the characters supporting this clade, but it was based on three features: comb built on bark without pulp foundation, material of coarse chips, and envelope reinforcement by secretion. His results differed from Carpenter's, which were based mostly on adult morphology, in placing *Synoeca* as sister-group of *Metapolybia*, with *Asteloeca* most closely related in turn; relationships of *Occipitalia* and *Clypearia* were not resolved further. Wenzel and Carpenter (1994) combined the data matrices from Carpenter (1991) and Wenzel (1993), and added unpublished larval characters provided by JK; their analysis established *Occipitalia sulcata* and *Clypearia* as sister-groups. Characters supporting the branches were not detailed, but this relationship was based on six characters: tempora narrowed, forecoxa rounded, propodeal concavity broad and deep, metasomal segment I subpetiolate, two larval mandibular teeth with subsidiary tooth distinct, and comb heavily rein-

forced and obscuring initial construction. We now take up the matter of the distinction between *Occipitalia* and *Clypearia*.

## ADULT MORPHOLOGY

Richards' (1978) concept of *Occipitalia* being a composite of what are now considered two genera, his keys and diagnoses do not accurately distinguish *O. sulcata* from *Clypearia*. The crucial character given in his generic key (p. 10, couplet 16), "Gena narrow even in ♀" vs. "Gena normal, wide at least in ♀," is more precisely described in his diagnosis of *Clypearia* (p. 191) as "Outer orbits (gena) very narrow, at top never more than half as broad as eye, below retreating and much narrower." His key to species of *Occipitalia* (p. 198) separates *O. sulcata* from *A. traili* by, *inter alia*, "Gena about half as wide as eye." To be sure, *O. sulcata* has the gena wider than any species of *Clypearia*, but it is narrower than is typical in other epiponines. As well, the state is variable within *Clypearia*, with *C. weyrauchi* having the gena wider than other species we have examined (*viz.*, *C. apicipennnis*, *C. angustior*, *C. duckei* Richards and *C. naumanni*). Distinguishing *Occipitalia* from *Clypearia* on this basis is simply arbitrary partitioning of continuous variation. A similar situation for this particular character has been shown in the synonymy of *Pseudochartergus* with *Protopolybia* by Carpenter and Wenzel (1990).

Of the other characters discussed in Richards' diagnoses and keys, for only four are any differences at all stated between *O. sulcata* and *Clypearia*. These are, *seriatim*: (1) mandibles "rather long" in *Clypearia* vs. "short" in the composite diagnosis of *Occipitalia*. The mandibles of *Asteloeca* differ from *Clypearia*, not so much in length as in having the external margin drawn out into a flange; *O. sulcata* does not differ from *Clypearia*. (2) Clypeus "much longer than broad" in *Clypearia* vs. "about as wide as long" for *O. sulcata* in the key to species of *Occipitalia*. That dif-

ference holds, but again is continuous variation, with *O. sulcata* having the clypeus narrower than, say, *Asteloeca* (clypeus "much wider than long" in the same key). And again, the character is variable within *Clypearia*, with *C. weyrauchi* having the clypeus wider than the other species. Moreover, the clypeal apex is described as "feebly truncate" in both *Clypearia* and *O. sulcata*, a derived condition (*O. sulcata* having the truncation less pronounced and slightly narrower than in species of *Clypearia*), and the clypeal-eye contact in both is about as long as the width of the antennal socket. (3) Fore basitarsus "two and a half or (*C. angustior*) three times as long as broad" in *Clypearia* vs. "three and a half times as long as broad" in the composite diagnosis of *Occipitalia*. Again, this is continuous variation, and again even within *Clypearia*, and the character offers only an arbitrary basis on which to distinguish the two genera. (4) Metasomal segment I, which is of variable form in *Clypearia*; the petiole in *O. sulcata* is within this variation, similar in form to the petiole of *C. angustior*.

*Occipitalia* and *Clypearia* are thus at best poorly differentiated by the characters treated by Richards (1978). Taking up the characters listed by Raw (1985: table 1), of the three characters differentiating *Occipitalia* and *Clypearia*, two have already been discussed: #4, length of the clypeus, and #10, width of the gena (note that Raw listed an intermediate state for this latter character in *Occipitalia*). The remaining character, #3, whether the antero-dorsal edge of the propleura is folded out along its entire length or only in part, had only *Occipitalia* with the former state. The difference between this taxon and the others is minor at best, but in any case is simply an autapomorphy of *O. sulcata*.

Turning now to characters of the male, these show the usual sexual dimorphism in Polistinae—a statement that could replace most of the descriptions of males in Richards (1978). The antennae, clypeus,
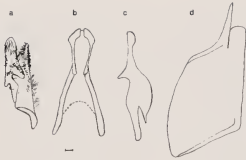
Fig. 1. Male genitalia of *Occipitalia sulcata*. a, volsella, lateral view; b, aedeagus, ventral view; c, aedeagus, lateral view; d, paramere, lateral view. The scale bar is 1 mm.



Fig. 2. Male genitalia of *Clypearia duckei*. a, apex of aedeagus, ventral view; b, volsella, lateral view; c, aedeagus, ventral view; d, aedeagus, lateral view; e, paramere, lateral view. The scale for b–e is the same as Fig. 1; a is drawn at about twice that magnification.

tempora, metasoma, and so forth, differ between the sexes *O. sulcata* in just the same way as is typical of other polistines. The more critical source of characters is male genitalia, and this character system was scarcely discussed in Richards' monograph. He briefly summarized (1978: 5) an unpublished survey of polistine genera by Vreugdenhil and van der Vecht, but the *Occipitalia* studied was *A. traili*. Of the species of *Clypearia*, males were known for only two, *C. angustior* and *C. duckei* Richards. Araujo (1951) published a photograph showing the genitalia in general aspect, but the genitalia of the single male specimen of the latter species were not studied by Richards. We have examined two species of *Clypearia* (*apicipennis* and *naumanni*) and the hitherto-undescribed male of *O. sulcata*, as well as *Asteloeca*, all five species of *Synoeca*, and five of *Metapolybia* (*bromelicola* Araujo, *cingulata* (F.), *docilis* Richards, *suffusa* (Fox) and an undescribed species).

The male genitalia of *O. sulcata* are illustrated in Fig. 1, and those of *C. duckei* in Fig. 2. The genitalia of the genera examined are basically similar, with some differences in detail of the shape of the aedeagus noted. In particular, the aedeagus of *Synoeca* is more attenuate than in the other four genera. These latter genera have the aedeagus apically broader, and the cuticular rods which form the aedeagus are more strongly sclerotized. As-

sessing the significance of this character will require thorough investigation of the other genera of Epiponini: it may be an autapomorphy of *Synoeca*, or else support the monophyly of a group comprising the other four genera. In any event, the male genitalia do not support the distinction of *Occipitalia* and *Clypearia* (cf. Figs. 1 and 2). Aside from the aedeagus, the only notable feature is the volsella of *S. surinama*, which has the digitus much more sharply pointed ventrally than any of the other species, an evident autapomorphy.

Regarding the three characters of the male genitalia mentioned by Richards (1978: 5) as distinguishing two groups of genera, the genitalia of *O. sulcata* fall into Group II (as do the other genera discussed here). However, the two groups are not distinct as stated. First, as shown in Fig. 1, Group II genitalia may have the aedeagus "serrate" beneath; the serration is simply very fine. Second, the medial lobes of the aedeagus (ventral process of Richards) differ in shape and size, rather than attachment to the cuticular rods. But it is not clear how, if at all, the two groups may be distinguished by the medial lobes, for these show considerable variation. And concerning the third character, hairs on the parameral spine, these are lacking in *O. sulcata* and the other genera examined

here. But this feature varies within Group I (*viz.*, a few short hairs in *Parachartergus*). The distinction of the two groups should be re-examined in the context of a comprehensive investigation of all the polistine genera, a task we will take up elsewhere.

## LARVAL MORPHOLOGY

Richards' (1978) key and description of the larva of *Clypearia* was based on a single species, *C. duckei*. He did not state on which species his description of *Occipitalia* was based, but it was *A. traili*, according to an unpublished manuscript preserved in the British Museum (Natural History). JK has studied the larva of *O. sulcata*, and it and *C. duckei* have the same condition of two larval mandibular teeth, with the subsidiary tooth distinct (secondarily derived condition). This is a synapomorphy between these two taxa. The only differences among the remaining larval features studied are: (1) setae on the cranium are very sparse and minute in *C. duckei* and are thick bristles in *O. sulcata*, the latter condition being more derived; (2) setae on the venter of thoracic segment I through abdominal segment I are thin and short in *C. duckei* vs. thick bristles in *O. sulcata*, the latter condition again being more derived; and (3) body spicules on anterior four or five segments are blunt or minutely dentate in *C. duckei* vs. pointed in *O. sulcata*, the former state being derived. These characters are often polymorphic or variable within other polistine genera, and so we view these differences as minor, having no more than specific value.

## NEST ARCHITECTURE

As already mentioned, the nests of several species of *Clypearia* have been described and illustrated. The nest of *O. sulcata* has also been illustrated; as noted by Richards (1978: 199), Evans and West-Eberhard (1970: fig. 92, not 85 as stated by Richards) figured its nest as "*Clypearia* sp."

Similar nest architecture has been regarded as evidence of close relationship by authorities on Polistinae (see, e. g. de Saussure 1853–1858; Ducke 1914; Richards 1978). Much of this view is now supported by modern analytic methods whereas other aspects are not (Carpenter and Wenzel 1990; Wenzel 1991, 1993). The regions where classical views differ from modern views are generally those where taxa are poorly known or where concepts of the polarity of character state transformations are critical. Both of the genera in question here are still poorly known in comparison to other South American genera. Statements not followed by a citation are based on specimens in the private collection of W. D. Hamilton (*C. duckei* and *A. traili*), and specimens collected by JMC and JWW and deposited in the AMNH.

The relevant aspects of nest architecture are those of the neotropical taxa that build combs as sessile structures (no supporting pedicel), and subsequently expand the nest along the substrate contiguously with the primary comb (astelocyttarus *sensu* Richards 1978) rather than by building a new comb upon the exterior of the primary envelope (phragmocyttarus *sensu* Richards). *Polybia* builds nests of the phragmocyttarus type, quite unlike those of the genera discussed here (*Asteloeca, Clypearia, Metapolybia, Occipitalia, Synoeca*). Although they are not all relevant to the morphological determination of the placement of *O. sulcata*, these latter five genera are discussed below because of overlapping architectural variation for which character polarity has yet to be determined. Taken in turn, the major elements of comparison are: the comb either entirely *versus* only partly attached to the substrate; the envelope thin and showing the original lines of construction *versus* later reinforced by addition of more pulp to the surface; and the structure of the nest entrance.

If the support is broad, the initial comb will be built entirely sessile upon it. If the

support is a narrow branch, *C. duckei*, and *A. traili*, project a planar comb beyond the margin of the branch, a trait that is probably plesiomorphic given that it is also found among many phragmocyttarus genera (Wenzel 1991: figs. 48–58). In contrast, *Metapolybia* and *Synoeca* will wrap a comb around a narrow branch so that all cells have their bases on the substrate, as perhaps will *C. angustior* (Araujo 1951). *O. sulcata* and *C. apicipennis* are intermediate between these extremes. Nests of *O. sulcata* will wrap partly around a narrow support before being extended beyond it. One specimen from near Iquitos, Peru (AMNH 901231–1), has cells around nearly half the circumference of a branch; however, these cells are oriented through only about 90 degrees relative to each other, rather than representing radii of the curve, and the bases of yet more lateral cells are built free of the substrate. Very similar to this is *C. apicipennis*, which builds all brood cells sessile on the branch, inside a bulging envelope. The space between the brood comb and the envelope is filled with structural, non-brood "cells" (Jeanne, pers comm. to JWW).

Nests of *C. duckei* and *O. sulcata* are built of a rough carton. The envelope rises abruptly from the substrate and is reinforced and disguised by subsequent addition of many fine particles that may differ in color and shape from the original carton (a trait widespread among epiponines), but *C. duckei* envelope may also have windows of pure secretion elsewhere. In contrast, both nests of *C. weyrauchi* collected by Jeanne (1979) and Weyrauch (now in the Fundación e Instituto Miguel Lillo, Tucumán, Argentina, and strikingly similar to that photographed by Jeanne) had envelopes that arose at a shallow angle from the substrate and were composed of fine, straight parallel lines of construction. *C. weyrauchi* and *A. traili* build a very smooth envelope that is glossy and thoroughly covered with secretion after completion. Intermediate be-

tween these two pairs of species, a nest of *C. angustior* was built by application of pulp in tortuous, fine stripes, short and spread in all directions; although the surface was rough, there were windows that consisted of pure secretion with no pulp (Araujo 1951: 55). This description would fit most *Metapolybia* nicely. When the back of the comb projects beyond the support, *C. duckei* and *O. sulcata* thicken it with pulp, obscuring cell bases. The comb sides are also thickened and do not show cell contours, and the cells may be partly flattened so as to provide a smooth exterior wall (*C. duckei*). In contrast, the exterior of a *C. angustior* nest (which did not project beyond the support) was reported to reflect the positions of cell walls (Araujo 1951), as does that of *A. traili* (which does project), and often *Metapolybia* and *Synoeca*. Jeanne's *C. apicipennis* did not have an envelope in contact with the walls of the brood cells (above), and there was no evidence of secondary thickening of the envelope anywhere (Jeanne, pers. comm. to JWW). *C. weyrauchi* (entirely sessile on the substrate) envelopes do not contact the cells. The *Asteloeca* nest collected by JMC and JWW (AMNH) and one recorded by W. D. Hamilton (unpublished notes) indicate that *A. traili* is unique among these species in that the comb back is extended beyond the substrate, but not reinforced by additional pulp, so that rows of convex cells bottoms are clearly visible.

In all astelocyttarus genera, expansion of the nest is accomplished by adding a new comb adjacent to, and contiguous with, the older comb. *Synoeca virginea* will sometimes build cells on the envelope (van der Vecht 1967; Overal 1982), but this is not known as a regular habit among the other *Synoeca* or other genera considered here. Richards' (1978: 199) statement regarding *Occipitalia* that "at a later stage cells were built on the envelope and covered with a new one" is based on notes by R. L. Jeanne, who is of the opinion that these cells were not normal and not part

of the regular comb that expands along the branch (Jeanne, pers. comm. to JWW). Ducke (1910) said that his nest of *C. apicipennis* was enlarged like *Synoeca*, but with additions more irregularly juxtaposed, and his photograph shows a nest growing in several sections along a branch. When *Synoeca* and *Metapolybia* build on an inclined surface, the expansion is directed upward. The new structure generally encompasses the original entrance hole (which is at the periphery of the envelope in the upper part of the nest), concealing it. In these two genera, the entrance is built as a short collar and is built separately from the last gap in the incipient envelope. *C. angustior* (Araujo 1951) and *C. duckei* both build short collars, the former peripherally and upward, the latter at least peripherally, perhaps directed upward (it is not yet known how these structures relate to the last gap in construction). In contrast, *C. apicipennis* has an entrance at the top, but without any collar or spout (Jeanne, pers. comm. to JWW). *O. sulcata* and *C. weyrauchi* have no collar or spout at the entrance, which in both cases is the last remaining gap in construction and is more central rather than peripheral in the envelope. Neither Jeanne's (1978) nor Weyrauch's nest of *C. weyrauchi* showed evidence of expansion, but one nest of *O. sulcata* that was apparently expanded (AMNH 901231–4) had two entrances, one at the center of the old envelope and one at the center of the contiguous new addition, as would be expected if the new envelope does not overlap the old entrance. *A. traili* has the entrance in the center of the envelope and built at the last remaining gap, but it orients a short collar downward.

Finally, two other behavioral traits are noteworthy and deserve more attention. First, all of the six *O. sulcata* colonies JMC and JWW collected (and the several more they did not) were in close association with the nests of *Azteca* ants, sometimes only centimeters away. Hamilton (1972:

225), Richards (1978: 199, discussing nests collected by Hamilton) and Chadab (1979: 162) have all commented on the association, which appears to be obligate. It would be interesting to know to what extent the species of *Clypearia* share this trait; evidently *C. apicipennis* and *C. weyrauchi* do not, but Richards' (1978: 196) description of *C. duckei* gave label data as "in an ant complex" and Chadab (1979: table 49) listed this species as nesting with *Azteca* in Limoncocha, Napo Province, Ecuador. Secondly, some of these species remove the meconium through the mouth of the cell after an adult emerges (Jeanne 1980). Jeanne's study found that such hygienic behavior was present in *C. apicipennis*, *O. sulcata*, and *A. traili*, but not in *C. weyrauchi*, and evidently not in *Synoeca* or *Metapolybia*. At the time of Jeanne's publication, Richards had recently placed *O. sulcata* and *A. traili* in his new genus *Occipitalia*, so the fact that they shared this trait made more sense than it does now in light of what we propose to be a rather distant relationship between them.

The evidence from nest architecture is somewhat ambiguous as to the correct placement of *O. sulcata*, but several things are clear. The range of variation found in *Clypearia* for architectural traits (such as attachment to the substrate, reinforcement of original carton, and placement and structure of the nest entrance) includes the states typical of *O. sulcata*. Indeed, the species of *Clypearia* appear to have no unique synapomorphy among these traits to distinguish them from *O. sulcata*. Furthermore, *A. traili* is not more closely allied to *O. sulcata* than to *Clypearia* species, contrary to Richards' opinion, and would be placed awkwardly anywhere among the known forms.

## CONCLUSION

We have documented that there is no adequate basis, in adult or larval morphology or nest architecture, for separating *Occipitalia* from *Clypearia* at the generic

level. Regarding adult morphology, the features by which these genera differ are nothing more than the arbitrary partitioning of continuous variation. For the larvae, there are only minor, specific differences between the two species known. And nest architecture does not differ.

Richards (1978) was correct to remove *O. sulcata* and *A. traili* from *Polybia*. But his original concept of *Occipitalia* was not monophyletic, instead it was a composite of two distantly related species. Raw (1985) correctly separated *A. traili* from *Occipitalia*; as concluded by Raw and shown in Wenzel and Carpenter (1994) *A. traili* is more closely related to *Metapolybia*, as established by the synapomorphies of mandibular edge raised, first metasomal tergum abruptly expanded apically, and thyridium elongate. But with the recognition of *Asteloeca*, the distinction between *Occipitalia* and *Clypearia* is also largely removed. Synonymy of these two genera is thus indicated, and we establish that synonymy now.

*Clypearia* de Saussure, 1854: 165, as subgenus of *Polybia* Lepeletier, 1836.

Type species: *Polistes apicipennis* Spinola, 1851, by monotypy.

*Occipitalia* Richards, 1978: v, 11 (key), 198, as genus. NEW SYNONYMY.

Type species: *Polybia sulcata* de Saussure, 1854, by original designation.

*Occiitalia* [!] Richards, 1978: 16. Incorrect spelling of *Occipitalia*.

## ACKNOWLEDGMENTS

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# *Plynops,* a Peculiar New Genus and Ten New Species in the Tribe Euphorini (Hymenoptera: Braconidae: Euphorinae)

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*Abstract.*—*Plynops* Shaw, a new genus in the tribe Euphorini, is described and illustrated. The genus is characterized by bizarre modifications of the female head, which are hypothesized to be adaptations for host manipulation. The phylogenetic affinities of the genus are examined and a sister-group relationship with *Cryptoxilos* Viereck is hypothesized. Ten new species of *Plynops* are described: *braziliensis, carinatus, edwardi, falcatus, hansoni, masoni, megakephalos, minutus, pilatus,* and *riedeni.* A key to species is given, and phylogenetic relationships among the species are briefly discussed.

## INTRODUCTION AND HISTORICAL REVIEW

For several years the existence of an unusual new euphorine genus with bizarre head modifications (Figs. 1, 5–21) has been known among North American braconidologists, but until now the genus has not been described or discussed in the literature. The purpose of this paper is to describe the genus, so that it may be included in the *Identification Manual for New World Genera of the Family Braconidae,* currently in production.

The earliest known specimens of this genus (three males) were collected by Fritz Plaumann in Nova Teutonia, Brazil, in 1940 and 1941, but their significance was not recognized until recently. Two specimens were sent to the British Museum (Natural History) in London, where they were accessioned in 1957, and another was sent to the Canadian National Collection at Ottawa. However, these specimens remained essentially lost in the collections until they were recently rediscovered and sent to me by Drs. D. Quicke and M. Sharkey, respectively.

The first person apparently to recognize the identity of this taxon as a new genus was Mr. C.F.W. Muesebeck, working at the U.S. National Museum in the 1950s. A single female specimen was reared from *Canavalia* seeds in Nogales, Mexico, in May of 1953, and was later sent to Mr. Muesebeck for identification. The specimen now bears his identification label as "n.g. near *Euphorus*" (a junior synonym of *Leiophron*). However, Mr. Muesebeck did not publish on the new genus and species, and subsequently the Mexican specimen was loaned to Dr. W.R.M. Mason at the Canadian National Collection, at Ottawa.

Many years later, early in 1984, I was fortunate to visit the Canadian National Collection where I met Dr. Mason and he showed me specimens of this remarkable genus. By that time he had accumulated only three more specimens, representing two more new species from Ecuador. He indicated to me that he had known about the new genus for many years, but had delayed publishing on it because of the scarcity of specimens. We examined the specimens together and we both agreed that the new genus very closely resembled *Cryptoxilos* Viereck in the form of the petiolar sculpturing (Figs. 2, 4), wing venation (Fig. 22), and ovipositor structure, but

that the head morphology was bizarrely apomorphic (with the face deeply concave and densely lined with setae, mandibles enlarged and hooked, and with unusual protruberances below the antennae). Dr. Mason indicated that he had coined a manuscript name for the new genus, which he called *Plynops*. Since he indicated to me that he planned to eventually publish on the new genus, I did not include the taxon in my subsequent studies of the Euphorinae (Shaw, 1985, 1987).

A few years later, around 1989, I began a collaboration with Prof. Paul Hanson, of the Universidad de Costa Rica, to help develop a textbook to the *Hymenoptera of Costa Rica*. As a result of this effort, dozens of Malaise traps were operated at sites throughout the country, and many thousands of specimens of Braconidae were collected and prepared for study. One of the unexpected surprizes of this project was the accumulation of several additional new species of this new euphorine genus, in substantially greater numbers than had previously been seen elsewhere. For the first time, a description of the genus based on substantial specimen series seemed possible.

In 1991 I contacted Dr. Mason about this project, and we agreed to collaborate on the description of this new genus. However, due to his untimely death late in 1991, our plans for a joint paper were circumvented. Later, Dr. M. Sharkey sent me all the specimens he was able to locate, but no manuscript was discovered. Consequently, I've endeavored to describe this new genus and ten included species. Other than adopting Bill Mason's proposed name for the genus, my work presented here is completely original. One new species included here is named as a patronym in honor of Dr. Mason, for his numerous contributions to the study of the Hymenoptera.

## METHODS

The morphological terminology used here follows that of Shaw (1985, 1987), ex-

cept for the wing venation terminology, which is adapted to conform to more recently adopted changes (Huber & Sharkey, 1993). To facilitate comparision with previous work, the wing venation terms of Shaw (1985) are given parenthetically in the descriptive section. Body length was measured from the front of the head to the apex of the metasoma, exclusive of the antennae and ovipositor. Ovipositor length was measured, in lateral view, relative to the length of the metasoma exclusive of the ovipositor. Acronyms for collections are given in the acknowledgments section.

Figs. 3–10 were done using the Environmental Scanning Electron Microscope at the Western Research Institute. Uncoated specimens were examined at operating voltages of 11–19 kV.

To examine the phylogenetic placement of the new genus, the taxon was coded for the 45 phylogenetically-informative characters examined by Shaw (1987) and added to the matrix for the tribe Euphorini (see tables 1 & 2 of Shaw, 1987). The revised matrix was analyzed using the Hennig86 program. Since the character list and matrix for the Euphorini is already published (Shaw, 1987), and all the character states for *Plynops* are given in the description below, the entire character list and matrix is not repeated here. The author will provide a diskette copy of the matrix to any interested reader.

## PLYNOPS Shaw, New Genus

*Head.*—Ocular setae present; inter-ocular distance broad, shortest distance between eyes greater than clypeus width; median frontal carina absent; frontal sculpture punctate medially; antenna with 11–19 flagellomeres; apical flagellomere with tip rounded or tapering to a rounded apex, not acutely pointed; scape length short, 2.5× scape width or less; occipital carina complete; malar space very short, less than ¼ eye height; face and clypeus indented medially and weakly (males) to strongly (females) concave; facial concav-

Figs. 1–2.   1. Head of *Plynops hansoni*, anterior view. 2. Metasomal tergum 1 of *Plynops hansoni*, lateral view.

ity moderately to densely setose; mandible elongated, but curved apically, degree of mandibular overlap less than ½ mandible length; maxillary palpus 5-segmented; labial palpus 2-segmented.

*Mesosoma.*—Mesonotal disc nitid; notau-

Figs. 3–4.   3. Head of *Plynops braziliensis*, dorsal view. Note coarse surface sculpture extending to vertex. 4. Metasomal tergum 1 of *Plynops braziliensis*, dorsal view.

li indicated antero-laterally by coarse rugo-punctate sculpture, medially punctate; scutellar disc nitid; propodeal sculpture areolate; propodeum convex, without medial or posterior impression; petiolar notch absent; forewing vein R1 (metacarpus) desclerotized, absent except weak pigmentation basally; forewing vein 3RS (radius) desclerotized distally, free from wing margin; forewing vein 2RS (first intercubitus) absent, except for short free stub apically; forewing vein r-m (second intercubitus) absent; forewing vein RS+M (first cubital abscissa) strongly curved; forewing vein M (second cubital abscissa) absent distad of RS+M; forewing vein m-cu (recurrent) absent; forewing vein M+CU (medius) present; forewing vein 1cu-a (nervellus) postfurcal, relative to vein M (basal); forewing vein 2CUa (discoideus) varying from short stub (virtually absent) to well-developed; forewing vein 2CUb (subdiscoideus) absent; forewing vein 2–1A (brachius) absent; hindwing vein C+SC+R (costella and subcostella) absent; hindwing vein RS (radiella) absent; hindwing vein cu-a (nervellus) absent; hindwing vein A (submediella) absent; hind femur length/width ratio less than 6.

*Metasoma.*—Petiole of segment 1 with tergum and sternum not fused; petiolar sculpture rugo-costate; petiolar shape narrow, less than 3× broader apically than basally, at most ¾ as long as metasoma beyond petiole excluding ovipositor; glymma absent; petiolar spiracles anterior to middle of segment; tergite 2+3 length shorter than ¾ length of metasoma beyond petiole excluding ovipositor, several following segments exposed; syntergum 2+3 not overlapping ventrally; lateral fold of syntergum 2+3 absent; lateral suture on syntergum 2+3 absent (latero-tergites not differentiated); ovipositor and sheaths long and straight, varying from 0.4–2.3× metasoma length.

*Phylogenetic considerations.*—Phylogenetic analysis of the revised data matrix for

the tribe Euphorini resulted in one most parsimonious cladogram with a length of 109 and a consistency index of 54, as calculated by the "mhennig*" and "bb" options of the Hennig86 program. Aside from the insertion of *Plynops* as the sistergroup of *Cryptoxilos*, the addition of this new genus did not alter the topology of the previously published cladogram for the Euphorini (Shaw, 1987). Application of sucessive approximations to character weighting (using the "m*; bb*; xs w; cc;" options) resulted in a single stable solution after two iterations, and that tree also had the same topology.

A sister-group relationship between *Plynops* and *Cryptoxilos* is indicated by five putative synapomorphies: forewing vein M+Cu present and somewhat curved, hindwing vein C+SC+R absent, metasomal syntergum 2+3 short, ovipositor long and straight, and ovipositor sheaths long. These conditions were previously interpreted as synapomorphies for *Cryptoxilos* species (Shaw, 1985), but the monophyly of *Cryptoxilos* is still indicated by the extremely narrow inter-ocular distance in females of that genus (the eyes are strongly convergent ventrally, and nearly touching).

The monophyly of *Plynops* is indicated by several putative synapomorphies: the extremely wide inter-ocular distance with the face broadly concave and densely setose, medially punctate frontal sculpture, strongly concave clypeus, mandible enlarged, presence of forewing vein 2CUa, and postfurcal position of forewing vein 1cu-a.

*Discussion.*—*Plynops* will key to subfamily Euphorinae without difficulty with existing keys to braconid subfamilies (e.g. M. Shaw & Huddleston, 1991; Sharkey, 1993; S. Shaw, 1995). In existing keys to genera (e.g. S. Shaw, 1985; Marsh *et al.*, 1987) *Plynops* will key to *Cryptoxilos*, from which it can be distinguished by the synapomorphic characters listed above.

The striking head modifications of fe-

male *Plynops* are so bizarre that it is tempting to speculate about their probable function, but aside from a few plant associations, nothing is known about the biology of *Plynops*. Since these head modifications are sexually dimorphic, being most strongly expressed in the female, it seems likely that these features are adaptations to grasping the host during oviposition. Other such host-manipulating adaptations are known in the Euphorinae: females of *Cosmophorus* grasp their host with enlarged mandibles and females of *Streblocera* have raptorial antennae (Shaw, 1985). Presumably such adaptations would be useful for coping with adult host insects, which may be both highly mobile and densely sclerotized, as compared with immature hosts. The actual hosts of *Plynops* are unknown, but given the similarity of ovipositor form it seems reasonable to speculate that like its sister-group, *Cryptoxilos*, *Plynops* may attack small, densely sclerotized hosts such as adult bark beetles (Scolytidae). The association of one species with legume seeds suggests the possibility that bruchids may be attacked. Thus, the peculiar head of female *Plynops* may function as a "beetle clamp." The deep facial concavity, dense setal pads, associated carina, tubercles, and protuberances could all fit neatly over a small, cylindrical insect such as a bark beetle, while the enlarged mandibles

could function to clamp the host in place. The median facial carina of *Plynops carinatus*, new species, is oriented such that it might fit between the elytrae of a beetle host. At least one specimen examined here demonstrates the feasibility of this ovipositional method: a specimen of *Plynops edwardi*, new species, died with the ovipositor fully extended anteriorly, along the venter of the body. It runs between the coxae and anteriorly between the closed mandibles (see Fig. 10). If my "beetle clamp" hypothesis is correct, then the facial concavities of *Plynops* are unique features adapted to the parasitization of particular host species, and may possibly serve as a "lock and key" mechanism. It is hypothesized that the morphologically-based species proposed here will eventually be found to have separate hosts, which actually fit well into the unique facial concavities of each wasp species.

*Etymology.*—From the Greek *plynos* meaning basin, and the Greek *ops* meaning eye or face. The name *Plynops* refers to the basin-like concavity of the face, between the eyes, that characterizes this genus. The name was suggested to me by Dr. W.R.M. Mason.

*Distribution.*—Mostly Neotropical in distribution, the genus ranges from Mexico and southern Florida south to Peru and Brazil.

*Type species.*—*Plynops hansoni* Shaw, new species.

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KEY TO THE KNOWN SPECIES OF *PLYNOPS*

1   Lateral portion of frons, on line directly between antennal insertion and median ocellus, coarsely punctate and dull (Fig. 3) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
–   Lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining (Figs. 1, 5, 7, 9) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
2 (1) Coarse rugo-punctate sculpture of frons ending roughly on line between lateral ocellus and compound eye, vertex smooth and shining; 15–19 flagellomeres . . . . . . . . . . . . . . . 3
–   Coarse rugo-punctate sculpture of frons extending posteriorly to vertex, crossing well beyond line between lateral ocellus and compound eye, vertex partly rough and dull (Fig. 3); 13–14 flagellomeres . . . . . . . . . . . . . . . . . .*Plynops braziliensis* Shaw, new species
3 (2) 15–16 flagellomeres . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
–   18–19 flagellomeres . . . . . . . . . . . . . . . . . . . . . *Plynops megakephalos* Shaw, new species

4 (3) Median area of facial concavity smooth and shining, without a vertical carina (Fig. 10)
......................................... ***Plynops edwardi*** Shaw, new species
– Median area of facial concavity with a strong vertical carina narrowly bordered by
coarse, dull punctation (Fig. 8) ................. ***Plynops carinatus*** Shaw, new species
5 (1) Facial concavity dorsally margined by a carinate edge that separates the concavity from
the frons (Fig. 12); area just below each antenna prolonged anteriorly as a roughly
triangular projection, in dorsal view (Figs. 5, 7, 9) ............................... 6
– Facial concavity not margined dorsally, grading smoothly onto the frons; area just below
each antenna not prolonged anteriorly ...................................... 8
6 (5) Head, in dorsal view, with the dorsal margin of the facial concavity forming a U-shaped
depression between the antennal insertions (Figs. 7, 9) ........................... 7
– Head, in dorsal view, with the dorsal margin of the facial concavity forming a V-shaped
depression between the antennal insertions (Fig. 5) .. ***Plynops hansoni*** Shaw, new species
7 (6) Triangular projection below antenna (in dorsal view) extending anteriorly beyond an-
tennal insertion for a distance equal to *twice* the diameter of the antennal socket (Figs.
9) .......................................... ***Plynops riedeni*** Shaw, new species
– Triangular projection below antenna (in dorsal view) extending anteriorly beyond an-
tennal insertion for a distance equal to the diameter of the antennal socket (Fig. 7)
......................................... ***Plynops masoni*** Shaw, new species
8 (5) Dorso-lateral areas of facial concavity only sparsely setose; facial setae normal: short,
straight, and not forming thick, brush-like pads; lower median area of facial concavity,
near dorsal clypeal margin, either with a single triangular projection, or none; 10–11
flagellomeres .................................................... 9
– Dorso-lateral areas of facial concavity densely lined with long, curved setae forming
thick, brush-like pads (Figs. 20–21); lower median area of facial concavity, near dorsal
clypeal margin, produced into *two* sharp, thorn-like spines (Fig. 21); 12 flagellomeres
......................................... ***Plynops pilatus*** Shaw, new species
9 (8) Mandible long and sickle-like (Figs. 6, 19); lower median area of facial concavity, near
dorsal clypeal margin, with a single triangular projection (Fig. 19); face, in lateral view,
with only a trace of a section visible in front of the eye, below the antenna, visible
portion narrower than antennal socket (Fig. 18) ..... ***Plynops falcatus*** Shaw, new species
– Mandible not so long and sickle-like (Fig. 17); lower median area of facial concavity,
near dorsal clypeal margin, without a triangular projection (Fig. 17); face, in lateral view,
with a distinct section visible in front of the eye, below the antenna, that is about as
wide as antennal socket (Fig. 16) ................. ***Plynops minutus*** Shaw, new species

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**Plynops braziliensis** Shaw, new species
(Figs. 3–4)

*Description of male.*—Body length 2.0–2.3
mm; lateral portion of frons, on line di-
rectly between antennal insertion and me-
dian ocellus, coarsely rugo-punctate and
dull; coarse rugo-punctate sculpture of
frons extending posteriorly to vertex,
crossing well beyond line between lateral
ocellus and compound eye, vertex partly
rugo-punctate and dull; 13–14 flagellom-
eres; forewing vein 2CUa well-developed,
sclerotized portion about as long as hind
coxa.

Color: head dark brown, except face yel-
lowish brown; antenna yellowish brown
basally, gradually darker brown apically;
mandible yellowish brown, except tips
reddish brown to black apically; palpi
pale brownish white; mesosoma, wing ve-
nation, and metasoma dark chocolate
brown; legs yellowish brown, except hind
coxa basally and tips of tarsi dark brown.

*Female.*—Unknown.

*Material Examined.*—Holotype: male,
Brazil, Nova Teutonia, 2.xi.1940, F. Plau-
mann, B.M. 1957–341, BMNH. Paratypes:
1 male, same data except 3.iv.1941,

Figs. 5–10. 5. Head of *Plynops hansoni*, dorsal view. 6. Mandibles of *Plynops falcatus* in closed position, anterior view. 7. Head of *Plynops masoni*, dorsal view. 8. Head of *Plynops carinatus*, antero-lateral view. 9. Head of *Plynops riedeni*, dorsal view. 10. Head of *Plynops edwardi*, antero-lateral view.

BMNH; 1 male, same data except 27°11'S, 52°23'W, 300–500m, 10.iii.1941, CNC.

*Distribution.*—At present known only from three specimens all from Nova Teutonia, Brazil. No other *Plynops* species have been recorded from Brazil.

*Biology.*—Unknown.

*Remarks.*—*Plynops braziliensis* can be distinguished from all other *Plynops* species by the more extensive coarsely rugo-punctate sculpture on the upper regions of the head (Fig. 3). Coarse rugo-punctate sculp-

ture of the lateral frons is a synapomorphy shared with three other species: *carinatus*, *edwardi*, and *megakephalos*, but none of these three have coarse rugo-punctate sculpture extending fully onto the vertex. Also, these three species have 15–19 flagellomeres, while *braziliensis* has 13–14 flagellomeres.

The recognition of *braziliensis* as a species poses a particular problem, since it is based entirely on males, while the three most closely related species are based entirely on females. Thus, it is impossible to judge to what extent the differences expressed in *braziliensis* may be due to sexual dimorphism, and the possiblility that *braziliensis* is actually the male of another species cannot be totally ruled out. Nevertheless, the variation noted above, along with the widely separated distributions of the populations involved, indicates that the best course of action at present is to hypothesize this as a separate species.

*Etymology.*—Named for the type-locality.

### Plynops carinatus Shaw, new species
(Fig. 8)

*Description of female.*—Body length 2.7 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, coarsely rugo-punctate and dull; coarse rugo-punctate sculpture of frons ending roughly on line between lateral ocellus and compound eye, vertex smooth and shining; 16 flagellomeres; median area of facial concavity with a strong vertical carina narrowly bordered by coarse, dull punctation; forewing vein 2CUa well-developed, sclerotized portion about as long as hind coxa; ovipositor length 1.4× metasoma length.

Color: head and antenna dark chocolate brown, except pedicel yellowish brown; mandible yellow, except tips reddish brown to black apically; palpi pale brownish white; mesosoma, wing venation, and metasoma dark chocolate brown, except membranous ventral parts of metasoma

white; legs medium to dark brown, except coxa and trochanters pale brownish white.

*Male.*—Unknown.

*Material Examined.*—Holotype: female, Ecuador, Napo Province, Huahua Surnaco, km. 44 on Hollin-Loreto Road, xii.1989, MT (Malaise trap), M.J. Wasbauer, H. Real, CNC. Paratype: 1 female, Ecuador, Pastaza Province, 25 km. N. of Puyo, 1000m, montane moss forest, 4.vii.1976, S. & J. Peck, CNC.

*Distribution.*—Known only from Ecuador.

*Biology.*—Associated with montane moss forest.

*Remarks.*—*Plynops carinatus* can be distinguished from all other *Plynops* species by the presence of a strong vertical carina, narrowly bordered by coarse, dull punctation, along the median area of the facial concavity (Fig. 8). In other respects it is quite similar to *Plynops edwardi* from Costa Rica, but that species lacks such a median carina, and the facial concavity is smooth and shining medially (Fig. 10). Also *Plynops carinatus* has darker leg coloration and the ovipositor is slightly shorter than in *Plynops edwardi*.

*Etymology.*—From the Latin *carina* for a ridge, in reference to the facial ridge that is diagnostic for this species.

### Plynops edwardi Shaw, new species
(Figs. 10, 13–14)

*Description of female.*—Body length 2.2–2.6 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, coarsely rugo-punctate and dull; coarse rugo-punctate sculpture of frons ending roughly on line between lateral ocellus and compound eye, vertex smooth and shining; 15–16 flagellomeres; median area of facial concavity smooth and shining, without a vertical carina; forewing vein 2CUa well-developed, sclerotized portion about as long as hind coxa; ovipositor length 1.5–2.3× metasoma length.

Color: head and antenna dark chocolate
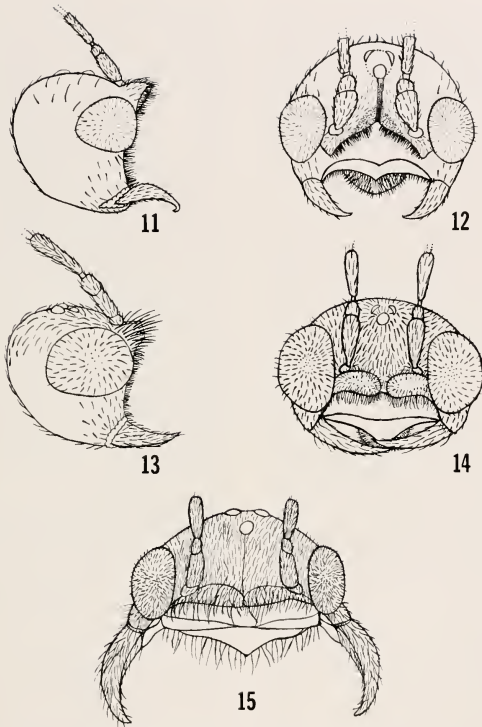
Figs. 11–15. 11. Head of *Plynops hansoni*, lateral view. 12. Head of *Plynops hansoni*, anterior view. 13. Head of *Plynops edwardi*, lateral view. 14. Head of *Plynops edwardi*, anterior view. 15. Head of *Plynops megakephalos*, anterior view.

brown, except scape and pedicel yellowish brown; labrum yellow; mandible yellow, except tips reddish brown to black apically; palpi pale brownish white; mesosoma, wing venation, and metasoma dark chocolate brown, except membranous ventral parts of metasoma white; legs light to medium brown, except coxa and trochanters white.

*Male.*—Unknown.

*Material Examined.*—Holotype: female, Costa Rica, Puntarenas Province, Golfo

Dulce, 24 km. W. Piedras Blancas, 200m, iii-vi.1990, P. Hanson, RMSEL. Paratypes: 1 female, same data; 1 female, same data except xii.1989-iii.1990; 1 female, same data except xii.1991; 1 female, same data except vii.1992; 1 female, Costa Rica, San Vito, Las Cruces, 17.viii-12.ix.198?, B. Gill. RMSEL, UCR.

*Distribution.*—Southern Costa Rica.

*Biology.*—Associated with moist primary tropical forest.

*Remarks.*—*Plynops edwardi* is similar to *Plynops carinatus* from Ecuador, but *edwardi* lacks a median facial carina (Fig. 10), and the facial concavity is smooth and shining medially (see Remarks above for *carinatus*).

Although not specifically mentioned on the labels, all the specimens from the Golfo Dulce site were sampled via Malaise traps. According to Prof. Hanson, the traps 24 kilometers west of Piedras Blancas were situated in the primary tropical forest at the Reserva Forestal Golfo Dulce, at coordinates of 8°46'N and 83°24'W. Originally one trap was placed about 50 meters down a trail into the primary forest, in a shaded situation. In October 1990 a second trap was situated at the very edge of the same forest. These traps were maintained locally by Maria Salablanca Nieto.

*Etymology.*—This species is named in honor of my father, Mr. Edward B. Shaw, of Boyne City, Michigan, in grateful recognition of his unswerving support for my entomological pursuits since early childhood. His assistance with aquiring and manufacturing nets, cages, and other collecting materials, along with leading collecting expeditions too numerous to count, were crucial elements in my advancement to a career as a naturalist, a scientist, and a professional entomologist.

## Plynops falcatus Shaw, new species
(Figs. 6, 18–19)

*Description of female.*—Body length 1.0–1.1 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining; facial concavity not margined dorsally, grading smoothly onto frons; area just below each antenna not prolonged anteriorly; dorsolateral areas of facial concavity only sparsely setose; facial setae normal: short, straight, and not forming thick, brush-like pads; lower median area of facial concavity, near dorsal clypeal margin, with single triangular projection; 11 flagellomeres; mandible long and sickle-like; face, in lateral view, with only a trace of a section visible in front of the eye, below the antenna, visible portion narrower than antennal socket; forewing vein 2CUa virtually absent, reduced to a short stub; ovipositor length 0.7–0.8× metasoma length.

Color: head dark chocolate brown, except antenna yellowish brown; mandible yellow, except tips reddish brown apically; palpi pale brownish white; mesosoma, pterostigma, and metasoma dark chocolate brown; wing venation and legs light yellowish brown.

*Male.*—Unknown.

*Material Examined.*—Holotype: female, Florida, Monroe County, Sugarloaf Key, Key Deer Refuge, SE1, S23, 6.vi-29.vii.1986, S.&J. Peck, 86–32, forest hammock Malaise, FIT, CNC. Paratype: 1 female, same data except S25, Kitchings, hardwood hammock forest, 26.ii-6.vi.1986, 86–29, CNC.

*Distribution.*—Known only from Sugarloaf Key, Florida. *Plynops falcatus* has the most restricted distribution of any known *Plynops* species.

*Biology.*—Associated with tropical hardwood forest vegetation (hammock) of the Florida Keys.

*Remarks.*—The exceptionally small body size and short ovipositor sets this species apart from other *Plynops*, with the exception of *Plynops minutus*. However, *Plynops falcatus* can be immediately distinguished from this and all other *Plynops* species by the presence of long and sickle-like mandibles (figs. 6, 19), and a single triangular

projection on the lower median area of the facial concavity, near the dorsal clypeal margin (Fig. 19).

*Etymology.*—From the Latin *falcatus* meaning "sickle-shaped," in reference to the form of the mandible.

**Plynops hansoni** Shaw, new species
(Figs. 1–2, 5, 11–12, 22)

*Description of female.*—Body length 1.5–2.0 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining; facial concavity dorsally margined by a carinate edge that separates the concavity from the frons; area just below each antenna prolonged anteriorly as a roughly triangular projection (in dorsal view); head, in dorsal view, with the dorsal margin of the facial concavity forming a V-shaped depression between the antennal insertions; 11 flagellomeres; forewing vein 2CUa present as a short branch, sclerotized portion about ½ as long as hind coxa; ovipositor length 0.7–0.9× metasoma length.

Color: head very dark brown to almost black; antenna dark chocolate brown, except scape and pedicel yellowish brown; mandible yellow, except tips reddish brown apically; palpi pale brownish white; mesosoma and metasomal tergum 1 very dark brown to almost black; wing venation, and remainder of metasoma dark brown, except membranous ventral parts of metasoma white; legs light to medium brown, except coxa and trochanters yellowish brown.

*Male.*—As female except body length shorter, 1.2 mm; face only slightly excavated and less densely setose, facial area lacking carinate margins and triangular projections; mandibles slightly shorter, less hooked apically; antenna and legs lighter, yellowish brown.

*Material Examined.*—Holotype: female, Costa Rica, Puntarenas Province, Road to Rincon, 10 km. west of Pan-American Highway, 100m, iii–v.1989, P. Hanson & l. Gauld, RMSEL. Paratypes: 3 females,

same data; 2 females, Costa Rica, Puntarenas Province, Reserva Forestal Golfo Dulce, 10 km. west of Piedras Blancas, 100m, vi–viii.1989, P. Hanson; 1 female, Costa Rica, Puntarenas Province, R.F. Golfo Dulce, 24 km. west of Piedras Blancas, 200m, vi–viii.1989, P. Hanson; 4 females, same data except xii.1991; 1 female, 1 male, same data except ii.1992; 9 females, same data except x–xi.1992; 2 females, Costa Rica, Puntarenas Province, Golfo Dulce, 5 km. west of Piedras Blancas, 100m, xi.1990, P. Hanson; 2 females, same data except xii.1990; 1 female, Costa Rica, Puntarenas Province, R.F. Golfo Dulce, 3 km. SW. Rincon, 10m, ii.1992, P. Hanson; 7 females, Puntarenas Province,P.N. Corcovado, Est. Sirena, 50m, x–xii.1990. RMSEL, UCR.

*Distribution.*—Various sites in Puntarenas Province, Costa Rica.

*Biology.*—Associated with moist primary tropical forest habitats at elevations from 10–200 meters on the Osa Peninsula.

*Remarks.*—*Plynops hansoni* is one of three species that have a pronounced synapomorphic triangular (in dorsal view) projection below each antenna, the other two being *Plynops masoni* and *Plynops riedeni* (see Figs. 5, 7, 9). *Plynops hansoni* can be distinguished from these, and all other *Plynops* species, by the profile of the space between these projections, which in dorsal view is distinctly V-shaped (Fig. 5). The profile of this space is U-shaped in both *Plynops masoni* and *Plynops riedeni* (Fig. 7, 9).

All of the specimens of *Plynops hansoni* were sampled via Malaise traps set by Prof. Paul Hanson, on, or in route to, the Osa Peninsula. The traps situated 24 kilometers west of Piedras Blancas are discussed above, under *Plynops edwardi*. The trap located 10 kilometers west of Piedras Blancas (=10 km. W. of Pan-American Highway) was situated at coordinates of 8°45'N and 83°18'W, placed just inside a primary forest, at a mostly shaded site. This trap was destroyed by a fallen tree
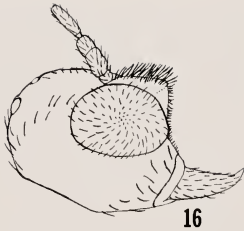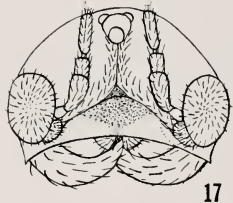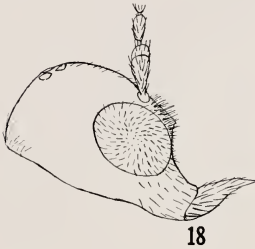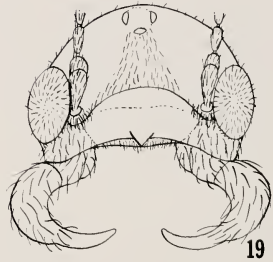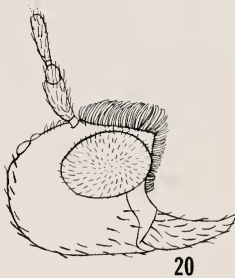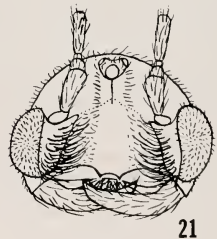
Figs. 16–21.  16. Head of *Plynops minutus*, lateral view. 17. Head of *Plynops minutus*, anterior view. 18. Head of *Plynops falcatus*, lateral view. 19. Head of *Plynops falcatus*, anterior view. 20. Head of *Plynops pilatus*, lateral view. 21. Head of *Plynops pilatus*, anterior view.

after 1–2 years of operation. The trap located 3 kilometers southwest of Rincon was situated at the edge of a primary forest, and was maintained by Moises Perez Parra and family.

*Etymology.*—This species is named in honor of Professor Paul Hanson, of the Universidad de Costa Rica, at San Pedro, in appreciation for several years devoted to the maintenance of Malaise traps, and subsequent sorting of samples too numerous to count. Without his collaboration, five of the species treated here (including this species), would not have been available for study.

**Plynops masoni** Shaw, new species
(Figs. 7)

*Description of female.*—Body length 1.6–1.9 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining; facial concavity dorsally margined by a carinate edge that separates the concavity from the frons; area just below each antenna prolonged anteriorly as a roughly triangular projection (in dorsal view); head, in dorsal view, with the dorsal margin of the facial concavity forming a U-shaped depression between the antennal insertions; triangular projection below antenna (in dorsal view) extending anteriorly beyond antennal insertion for a distance equal to the diameter of the antennal socket; 11 flagellomeres; forewing vein 2CUa reduced to a short stub, sclerotized portion about $\frac{1}{8}$ as long as hind coxa; ovipositor length 0.5–0.9× metasoma length.

Color: head reddish brown, except facial concavity yellowish brown; antenna medium brown, except scape and pedicel yellowish brown; mandible yellow, except tips reddish brown apically; palpi pale brownish white; mesosoma, wing venation, and metasomal tergum 1 dark reddish brown; remainder of metasoma dark brown to yellowish brown, except membranous ventral parts of metasoma white; legs light to medium brown, except coxa

and trochanters yellowish brown to yellowish white.

*Male.*—Unknown.

*Material Examined.*—Holotype: 1 female, Ecuador, Pichincha, 47 km. S. Santo Domingo de los Colorados, Rio Palenque Station, Pacific lowland rainforest, 1–14.vii.1975, A. Forsyth, CNC. Paratype: 1 female, same data except 200m, vi.1976, Peck, CNC.

*Distribution.*—Known only from the type-locality in Pichincha, Ecuador.

*Biology.*—Associated with Pacific lowland rainforest.

*Remarks.*—*Plynops masoni* is similar to *Plynops riedeni* from Costa Rica, but differs from that species by having much shorter triangular projections below the antennae (Fig. 7).

*Etymology.*—This species is named in honor of Dr. W.R.M. Mason in recognition of his many contributions to the study of braconid wasps, and in appreciation for first calling to my attention this interesting new genus.

*Plynops megakephalos* Shaw, new species
(Figs. 15)

*Description of female.*—Body length 2.7–3.9 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, coarsely rugo-punctate and dull; coarse rugo-punctate sculpture of frons ending roughly on line between lateral ocellus and compound eye, vertex smooth and shining; 18–19 flagellomeres; forewing vein 2CUa well-developed, sclerotized portion slightly longer than hind coxa; ovipositor length 1.5–1.6× metasoma length.

Color: head very dark chocolate brown, nearly black; antenna dark brown, except scape, pedicel, and apical 6 flagellomeres yellowish brown; labrum yellowish brown; mandible yellowish brown, except tips reddish brown to black apically; palpi pale brownish white; mesosoma, wing venation, and metasoma very dark chocolate

Fig. 22.   Wings of *Plynops hansoni*.

brown to nearly black; legs medium to dark brown, except coxa and trochanters light brownish white.

*Male.*—Unknown.

*Material Examined.*—Holotype: female, Costa Rica, Heredia, Estacion Biologia La Selva, 50–150m, 10°26′N, 84°01′W, 2.v.1993, INBio-OET, bosque primario, M/05/084, INBio Barcode CR1001–227693, INBio. Paratype: 1 female, same data except 2.iv.1993, M/05/052, INBio Barcode CR1001–239856, INBio.

*Distribution.*—Known only from the type-locality at the La Selva Biological Station, Heredia Province, Costa Rica.

*Biology.*—Associated with moist primary tropical forest.

*Remarks.*—Coarse rugo-punctate sculpture of the lateral frons is a synapomorphy shared with three other species: *braziliensis, carinatus,* and *edwardi,* but *Plynops megakephalos* can be distinguished from these, and all other *Plynops* species, by its large body size, exceptionally broad head (Fig.

15), and long flagellum. *Plynops megakephalos* has more flagellomeres (18–19) than any other *Plynops* species.

These specimens were collected during the ALAS Project (Arthropods of La Selva), but they were recognized as *Plynops* and brought to my attention by Geraldine Wright and Carlie Miller who were studying in Costa Rica during the summer of 1994, with support from an NSF-REU grant.

*Etymology.*—Derived from the Greek *megakephalos,* meaning "large-headed."

**Plynops minutus** Shaw, new species
(Figs. 16–17)

*Description of female.*—Body length 0.9– 1.6 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining; facial concavity not margined dorsally, grading smoothly onto the frons; area just below each antenna not prolonged anteriorly; dorso-lateral areas of facial concavity only

sparsely setose; facial setae normal: short, straight, and not forming thick, brush-like pads; lower median area of facial concavity, near dorsal clypeal margin, without a triangular projection; mandibles not long and sickle-like; face, in lateral view, with a distinct section visible in front of the eye, below the antenna, that is about as wide as antennal socket; 11 flagellomeres; forewing vein present as a short branch, sclerotized portion about ¼ as long as hind coxa; ovipositor length 0.4–1.3× metasoma length.

Color: head dark chocolate brown to nearly black, except antenna yellowish brown to brown; mandible yellow, except tips reddish brown apically; palpi pale brownish white; mesosoma, pterostigma, and metasoma dark chocolate brown to nearly black; wing venation and legs medium to dark brown.

*Male.*—As female except face less strongly excavated; body length 1.2 mm; 10 flagellomeres; antenna and legs lighter, yellowish brown.

*Material Examined.*—Holotype: female, Costa Rica, Puntarenas Province, Golfo Dulce, 3 km. SW. Rincon, 10m, xii.1989-iii.1990, P. Hanson, RMSEL. Paratypes: 1 female, Mexico, Nogales, 8.v.1953, with *Canavalia* seeds, 72857, n.g. near *Euphorus* det. Mues., USNM; 1 female, Peru, Madre de Dios, Puerto Maldonado, 6–11.i.1984, L. Huggert, CNC; 1 female, Costa Rica, Heredia Province, Puerto Viejo, OTS, La Selva, 100m, iv.1991, P. Hanson, UCR; 1 female, Costa Rica, Puntarenas Province, Peninsula Osa, Puerto Jimenez, 10m, vi.1991, P. Hanson, grassy, weedy site, UCR; 1 male, same locality as holotype except ii-iii.1989, P. Hanson & I. Gauld, RMSEL.

*Distribution.*—This species has the broadest distribution of any *Plynops* species, ranging from Central America (Mexico and Costa Rica) to Peru.

*Biology.*—The Mexican specimen is associated with seeds of *Canavalia* (jack bean), a member of the Leguminosae. The

species occurs in habitats ranging from shaded, moist, primary forests, to very disturbed, sunny, weedy sites.

*Remarks.*—This tiny species is similar to *Plynops falcatus*, which also has a very small body size and short ovipositor. *Plynops minutus* differs from *falcatus* in the form of the mandibles, which are not so strongly sickle-shaped (Fig. 17), by lacking a triangular projection medially in the facial concavity (Fig. 17), and by having the lateral borders of the face, below the antenna, more noticeably protruding in lateral profile (Fig. 16).

The Costa Rican specimens were all collected by Malaise traps set by Prof. Paul Hanson. The trap located 3 kilometers southwest of Rincon was situated within a, more or less, primary forest (the understory at this site was cleared) on a very steep, shaded slope. The trap at La Selva was situated within a virgin primary forest. In stark contrast to these, the trap at Puerto Jimenez was located in full sun, in a grassy, extremely disturbed site with weedy bushes and trees nearby. Judging from these collecting sites, it appears that *Plynops minutus* is adapted to a broader range of habitats than other *Plynops* species, which may account for its broader distribution.

*Etymology.*—Derived from the Latin *minutus*, meaning "little."

**Plynops pilatus** Shaw, new species
(Figs. 20–21)

*Description of female.*—Body length 2.2 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining; facial concavity not margined dorsally, grading smoothly onto the frons; area just below each antenna not prolonged anteriorly; dorso-lateral areas of facial concavity densely lined with long, curved setae forming thick, brush-like pads; lower median area of facial concavity, near dorsal clypeal margin, produced into two sharp, thorn-like spines; 12 flagellomeres; fore-

wing vein 2CUa present as a short branch, sclerotized portion about ¼ as long as hind coxa; ovipositor length 0.8× metasoma length.

Color: head dark chocolate brown; antenna dark brown, except scape and pedicel yellowish brown; mandible yellow, except tips reddish brown apically; palpi pale brownish white; mesosoma, pterostigma, wing venation, and metasoma dark chocolate brown; legs medium yellowish brown.
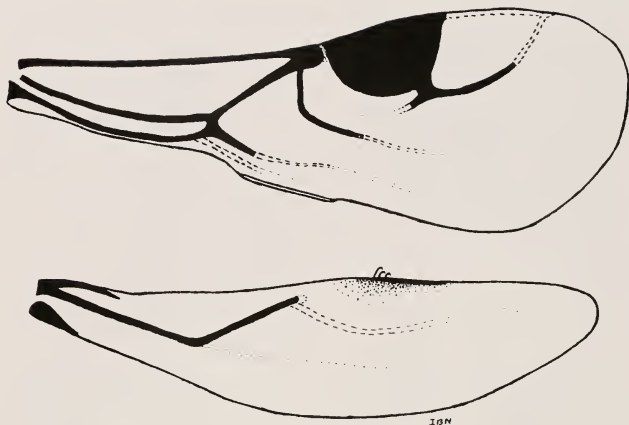
*Male.*—Unknown.

*Material Examined.*—Holotype: female, Costa Rica, San Jose Province, San Antonio de Escazu, 1300m, iv.1987, Col. W. Eberhard, RMSEL.

*Distribution.*—Known only from the type-locality in Costa Rica.

*Biology.*—Unknown.

*Remarks.*—*Plynops pilatus* can be distinguished from all other *Plynops* species by the presence of thick, brush-like setal pads on the dorso-lateral areas of the facial concavity (Figs. 20–21), and also by the presence of two sharp, thorn-like spines on the lower median area of facial concavity, near dorsal clypeal margin (Fig. 21).

*Etymology.*—From the Latin *pilatus,* meaning "grown hairy."

**Plynops riedeni** Shaw, new species
(Figs. 9)

*Description of female.*—Body length 1.8–2.1 mm; lateral portion of frons, on line directly between antennal insertion and median ocellus, smooth and shining; facial concavity dorsally margined by a carinate edge that separates the concavity from the frons; area just below each antenna prolonged anteriorly as a roughly triangular projection (in dorsal view); head, in dorsal view, with the dorsal margin of the facial concavity forming a U-shaped depression between the antennal insertions; triangular projection below antenna (in dorsal view) extending anteriorly beyond antennal insertion for a distance equal to twice the diameter of the antennal socket; fore-

wing vein 2CUa present as a short branch, sclerotized portion about ¼ as long as hind coxa; ovipositor length 0.9–1.3× metasoma length.

Color: head very dark brown to almost black, except triangular projections and lower ½ of facial concavity yellowish brown; antenna dark chocolate brown, except scape and pedicel yellowish brown; mandible yellow, except tips reddish brown apically; palpi pale brownish white; mesosoma and metasomal tergum 1 very dark brown to almost black; wing venation, and remainder of metasoma dark brown, except membranous ventral parts of metasoma white; fore leg yellowish brown; middle and hind legs light to medium brown, except coxa and trochanters yellowish brown.

*Male.*—Unknown.

*Material Examined.*—Holotype: female, Costa Rica, Heredia Province, 3 km. S. Puerto Viejo, OTS, La Selva, 100m, ii-iii.1993, P. Hanson, RMSEL. Paratype: female, Costa Rica, Alajuela Province, 10°27′N, 84°05′W, Los Chiles de Aguas Zarcas, cafe, 300m, xi.1989, mixed coffee plantation, R. Cespedes, UCR.

*Distribution.*—This species is known only from two sites in Costa Rica, on the northern part of the Caribbean coastal plain.

*Biology.*—Recorded from both moist primary forest at La Selva, and a mixed coffee plantation at Los Chiles de Aguas Zarcas.

*Remarks.*—*Plynops riedeni* is one of three species that have a pronounced triangular (in dorsal view) projection below each antenna, the other two being *Plynops masoni* and *Plynops hansoni. Plynops riedeni* can be distinguished from these, and all other *Plynops* species, by the exceptionally large size of the triangular projection below the antenna, which extends anteriorly beyond antennal insertion for a distance equal to twice the diameter of the antennal socket (Fig. 9).

*Etymology.*—This species is named in

honor of my father-in-law, Dr. James A. Rieden, of Bloomfield Hills, Michigan.

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# Phenology of Ammophiline Wasps in a Premontane Wet Forest in Costa Rica (Hymenoptera, Sphecidae, Ammophilini)

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*Abstract.*—Population fluctuations sampled by Malaise traps are reported for three species of *Ammophila* and three species of *Eremnophila* during a 16 month period at Finca Montezuma in Guanacaste Province, Costa Rica. Populations of *Ammophila centralis* Cameron and *Eremnophila melanaria* (Dahlbom) reach their peak during the wet season, and populations of *Ammophila picipes* Cameron and *Eremnophila aureonotata* (Cameron) are greatest during the dry season. *Ammophila gaumeri* Cameron and *Eremnophila opulenta* (Lepeletier) were infrequently taken at the site, and no conclusions regarding them are possible. *Podalonia montana* (Cameron) is recorded from Costa Rica for the first time.

Three genera of Ammophilini occur in Costa Rica, *Ammophila* Kirby, *Eremnophila* Menke, and *Podalonia* Fernald. In this paper we report on population fluctuations of species in the first two genera at one location in northwestern Costa Rica over a period of 16 months in 1992 and 1993. Janzen (1983) described a variety of factors that possibly have roles in regulating insect populations throughout the year in Costa Rica, particularly in the lowlands of Guanacaste Province, but he stressed that "... we know next to nothing about the ecology of almost all Costa Rican insects." This is certainly true of the ammophiline wasps. While our data suggest that population fluctuations throughout the year appear to be influenced by rainfall/temperature in some species, we know nothing about the influence of other environmental factors such as sunlight, wind, parasites, etc. We do not know how long adults live, or how many generations each species has per year. We do not know if their population fluctuations are tied to prey availability and abundance. For that matter, we know nothing

about the prey of Costa Rican ammophilines other than that they take caterpillars.

The study site was premontane wet forest in the transition between wet and dry zones located at Finca Montezuma, Guanacaste Province. This finca is located 3 km southeast of Rio Naranjo (lat. 10° 42", long. 85° 5") at an altitude of 450 m. Total precipitation at Finca Montezuma averages about 2200 mm per year, with the majority of rainfall occurring from June through December (Fig. 1). Defoliation is not total during the drier part of the year because of mist blown by trade winds over the continental divide from the wet zone. Flowering plants are common throughout the year. Temperature at Finca Montezuma fluctuates about 3° C during the year and reaches its maximum during the dry season (Fig. 2).

One of us, Parker, operated 12 Malaise traps continuously for several years at Finca Montezuma. The traps used were of various designs and set up at the ecotone between forests and crop lands. Most traps were between the edge of the

**Rainfall, Finca Montezuma, 1992-1993**
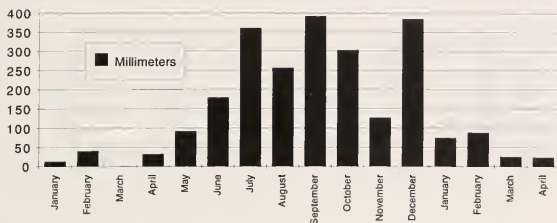


Fig. 1. Bar graph showing rainfall in millimeters at Finca Montezuma from January 1992 to April 1993.

forest and coffee plantations, but some traps were placed along roads that ran through the forest. The collecting heads of the traps were sprayed with locally purchased insecticide; the insects trapped in the bottles died rapidly. The trap bottles were emptied daily and the insects sorted and stored. The Ammophilini taken in the traps during 1992 and the first four months of 1993 were placed in bags of 70% alcohol and sent to Menke for identification. Menke then tallied the numbers of each sex for each species on

a monthly basis and plotted them on graphs (Figs. 3-8).

Four species of *Ammophila* (*picipes* Cameron, *centralis* Cameron, *gaumeri* Cameron and *procera* Dahlbom) and three species of *Eremnophila* (*aureonotata* (Cameron), *melanaria* (Dahlbom), and *opulenta* (Lepeletier)) are known in Costa Rica. *Ammophila procera* was the only wasp not taken in the traps during the survey, although it occurs at lower elevations in Guanacaste Province. The absence of *procera* in the traps may indicate that it occupies different

**Temperature, Finca Montezuma, 1992-1993**
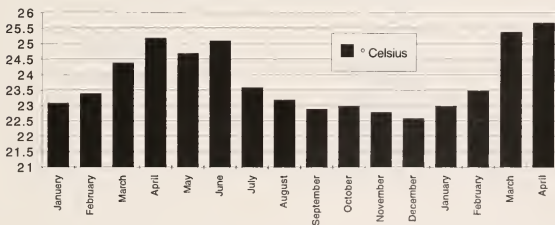


Fig. 2. Bar graph showing temperature fluctuations in Celsius at Finca Montezuma from January 1992 to April 1993.

**Ammophila picipes, 1992-1993**
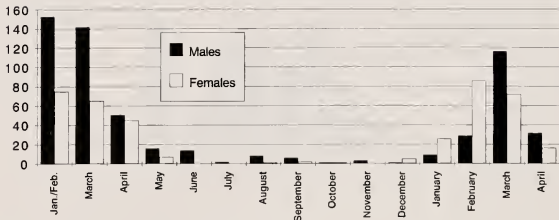


Fig. 3. Bar graph showing number of males and females of *Ammophila picipes* taken at Finca Montezuma from January 1992 to April 1993.

habitats. One example of the genus *Podalonia* was taken during the survey, a male of *montana* (Cameron) captured in February, 1992. This specimen proves that all three genera occur at the survey site, but more importantly, it represents the first record of this species in Costa Rica. *Podalonia montana* was known previously from Mexico, Guatemala and Nicaragua. Three females of *montana* have since been found among material collected by Parker at Finca Montezuma, using an insect net, in February and March 1992.

The most common species at the site was *A. picipes*, which is ubiquitous throughout Mexico and Central America and extends into Arizona, New Mexico and Texas. The second most abundant taxon is *E. aureonotata*, a species that is common over most of the eastern half of North America and which ranges south as far as Guanacaste Province, Costa Rica. The remaining species taken in the traps were far less abundant, particularly *E. melanaria* and *E. opulenta*. However, *E. melanaria* is a common species over most of

**Ammophila centralis, 1992-1993**
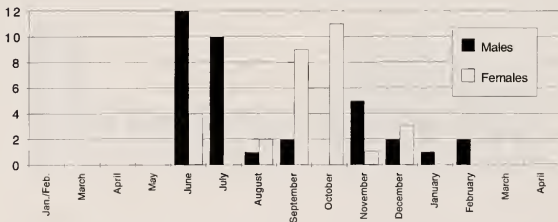


Fig. 4. Bar graph showing number of males and females of *Ammophila centralis* taken at Finca Montezuma from January 1992 to April 1993.

**Ammophila gaumeri, 1992-1993**
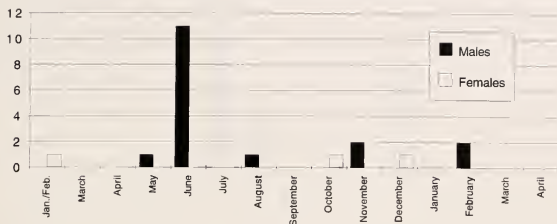


Fig. 5. Bar graph showing number of males and females of *Ammophila gaumeri* taken at Finca Montezuma from January 1992 to April 1993.

its range, which extends from tropical Mexico to Argentina. *Eremnophila opulenta* has a similar distribution but is less frequently collected. *Ammophila centralis* ranges from the southern tip of Texas to the xeric regions of northwestern Venezuela, and *A. gaumeri* has a similar distribution although it does not occur north of tropical Mexico.

When the plotted population fluctuations for these species during the period covered (Figs. 3-8) are compared with rainfall for the same period (Fig. 1), some obvious differences can be seen. Two species in each genus have highest population levels at different times of the year. The wet season group (*A. centralis* and *E. melanaria*) seems absent during the major part of the dry season. On the other hand, the dry season group (*A. picipes* and *E. aureonotata*), occurs throughout the year. The other species, *A. gaumeri* and *E. opulenta* occur at such a low density at Finca Montezuma that no conclusions can be made

**Eremnophila aureonotata, 1992-1993**
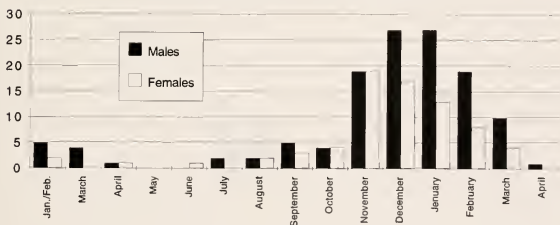


Fig. 6. Bar graph showing number of males and females of *Eremnophila aureonotata* taken at Finca Montezuma from January 1992 to April 1993.

**Eremnophila melanaria, 1992-1993**
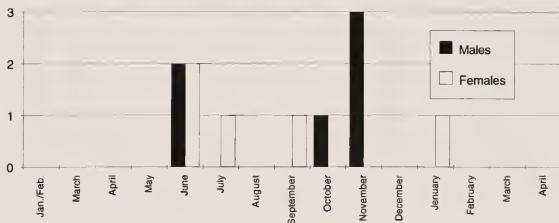


Fig. 7. Bar graph showing number of males and females of *Eremnophila melanaria* taken at Finca Montezuma from January 1992 to April 1993.

except to say that *gaumeri* is present sporadically through the year, with an apparent peak in June, the beginning of the wet season (Fig. 5). The two females of *opulenta* were taken in the rainy season (Fig. 8).

Temperature (Fig. 2) may also be a factor in population fluctuations of these wasps. Certainly its fluctuations at Finca Montezuma complement our data on wasp distribution based on rainfall.

To obtain wholly satisfying results would require operating traps for several years, carefully monitoring species taken

in each trap, rather than pooling the samples as was done here. We have no data on the efficacy of trapping populations of *Ammophila, Eremnophila,* and *Podalonia* with Malaise traps. Our data could be artificial, but there seems to be seasonal separation of species based on rainfall and temperature.

## ACKNOWLEDGEMENTS

**Eremnophila opulenta, 1992-1993**
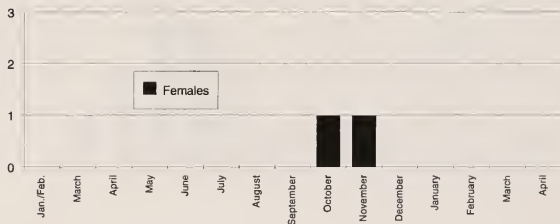


Fig. 8. Bar graph showing number of females of *Eremnophila opulenta* taken at Finca Montezuma from January 1992 to April 1993.

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# The Ammophilini of Costa Rica; An Identification Guide (Hymenoptera: Sphecidae: Sphecinae)

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*Abstract.*—Three genera (*Ammophila* Kirby, *Eremnophila* Menke and *Podalonia* Fernald) and nine species of Ammophilini are recorded from Costa Rica and a key and illustrations provided for their identification. *Ammophila* is represented by *centralis* Cameron, *gaumeri* Cameron, *picipes* Cameron, and *procera* Dahlbom; *Eremnophila* by *aureonotata* (Cameron), *melanaria* (Dahlbom) and *opulenta* (Lepeletier); and *Podalonia* by *atriceps* (Smith) and *montana* (Cameron). The following new synonyms are proposed: *Ammophila consors* Cameron, 1888, and *A. nigrocaerulea* Cameron, 1888 = *Ammophila centralis* Cameron, 1888; *Ammophila communis* Cresson, 1865, *A. alpestris* Cameron, 1888, and *Podalonia communis* ssp. *intermedia* Murray, 1940 = *Podalonia atriceps* (Smith), 1856. *A. piceiventris* Cameron, 1888 is treated as a tentative synonym of *P. atriceps* (Smith). *Ammophila gaumeri* Cameron is recorded from Venezuela. Records of *Podalonia robusta* (Cresson) in Costa Rica are shown to be erroneous.

## INTRODUCTION

Publication of the book, *The Hymenoptera of Costa Rica* (Hanson and Gauld, 1995), will doubtless foster considerable interest in the wasps of the country, as will the keys to genera of Neotropical Sphecidae by Menke and Fernández (in press). The following is the first of a series of papers dealing with the identification of Costa Rican Sphecidae.

The ammophiline wasps are among the larger sphecids in Costa Rica, but because of their slender build, they are less conspicuous than their cousins in the genera *Sphex* and *Isodontia*. Nevertheless, they are fairly commonly collected. The wasps are predators of lepidopterous caterpillars, although nothing has been published on the biology of any Costa Rican ammophiline. Three genera are known in Costa Rica, *Ammophila* Kirby, *Eremnophila* Menke, and *Podalonia* Fernald, containing four, three, and two species, respectively (Hanson and Menke, 1995; Menke and Parker, 1996). Our knowledge of the distribution

of ammophiline species in Costa Rica is fragmentary, but the rapidly growing collection of the Instituto Nacional de Biodiversidad in Santo Domingo (INBio), Costa Rica should improve this situation dramatically in the coming years. Menke and Parker (1996) provided phenological data for some species of Ammophilini at one site in Guanacaste Province, Costa Rica. Populations of some species reach their zenith in the dry season, others in the wet season.

The Costa Rica/Panamá section of Central America is a zoogeographical crossroads between the North American and South American sphecid faunas (Hanson and Menke, 1995). Some northern elements extend south to the seasonally dry Guanacaste Province of northwestern Costa Rica, and apparently go no farther. Within the Ammophilini, *Ammophila procera* Dahlbom, *Eremnophila aureonotata* (Cameron), and *Podalonia montana* Cameron have this pattern. For some northern taxa, Panamá is the southern limit, and *Podalonia atriceps* (Smith) is the only example

in the Ammophilini. Some South American species occur as far north as Panamá or Costa Rica. The common South American wasp *Eremnophila binodis* (Fabricius) is the only ammophiline with this pattern, and so far, it is known only as far north as central Panamá. The remaining Costa Rican ammophilines are more widespread.

## SOURCES OF MATERIAL

I would like to thank Terry Griswold, Bee Biology and Systematics Research Lab., Utah State University, Logan, Utah; Paul Hanson, Universidad de Costa Rica, San Jose, Costa Rica; and Jesús Armando Ugalde Gómez, INBio, Santo Domingo de Heredia, Costa Rica, for allowing me to study their Ammophilini. Frank Parker, also at Utah State University, sorted through his extensive Costa Rican material housed at the University, and sent interesting specimens to me for study. Colin Vardy, The Natural History Museum,

London, lent types for study. Depositories for types and other material listed in this paper are identified by city names in capital letters. These institutions are listed below.

The Natural History Museum, London, England (LONDON).

Zoologiska Institutionen, Lund, Sweden (LUND).

Università di Torino, Torino, Italy (TURIN).

Museo Civico di Storia Naturale, Genova, Italy (GENOA).

Museum fur Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany (BERLIN).

Academy of Natural Sciences, Philadelphia, Pennsylvania (PHILADELPHIA).

National Museum of Natural History, Washington D.C. (WASHINGTON).

Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah (LOGAN).

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KEY TO GENERA AND SPECIES OF AMMOPHILINI IN COSTA RICA

1. Sternum I not tapering distad (ventral view), meeting and often overlaping base of II (Fig. 2); spiracle of tergum I located before apex of sternum I (lateral view, Fig. 1) . . . .
   *Podalonia* Fernald . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
   – Sternum I tapering distad, not reaching base of II, intervening space usually long and consisting of membrane and a ligament (Fig. 4); spiracle of tergum I (lateral view) usually located at or beyond level of sternum I apex (Fig. 3) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

2. Female: gaster red, free margin of clypeus with four, large, irregular teeth; male terga I-II broadly black (red only laterally), III nearly all black; Guanacaste Province at elevations below 600 m . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. montana* (Cameron)
   – Female: entirely black, free margin of clypeus without teeth; male terga I-III entirely red (III may be narrowly black distally); generally at elevations of 1000 m or more . . . . . .
   . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. atriceps* (Smith)

3. Episternal sulcus curving posterad from subalar fossa to scrobe, then extending obliquely ventrad to anteroventral area of mesopleuron (Figs. 5, 7); entirely black wasps with conspicuous spots of appressed silver setae on mesopleuron and propodeal side . . . . . . . .
   *Eremnophila* Menke . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
   – Episternal sulcus extending straight down from subalar fossa (Fig. 6), not curving toward scrobe (area in front of scrobe may be depressed, connecting with episternal sulcus), sulcus sometimes ending at level of pronotal lobe (Fig. 9); abdominal terga I-II often red; side of thorax with or without conspicuous spots of appressed silver setae . . . . . . . . . . . . 6

4. Scutum anteromedially with large area of appressed silver or golden setae, surface anterolaterally densely transversely carinate; male sternum VIII with prominent median tubercle; Guanacaste Prov . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. aureonotata* (Cameron)

– Scutum without appressed silver or golden setae, surface punctate anterolaterally; male sternum VIII without tubercle; widespread in Costa Rica . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5. Setae forming appressed silver mesopleural spot arranged in a swirled, circular pattern (Figs. 7–8); mesopleuron with digiform or conical tubercle anteroventrally (Figs. 7–8); male gastral sternum I (not petiole) flat in lateral profile . . . . . . . . . *E. opulenta* (Lepeletier)

– Setae forming silver mesopleural spot arranged in sinuate pattern; mesopleuron with angular bulge anteroventrally; male gastral sternum I with angular bulge at distal third in lateral profile . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. melanaria* (Dahlbom)

6. Pronotal collar and scutum coarsely, transversely ridged; Guanacaste Province . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. procera* Dahlbom

– Pronotal collar and scutum smooth, not cross-ridged; widespread in Costa Rica . . . . . . . . 7

7. Erect setae of head and thorax pale; mesopleuron with linear band of appressed silver setae (usually sharply defined) that extends along mesopleural suture from base of mid-coxa to just beneath tegula (Fig. 6); epternal sulcus ending at level of scrobe (Fig. 9)
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. picipes* Cameron

– Erect setae of head and thorax black; mesopleuron with broad, non-linear silver spot adjacent to mesopleural suture, or appressed mesopleural setae sparse, not forming a discrete silver band or spot; epternal sulcus extending past level of scrobe to ventral region of mesopleuron (Fig. 6) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

8. Female, abdomen with six visible terga . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

– Male, abdomen with seven visible terga . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

9. Mesopleural silver spot larger than pronotal lobe, broadly triangular, extending from scrobe to near midcoxa; abdominal terga I-II usually partially or largely red (rarely all black); black part of abdomen without bluish-green tint . . . . . . . . . . . *A. centralis* Cameron

– Mesopleural silver spot, if present, usually smaller than pronotal lobe, located next to midcoxa (spot rarely extending to level of scrobe as a narrow band); abdomen black; body, especially abdomen, with bluish-green tint . . . . . . . . . . . . . . . . . *A. gaumeri* Cameron

10. Apex of gonoforceps drawn out into a long, narrow, parallel-sided and largely asetose process that is longer than outer spur of hindtibia, and truncate apically; edge of gono-forceps lateral to base of apical process fringed with one to three long, slender, pale setae (Fig. 10) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*A. centralis* Cameron

– Apex of gonoforceps extended as a fingerlike, incurved lobe, acuminate apically, its outer edge densely fringed with short setae; edge of gonoforceps lateral to base of lobe fringed with many long, stout, black setae (Fig. 11) . . . . . . . . . . . . . . . . . . . . . A. gaumeri Cameron

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## AMMOPHILA W. Kirby

Fernald's (1934) revision of the North American and Mexican members of this genus is of little use for various reasons. Murray (1938) clarified the status of a few species and provided a partial key. I (Menke, 1964a, b, 1965, 1966b, 1967, 1970) described many new species, established species groups, and new synonymy, but my revision of the New World fauna is still in progress. The four Costa Rican species are divided among three species groups: *picipes* Cameron is in the *urnaria* group (Menke, 1966b), *procera* is in the *procera* group (Menke, 1964a), and *centralis*

Cameron and *gaumeri* Cameron belong to the *nigricans* group (Menke, 1970).

## Ammophila centralis Cameron
(Fig. 10)

*Ammophila centralis* Cameron, 1888:6. Lectotype: male, El Reposo, Guatemala (LONDON), designated by Menke, 1976:151.

*Ammophila consors* Cameron, 1888:12. Lectotype: male, N. Yucatán, México (LONDON), designated by Menke, 1976:151. **New synonym.**

*Ammophila nigrocaerulea* Cameron, 1888:12. Syntypes: females, San Gerónimo, Guatemala (LONDON). **New synonym.**

*Ammophila centralis* occurs from ex-
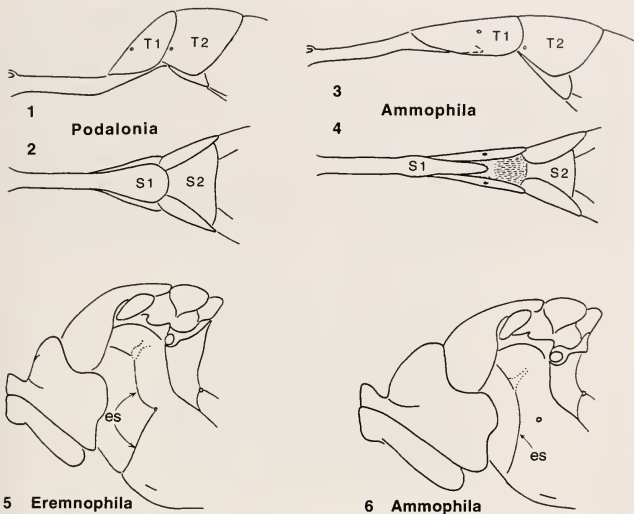
Figs. 1–6. Figs. 1–2. First two abdominal segments of *Podalonia*. 1, lateral profile; 2, ventral view. Figs. 3–4. First two abdominal segments of *Ammophila*. 3, lateral profile; 4, ventral view. Figs. 5–6. Lateral view of thorax showing episternal sulcus (es). 5, *Eremnophila*; 6, *Ammophila*.

treme southern Texas (Hidalgo and Cameron Counties) through Central America. I have also collected the species in xeric areas of northwestern Venezuela (Zulia: 6 km W La Concepcion; Lara: 20 km E Carora; and Aragua: Ocumare de la Costa) and even in the Orinoco River basin of that country (Guarico: Hato Masaguaral, 44 km S Calabozo, see Menke & Carpenter, 1985). In Costa Rica *centralis* has been collected in Guanacaste and San José Provinces. In Guanacaste Province *centralis* reaches its highest population levels during the rainy season (Menke and Parker, 1996).

I studied the type material of Cameron's three names in 1964, and listed *consors* and *nigrocaerulea* as synonyms of *centralis* (Menke, 1976), but I did not indicate that the synonymy was new. I do so now. Occasional females of *centralis* are entirely black and are thus similar to the all black *gaumeri*. Black females of *centralis* have a broad triangular patch of appressed silver setae on the mesopleuron, and the body lacks the bluish tint common in *gaumeri*. In *gaumeri* the mesopleural silver patch is located near the midcoxa and typically is smaller than the pronotal lobe. The first gastral segment of most females of *centralis* is largely red, as is tergum I (petiole). The male genitalia of *centralis* (Fig. 10) readily separate this species from males of *gaumeri* (Fig. 11).

## Ammophila gaumeri Cameron
### (Fig. 11)

*Ammophila gaumeri* Cameron, 1888:4 Lectotype: female, N. Yucatán, México (LONDON), designated by Menke, 1976:152.

*Ammophila micans* Cameron, 1888:5. Syntypes: females, San Gerónimo, Guatemala (LONDON). Synonymy by Fernald, 1934:114.

*Ammophila gaumeri* ranges from tropical México to the xeric regions of northwestern Venezuela, but it is never as commonly collected as *centralis* with which it is easily confused. In Costa Rica the species is known only from Guanacaste Province (Menke, 1991, Menke and Parker, 1996). The Venezuelan records for *gaumeri* have never been published, but in 1976 and 1981 I collected it in the states of Aragua (Ocumare de la Costa) and Zulia (Los Angeles del Tucuco) (WASHINGTON).

This species is entirely black, and females in fresh condition have areas of microsetae with a bluish caste. This is particularly noticeable on the gaster, mesopleuron, and thoracic dorsum. In addition, females usually have only a small patch of appressed silver setae on the mesopleuron, and it is near the midcoxa. This patch is usually smaller than the pronotal lobe. In one female from Costa Rica the patch is expanded upward along the mesopleural suture and extends onto the hypoepimeral area (Estación Experimental Enrique Jiménez Nuñez, 20 km SW of Cañas, Guanacaste Prov.; LOGAN). Males of *gaumeri* and *centralis* are very similar, but the genitalia readily separate them (see Figs. 10–11).

I examined Cameron's types of *micans* in 1964 and confirm Fernald's synonymy with *gaumeri*.

## Ammophila picipes Cameron
### (Fig. 9)

*Ammophila picipes* Cameron, 1888:11. Holotype: male, Temax, Yucatán, México (LONDON).

*Ammophila alticola* Cameron, 1888:10. Holotype: male, Volcán de Chiriquí, Panamá (LONDON). Synonymy by Menke, 1965:2392.

*Ammophila volcanica* Cameron, 1888:17. Holo-

type: female, Volcán de Chiriquí, Panamá (LONDON). Synonymy by Menke, 1965: 2392.

*Ammophila chiriquensis* Cameron, 1888:18. Holotype: female, Volcán de Chiriquí, Panamá (LONDON). Synonymy by Menke, 1965: 2392.

*Ammophila picipes* occurs from northern Panamá to Texas and southern Arizona, and it is the most commonly collected species of *Ammophila* in Costa Rica. It is a dry season species, at least in Guanacaste Province (Menke and Parker, 1996).

The long band of appressed silver setae on the mesopleuron is distinctive (Fig. 9), but in some females of *picipes* from higher elevations the appressed silver pubescence of the mesopleuron (and propodeal side) is more extensive (San Isidro General, Puntarenas Prov., 600 m, LOGAN). In these specimens the setal patches of the mesopleuron and propodeal side lose their sharp margins because the integument is generally fairly densely covered with appressed silver setae. Even the scutum and propodeal dorsum are often silvery in such material. Most of the *picipes* that I have seen from Panamá have this expanded coverage of appressed silver setae on the thorax.

*Ammophila picipes* is similar to the widespread, common South American species *gracilis* Lepeletier, but until both can be thoroughly studied, I consider them distinct.

## Ammophila procera Dahlbom

*Ammophila procera* Dahlbom, 1843:15. Holotype: female, "N. America" (LUND).

*Ammophila procera* Lepeletier, 1845:376. Holotype: female, "Am. Sept." (TURIN), nec Dahlbom, 1843. Synonymy by Menke, 1965:2392.

*Ammophila saeva* Smith, 1856:222. Lectotype: female, California (LONDON), designated by Menke, 1976:153. Synonymy by Fernald, 1934:44.

*Ammophila gryphus* Smith, 1856: 222. Lectotype: female, Charlston, Florida (LONDON), designated by Menke, 1976:153. Synonymy by Fernald, 1934:44.

*Ammophila barbata* Smith, 1873:260. Syntypes:
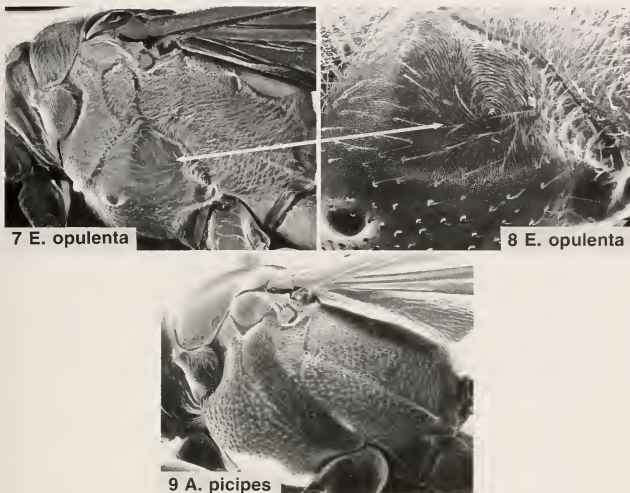
Figs. 7–9. Fig. 7. Scanning electron photomicrographs of left side of thorax. 7–8, *Eremnophila opulenta*, 8 is closeup of whorled setae; 9, *Ammophila picipes*.

females, México (missing). Synonymy by Fernald, 1934:44.

*Ammophila ceres* Cameron, 1888:8. Holotype: male, San Gerónimo, Guatemala (LONDON). Synonymy by Fernald, 1934:44. Menke (1976:153) unnecessarily designated this specimen as lectotype.

*Ammophila championi* Cameron, 1888:9. Lectotype: female, San Gerónimo, Guatemala (LONDON), designated by Menke, 1976:153. Synonymy by Fernald, 1934:44.

*Ammophila striolata* Cameron, 1888:10. Holotype: female, Ventanas, Durango, México (LONDON). Synonymy by Fernald, 1934:44.

*Ammophila procera* is found throughout North America, and its range extends from southern Canada southward through México and into Central America. It occurs as far south as Costa Rica (Menke, 1991), where it is known only from Guan-

acaste Province (Estacion Experimental Enrique Jimenez Nuñez, 20 km SW Cañas; Finca Jenny, 30 km N Liberia. This is probably about the southern limit of its range.

The cross-ridged scutum and pronotal collar of *procera* are unique features among Costa Rican *Ammophila* and immediately identify it.

I examined the type material of all of the Smith (except *barbata*) and Cameron names in the above synonymy in 1964 and can confirm Fernald's synonymy. As to *barbata*, Smith's description strongly suggests that it is a synonym of *procera*. It is apparently an example of the entirely black *procera* occasionally found in México. Searches for type material of *barbata* at the Natural History Museum in London and the Museum at Oxford have been fruitless.

## EREMNOPHILA Menke

This genus is endemic to the New World, but eight of its nine species are restricted to the Neotropical Region. I reviewed the genus (as a subgenus of *Ammophila*), segregated the species into groups, and keyed the species (Menke, 1964c). *Eremnophila* was subsequently elevated to genus (Menke, 1966a). Three species are currently known in Costa Rica, but a fourth, *binodis* (Fabricius), may be discovered in the southern end of the country because it is known from central Panamá. *Eremnophila binodis* is a common wasp in South America.

### Eremnophila aureonotata (Cameron)

*Ammophila aureonotata* Cameron, 1888:7. Lectotype: male, Valladolid, Yucatán, México (LONDON), designated by Menke, 1964:881.

This wasp occurs commonly in eastern North America east of the 100th meridian from southern Canada to Florida and Texas. I (Menke 1964) recorded *aureonotata* from México to El Salvador in Central America, and subsequently noted its presence in Guanacaste Province, Costa Rica (Menke 1991). It is likely that this is the southern limit of the range of *aureonotata*. I have not seen it from other parts of Costa Rica. Population levels of *aureonotata* are highest during the dry season in Guanacaste Province (Menke and Parker, 1996).

The South American species, *binodis*, occurs as far north as central Panamá, and it is similar to *aureonotata*. The scutum of *binodis* is cross carinate like *aureonotata* but *binodis* usually lacks the appressed gold setae found on the scutum of *aureonotata*. The male genitalia also differ (see illustrations in Menke, 1964c).

### Eremnophila opulenta
(Guérin-Méneville)
(Figs. 7–8)

*Ammophila opulenta* Guérin-Méneville, 1838:261. Holotype: female, Pará, Brasil (GENOA).
*Ammophila bimaculigera* Strand, 1910:129. Lec-

totype: female, Villa Morra, Paraguay (BERLIN), designated by Menke, 1964:878. Synonymy by Menke, 1964:878.

This large wasp occurs from tropical México to Argentina. In Costa Rica it is the least commonly collected species of *Eremnophila*. The mesopleural tubercle and whorled nature of the mesopleural silver patch (Figs. 7–8) easily identify this wasp.

### Eremnophila melanaria (Dahlbom)

*Ammophila melanaria* Dahlbom, 1843:15. Lectotype male: "Brasilia" (LUND), designated by Menke, 1964:878.
*Ammophila miliaris* Cameron, 1888:3. Lectotype: female, Bugaba, Panamá (LONDON), designated by Menke, 1964:878.
*Ammophila iridipennis* Cameron, 1888:5. Lectotype: female, Zapote [= El Zapote], Guatemala (LONDON), designated by Menke, 1964:878.
*Ammophila velutina* Schrottky, 1910:31. Holotype: female, San Ignacio, Argentina, (location unknown, possibly destroyed). Synonymy tentative.
*Ammophila lobicollis* Cameron, 1912:428. Holotype: female, Demerara, British Guyana (LONDON). Synonymy by Menke, 1964:878.

*Eremnophila melanaria* ranges from tropical México south to Argentina. The species is generally distributed in Costa Rica, and is most commonly collected in the wet season in Guanacaste Province (Menke and Parker, 1996).

It is still not clear whether the South American population of *melanaria* is distinct from the Central American one. As I mentioned and illustrated (Menke, 1964c), there appear to be slight differences between these populations in the male genitalia. I am still unable to resolve this problem, but if the Central American material proves to represent a separate species, the name *miliaris* (Cameron) would apply, with *iridipennis* as a synonym.

Unless Schrottky's material of *velutina* can be found, the status of the species will remain in doubt. However, the name is either a synonym of *melanaria* or *opulenta*.

## Podalonia Fernald

Murray (1940) revised this genus for the New World. He recorded two species from Costa Rica, *communis* Cresson and *robusta* (Cresson). *Podalonia communis* is a commonly collected wasp in the western half of North America and it extends south to Costa Rica, but as I relate below, the proper name for the species is *atriceps* Smith. *Podalonia robusta* was recorded from Costa Rica by Murray based on one male specimen, but as I demonstrate below, his record is erroneous. The specimen is actually *atriceps*. Menke and Parker (1996) reported the first record of *Podalonia montana* Cameron in Costa Rica. Thus, there are still two species of the genus in the country, *atriceps* and *montana*.

### Podalonia atriceps (Smith), new status
### (Figs. 12–19, 21–23)

*Ammophila atriceps* Smith, 1856:221. Female, male, México. Lectotype: male, designated by Menke, 1976:144. (LONDON).

*Ammophila communis* Cresson, 1865:462. 40 males, Colorado Territory. Lectotype: male designated by Cresson, 1916:94. (PHILADELPHIA). **New synonym**.

*Ammophila alpestris* Cameron, 1888:21. Syntypes: males, Volcán de Chiriquí, 4000–6000 feet, Panamá. (LONDON). **New synonym**.

*Ammophila piceiventris* Cameron, 1888:22. Holotype: female, Quezaltenango, Guatemala, 7800 feet (LONDON). Tentative synonymy.

*Podalonia communis intermedia* Murray, 1940:29. Holotype: male, Distrito Federal, México (WASHINGTON). **New synonym**.

In *Sphecid Wasps of the World* (Bohart and Menke, 1976) I listed *atriceps* (Smith) as a subspecies of *communis* with *alpestris* as a synonym (I should have added "new synonym"). This presentation of facts was erroneous in two ways. First, Smith's *atriceps* is the oldest available name and must be used for the species. Second, the lectotype of *atriceps* is not identical with the syntypes of *alpestris* although they appear to be conspecific. I studied syntypes of both taxa in 1964 at The Natural History Museum, London and can confirm that the genitalia of *alpestris* agree with those of *atriceps* (Figs. 12, 16). However, specimens of *atriceps* from Costa Rica and Panamá have erect pale setae on the male clypeus (all black in typical *atriceps*), and the name *alpestris* was based on this population.

Smith (1856) described *atriceps* from a female and a male. Since he did not designate a holotype in the original description, both specimens are syntypes. Fernald (1927:35) and Murray (1940:30) studied the male but noted the female was missing. Both authors mistakenly regarded the female as the holotype, and Murray declared that it must be an *Ammophila*. Consequently Murray did not apply the name *atriceps* in *Podalonia*.

My designation (Menke 1976) of the male as lectotype resulted in the assignment of *atriceps* to *Podalonia*. The genitalia of the lectotype agree with the traditional interpretation of *communis* (Murray 1940). In fact, Murray noted that the genitalia of Smith's male of *atriceps* were identical to *communis*, and furthermore, that the male of *atriceps* was conspecific with Cameron's *alpestris*.

Murray treated *alpestris* as a Costa Rican/Panamanian subspecies of *communis* (i.e., *atriceps*) because of slight external morphological differences. The female clypeus was "... slightly more bulging in the middle than in typical *communis*" and the arolium was "... large, being considerably larger than in typical *communis* and almost as large as in *violaceipennis*." These female differences do not withstand scrutiny. The size of the arolium depends on the degree of its inflation, and the convexity of the clypeus varies. Murray differentiated the male of *alpestris* from *communis* by the presence in the former of erect white setae on the clypeus (all black in *communis*). The pale clypeal setae of the male differentiates the Costa Rican/Panamanian *alpestris* from typical *atriceps*. In addition, the erect setae on the gena are also pale in *al-*

Figs. 10–11. Scanning electron photomicrographs of male genitalia of *Ammophila* in lateral profile. 10, *A. centralis* (30 km n Liberia, Guanacaste Prov. Costa Rica), 11, *A. gaumeri*. (Quezaltepeque, El Salvador).

*pestris* (unlike *atriceps*). The erect setae of the male thoracic pleura are extensively pale in *alpestris*, and even the coxae and lateral areas of the pronotal collar and scutum sometimes have pale erect setae. In typical *atriceps* pale setae are restricted to the pleura and are often intermixed with black setae. Murray (1940:31) also noted that the shape of the male clypeus varied in *alpestris*, some specimens looking like typical *atriceps*, others being more broadly truncate. I have examined the large series of males from La Carpentera [1200–1800m], Costa Rica, collected by W. Mann in April 1924 (WASHINGTON) studied by Murray, and can confirm the clypeal variation, but most specimens are more or less typical of *atriceps*. Perhaps this variation is to be expected at the extreme southern end of the species' range.

One male from La Carpentera was misidentified by Murray (1940:64) as *robusta* (Cresson). Apparently Murray misassociated the genitalia of this specimen with

those from a male of *robusta*, and on that basis erroneously recorded Cresson's species from Costa Rica.

I have studied the holotype of Cameron's *piceiventris*, as well as three females from Totonicapam, Guatemala, mentioned in the original description as "probably referable to the same species." There is also another female from the type locality, and it, and the Totonicapam specimens, are smaller (13–15 mm long) than the type (19 mm), and entirely black. These four are undoubtedly examples of *atriceps*, but the identity of the holotype of *piceiventris* is puzzling. Murray (1940), who did not study the type, treated it as a questionable synonym of *communis* (i.e., *atriceps*). The problem with this specimen is that abdominal terga II-V are amber rather than black as noted by Cameron and shown by his figure 7 on plate II. Small areas of the thorax, especially the pronotum and legs, have similar coloration. The holotype may simply have been collected in some type of flu-
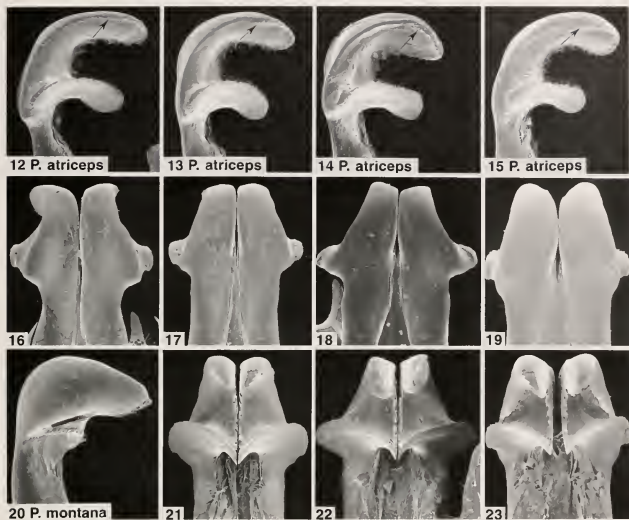
Figs. 12–23. Scanning electron photomicrographs of male genitalia of *Podalonia*, all but 20 are *atriceps*. 12–15, penis valve head in lateral profile (arrow marks end of row of teeth); 12, specimen from Volcan de Chiriquí, Panamá; 13, specimen from La Carpentera, Costa Rica; 14, specimen from Paria Canyon, Arizona; 15, specimen from Boulder, Colorado. 16–19, dorsal view of penis valve head shown in 12–15, respectively. 20. penis valve head of *P. montana* in lateral profile, specimen from Ahuacatlan, México. 21–23, ventral view of penis valve head shown in 13–15, respectively.

id that brought on discoloration, because the specimen otherwise looks like *atriceps*.

Murray's (1940:29) description of the subspecies *Podalonia communis intermedia* was based on a single male from the Federal District of México. It differs from North American material of the species, and from the Costa Rican/Panamanian population, in having an entirely black abdomen. I have examined the holotype (WASHINGTON) and agree with Murray that the genitalia are identical with those of *communis* (i.e., *atriceps*, see Figs. 12–13, 16–17). I have also found five additional males

of this taxon from San Marcos, Guatemala, elevation 3052 m (WASHINGTON), and one male from Cerro Verde, El Salvador (WASHINGTON). Apparently it is a melanic, high altitude form of *atriceps*. The erect body setae are black except on the mesopleura where pale and black setae are mixed just as in males of typical *atriceps*. It is likely that Murray's *intermedia* is a junior synonym of *piceiventris* Cameron, described from 7800′ in Guatemala, but males of the latter will have to be collected at the type locality to settle the matter.

The range of *atriceps* includes the west-
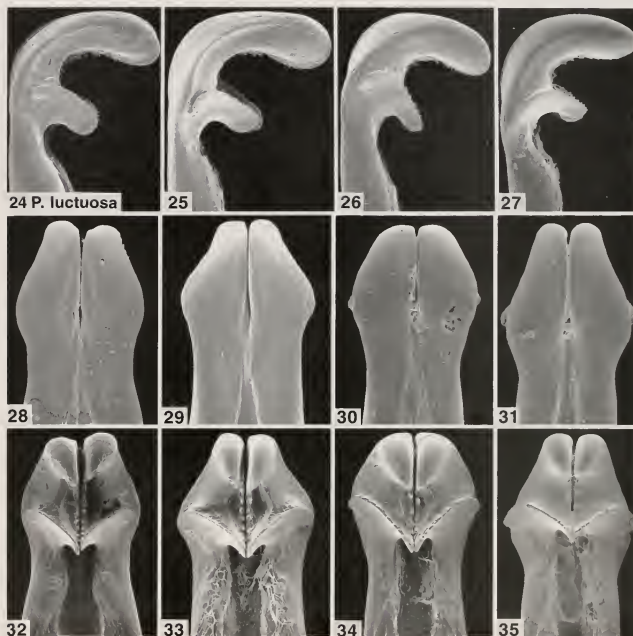
Figs. 24–35. Scanning electron photomicrographs of male genitalia of *Podalonia luctuosa*. 24–27, penis valve head in lateral profile (arrow marks end of row of teeth); 24, specimen from Hallelujah Junction, California; 25, specimen from Shoshone, Idaho; 26, specimen from "Cochetopa Natl. Forest", (probably Saguache Co.), Colorado; 27, specimen from Powell, Wyoming. 28–31, dorsal view of penis valve head shown in 24–27, respectively. 32–35, ventral view of penis valve head shown in 24–27, respectively.

ern half of North America, the central plateau of México, and Central America as far south as northern Panamá. Apparently it occurs only at high elevations in Mesoamerica, and differences between such isolated populations are to be expected. *Podalonia* has been poorly sampled in Central America; thus, I feel it would be premature to recognize the Costa Rican/Panamanian

*alpestris* and Mexican/Guatemalan/El Salvadoran *intermedia* (= *piceiventris*?) as subspecies of *atriceps*.

*Podalonia atriceps* is similar to *P. luctuosa* (Smith), another common North American species that is sympatric in the west, but which occurs across the continent in the north. In fact, Murray (1940) had difficulty separating females of *luctuosa* and *com-*

munis (i.e., *atriceps*). Of the separating features in couplet 29 of his key, only the deeply impressed frontal line of female *luctuosa* seems to separate it reliably from females of *communis* (i.e., *atriceps*) in which the frontal line is not impressed. But this difference may be artificial and needs careful scrutiny. The only differences between males of the two species are clypeal shape and structure of the penis valve (compare Figs. 12–14, 16–18, and 24–31). I have examined the material of both taxa in the collection of the National Museum of Natural History, Washington D.C., much of it identified by Murray, and there seems to be variation in the form of the male clypeus and penis valves of both species. The clypeal margin in *luctuosa* was said by Murray to be "more or less broadly transverse". By that he meant the straight or slightly concave portion of the free margin was broader than in *atriceps*. Generally this is true, but when many specimens are examined, the distinction is not always clear. The male genitalia appear more reliably diagnostic. The essential difference is the shape of the penis valve in dorsal outline. In *atriceps* the outer edge is abruptly angled at the point where the ventral toothed flange ends dorsad (Figs. 16–18). In *luctuosa* the outer edge of the penis valve is an uninterrupted arc at this point (Figs. 28–31). Another apparent difference is seen in the fringe of teeth along the inner, ventral margin of the penis valve head. In *atriceps* this row of teeth passes around the lower end of the penis valve head and extends dorsad for some distance (Figs. 12–15). In *luctuosa*, this row of teeth does not extend as far dorsad (Figs. 24–27). Examination of the penis valves of many males of *luctuosa* and *atriceps* from North America has demonstrated to me that in occasional specimens the dorsal outlines described above are not always clearly diagnostic (for example, see Fig. 19). However, in such doubtful cases, the fringe of teeth along the inner, ventral margin of the penis

valve head seems to be reliable for discrimination. Nonetheless, the separation of *atriceps* and *luctuosa* should be studied further.

## Podalonia montana (Cameron)
### (Fig. 20)

*Ammophila montana* Cameron, 1888:20. Holotype: male, Ventanas, Durango, México, 4000' (LONDON).

*Ammophila jason* Cameron, 1888:20. Holotype: female, San Gerónimo, Guatemala (LONDON). Synonymy by Murray, 1940:46.

*Ammophila quadridentata* Cameron, 1888:23. Holotype: female, Ventanas, Durango, México (LONDON). Tentative synonymy by Murray, 1940:46, confirmed here.

Bohart and Menke (1976) list this large wasp from México and Guatemala, and I have seen material from Nicaragua (WASHINGTON). Menke and Parker (1996) recorded *montana* from Costa Rica based on a single male and three females from Finca Montezuma, Guanacaste Province (LOGAN). Guanacaste Province may prove to be the southernmost range of *montana*. Collecting times were February and March suggesting that *montana* may be a dry season species.

The irregularly toothed female clypeus immediately identifies this sex of *montana*. The male abdominal terga of *montana* are black except I and II are red laterally. In males of *atriceps* terga I and II are entirely red. The penis valve heads of the male genitalia of these two species differ markedly (compare Figs.12, 20).

I examined the type material of Cameron's three names in 1964 and confirm Murray's (1940) synonymy.

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# First Chromosome Records for the Superfamily Ceraphronoidea and New Data for Some Genera and Species of Evanioidea and Chrysididae (Hymenoptera: Chrysidoidea)

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*Abstract.*—The first data on chromosome numbers and karyotypes of the Ceraphronoidea (Megaspilidae) are presented. New data is presented for one species of Gasteruptiidae (Evanioidea ) and 3 species in two genera of Chrysididae increasing our knowledge of karyotypes in these families. Phylogenetic implications of these data are briefly discussed.

Despite intensive chromosome study of parasitic wasps including the less derived groups of aculeate Hymenoptera during the last few years (see Gokhman and Quicke 1995 for review), some entire families and even superfamilies still remain totally or largely untouched by karyological investigation. The superfamilies Ceraphronoidea, Evanioidea and Chrysidoidea are among the latter. There are no data at present on chromosomes of these groups except for one gasteruptiid *Gasteruption breviterebrae* (listed under *Trichofoenus*, a junior synonym of *Gasteruption*), and one chrysidid, *Omalus djozanus hondonis* (Hoshiba and Imai 1993), and two chrysidoids from the family Bethylidae (Gokhman and Quicke 1995; table 1). In Hoshiba & Imai a chromosome number for a *Trichofoenus* sp. (a junior synonym of *Gasteruption*) is listed *loc. cit.* as a sphecid under the Larrinae, but this was apparently a mistake and Hoshiba (pers. comm.) has kindly had the specimen, identified as *Gasteruption breviterebrae* Watanabe. We have studied for the first time chromosome numbers and karyotype of the family Megaspilidae (the first records for the superfamily Ceraphronoidea), and a second species of *Gasteruption* and three species in two genera of Chrysididae for

which family there was previously only one published karyotype. Chromosome preparations were obtained from adult wasps collected from the wild at Silwood Park, Berkshire, U.K., during May-July 1995. Preparations were made according to the previously described protocol (Gokhman and Quicke 1995). Chromosomes were subdivided into four groups—metacentrics (M), submetacentrics (SM), subtelocentrics (ST) and acrocentrics (A) following Levan *et al.* (1964) and Imai *et al.* (1977). Voucher specimens are deposited in the Natural History Museum, London.

## RESULTS

### Ceraphronoidea: Megaspilidae

*Dendrocerus carpenteri* (Curtis). 2n = 18 (4M + 8SM + 6ST); NF = 36 (Fig. 1a). All chromosomes are obviously two-armed. Two pairs of metacentrics differ notably in size, the second is the smallest chromosome in the set. The submetacentric chromosomes show a continuous gradation in length. The third pair of subtelocentrics is much shorter than the other two.

### Evanioidea: Gasteruptiidae

*Gasteruption breviterebrae* (Watanabe). 2n = 28 (4M + 24A)

Table 1. Chromosome numbers in the Ceraphronoidea, Evanioidea and Chrysidoidea

| Taxon | n* | 2n* | Reference |
|---|---|---|---|
| **Ceraphronoidea** | | | |
| Megaspilidae | | | |
| *Dendrocerus carpenteri* (Curtis) | 9 | 18 | present paper |
| **Evanioidea** | | | |
| Gasteruptiidae | | | |
| *Gasteruption breviterebrae* Watanabe | *28* | 14 | Hoshiba & Imai 1993 |
| *Gasteruption jaculator* (L.) | *16* | 32 | present paper |
| **Chrysidoidea** | | | |
| Bethylidae | | | |
| *Epyris niger* Westwood | *14* | 28 | Gokhman and Quicke 1995 |
| *Laelius utilis* Cockerell | 10 | 20 | Gokhman and Quicke 1995 |
| Chrysididae | | | |
| *Chrysis viridula* L. | 21 | 42 | present paper |
| *Hedychridium ardens* (Coquebest) | ?19 | ?38 | present paper |
| *H. roseum* (Rossi) | 19 | 38 | present paper |
| *Omalus djozanus hondonis* (Tsuneki) | 19 | *38* | Hoshiba and Imai 1993 |

* In papers which only quote n or 2n, the other value has been surmised and is given in italics.

*Gasteruption jaculator* (L.). $2n = 32$ (8M + 8SM + 8ST + 8A); NF = 56 (Fig. 1b). Four pairs of acrocentrics were found in the karyotype. First pair of metacentric chromosomes is obviously larger than the others, and the last pair of submetacentrics is notably shorter than the preceding ones.

### Chrysidoidea: Chrysididae

*Hedychridium roseum* (Rossi). $2n = 38$ (6M + 12SM + 10ST + 10A); NF = 66 (Fig. 1c). Five pairs of acrocentric chromosomes are present in the karyotype. The last pairs of meta- and submetacentrics are obviously shorter than the other chromosomes of their respective types.

*Hedychridium ardens* (Latreille). $2n \approx 38$ A single metaphase plate with approximately 38 chromosomes was also found in this species.

*Chrysis viridula* L. $2n = 42$

### DISCUSSION

The above results, which are summarized in Table 1 and Fig. 1, provide new information about the chromosomes of various hymenopteran taxa that may be of use in elucidating phylogenetic relationships,

though at present too little is known about the variation in many families and superfamilies to draw any firm conclusions. Both the Ceraphronoidea and Evanioidea are currently believed to belong to the same clade which forms a sister group to the remaining Apocrita (Rasnitsyn 1988). Gokhman and Quicke (1995) hypothesised that the plesiomorphic haploid chromosome number in parasitic Hymenoptera (and therefore in the Apocrita as a whole) is likely to have been greater than 7, and most probably about 10 or 11. This agrees quite well with the value $n=9$ found for the megaspilid, *Dendrocerus carpenteri*. The considerably higher $n$ values in the *Gasteruption* species may represent a synapomorphy for the family, but the interspecific differences suggest that karyology man also be useful in species differentiation in this group. As for the Chrysidoidea, the higher chromosome numbers found in the Chrysididae compared with the two bethylids for which data are available, may represent a synapomorphy for the nominative family (see Brothers and Carpenter 1993). Of the chrysid genera investigated to date, *Hedychridium* and

a       b       c
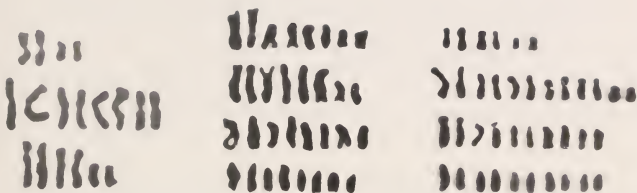


Fig. 1. Karyograms of the Ceraphronoidea, Evanioidea and Chrysidoidea. a, *Dendrocerus carpenteri* (Curtis); b, *Gasteruption jaculator* (L.); c, *Hedychridium roseum* (Rossi).

*Omalus*, both characterised by having $n=19$, belong to the Omalini, whereas the higher value of $n=21$ found for *Chrysis* (Chrysidini) may be an autapomorphy.

## ACKNOWLEDGEMENTS

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# Morphology of Antennal Gustatory Sensilla and Glands in Some Parasitoid Hymenoptera With Hypothesis on Their Role in Sex and Host Recognition

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*Abstract.*—On the basis of scanning and transmission ultrastructural investigations of nine species of parasitoids in four superfamilies along with scanning data on seven other species in three additional superfamilies, several new sensory and secretory antennal structures are defined. These are: uniporous gustatory sensilla (UGS), multiporous gustatory sensilla (MGS), male ventral (MVG) and lateral (MLG) glands, male and female dorsal gland (MDG, FDG), and accessory glands (AG) associated with MGS. Using these structures, two functional areas, "touch and taste area" and "release and spread area", are proposed in an attempt to associate them with behavior and to clear some nomenclatural problems in different taxa. It is suggested that the role of these areas is chemical communication during sexual and host recognition. Limited observations indicate that non-parasitoid Aculeata also have some of these structures.

## INTRODUCTION

The antennae of parasitic Hymenoptera are segmented appendages that have been subdivided in various ways. Although the antennae consist of a series of segments, we prefer the term antennomer. Most commonly the antennae are divided into scape with radicula, pedicel, anelli and flagellum (Fig. 1a) (e.g. Boucek 1988). However, these can often be further subdivided based on the modification of several antennomers. For example, often the distal antennomers are enlarged forming a clava with the remainder being called the funicle. This situation is common in females, but in certain taxa may also occur in males.

In general these various labeled antennomers are numbered according to the smaller subdivision resulting in, for example (Fig. 1a), six funicular antennomers and three claval antennomers. However, using such a system becomes cumbersome when comparing the morphology and function of the various antennomers be-

tween the sexes or between species, or in consideration of the evolutionary relationships of the various antennomers in different groups.

Another common system numbers the antennomeres consecutively from the scape or first antennomere (A1), pedicel (A2) and so on (Fig. 1b) and is followed here for the sake of uniformity and simplicity. For the same reason, but especially for the still controversial opinions about the true structure of anelli (Richards 1956; Graham 1969; Schauff 1986; Boucek 1988; Hayat 1990; Gauld and Bolton 1988), they are not numbered here.

Traditionally the antennae have been described as sensory appendages which may support a large number of sensilla of different types (Miller 1972; Richerson *et al.* 1972; Weseloh 1972; Voegele *et al.* 1975; Borden *et al.* 1978; Barlin and Vinson 1981; Cave and Gaylor, 1987; Bin *et al.* 1989; Navasero and Elzen 1991; Olson and Andow 1993). Using external features many different names have been proposed, possibly for the same type of structure, or in-
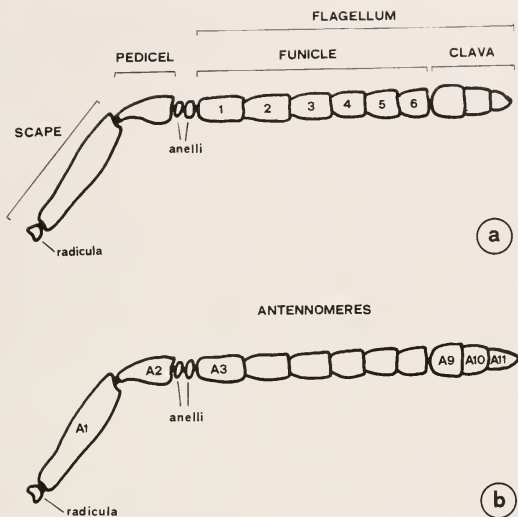
Fig. 1. Comparison of the different types of antennal terminology: a) traditionally used; b) adopted in the text.

versely one name may cover different structures, so causing confusion in the literature. Only through the study of internal details can the sensilla and associated structures be correctly defined and relatively few of these structures have been so studied with many others still to be investigated.

This has become more apparent as ultrastructural studies have revealed that some obvious features, as well as inconspicuous or obscured features and structures, thought to be sensilla, were actually release sites of glands (Dahms 1984; Bin and Vinson 1986; Bin et al. 1989; Pedata et al. 1993; Isidoro and Bin 1995). One other recent aspect is that some glands and sensilla can be in close association (Bin et al. 1989).

In this study only the sensory and secretory structures that probably come into contact for chemical communication during sexual and host recognition have been investigated. We provide new anatomical evidence for the function of some of the antennal structures. We also make comparisons among different taxa, reinterpret the functions of antennae in some groups of parasitoids, relating some of the structures to behavior. Some information on the Aculeata is included.

MATERIALS AND METHODS

The insects examined in this study are presented in Table 1. For scanning electron microscopy (S.E.M.) observations, males and females were anesthetized in $CO_2$, beheaded, and immediately im-

Table 1. The antennae of the species and sex examined with SEM and TEM are presented

| Taxa | Sex | SEM | TEM |
|------|-----|-----|-----|
| Ichneumonoidea | | | |
| Ichneumonidae | | | |
| *Cylloceria melancholica* Gravenhorst | ♂ | + | |
| *Ichneumon sarcitorius* L. | ♂ | + | |
| *Pimpla hypocondriaca* (Retzius) | ♂ | + | |
| Proctotrupoidea | | | |
| Diapriidae | | | |
| *Trichopria (?drosophilae)* (Perkins) | ♂ ♀ | + | + |
| *Coptera occidentalis* (Muesebeck) | ♂ ♀ | + | + |
| Ceraphronoidea | | | |
| Ceraphronidae | | | |
| *Aphanogmus steinitzi* Priesner | ♀ | + | |
| Chalcidoidea | | | |
| Aphelinidae | | | |
| *Encarsia asterobemisiae* (Vigg. & Mazz.) | ♀ | + | + |
| Mymaridae | | | |
| *Polynema striaticorne* (Girault) | ♀ | + | |
| Trichogrammatidae | | | |
| *Trichogramma brassicae* (Bedzenko) | ♀ | + | + |
| Platygastroidea | | | |
| Platygastridae | | | |
| *Amitus spiniferus* (Brethes) | ♂ ♀ | + | + |
| Scelionidae | | | |
| *Mantibaria anomala* Dodd | ♀ | + | + |
| *Telenomus chloropus* (Thomson) | ♀ | + | |
| *Trissolcus basalis* (Wollaston) | ♂ ♀ | + | + |
| *Trissolcus simoni* (Mayr) | ♀ | + | + |
| Chrysidoidea | | | |
| Dryinidae | | | |
| *Neodryinus typhlocybae* (Ashmead) | ♀ | + | + |
| Vespoidea | | | |
| Vespidae | | | |
| *Vespa crabro* (L.) | ♂ | + | |

mersed in 50% ethanol solution and kept overnight at 4°C. After dehydration in a graded ethanol series, the heads with antennae were critical point-dried in a Balzers Union CPD 020 unit, gold coated in a Balzers Union SCD 040 unit, and finally examined with Philips 501 B, Philips XL 20 and Jeol JSM 35. In some cases specimens were previously treated with Neutrase to remove secretions from the sensilla or with KOH to reveal additional release and spread structures (Bin and Vinson 1986).

The semi-schematic tridimensional drawings represent the results of transmission electron microscopy observations, either published (Bin *et al.* 1989; Isidoro and Bin 1995; Pedata *et al.* 1995) or "in preparation".

## RESULTS

### Gustatory Sensilla

Based on both external and internal morphology there is a group of sensilla that are relatively thick walled and have either one, or rarely a few, apical pores (uniporous) or have a numbers of pores

(multiporous) distributed on an area that varies in shape and size (Altner and Prillinger 1980; Zacharuk 1985). Further, these sensilla are only located in areas that are associated with touching the substrate, host or opposite sex (Weseloh 1972; Norton and Vinson 1974b; Bin *et al.* 1988; Vinson *et al.* 1988). For these reasons we have considered these sensilla as gustatory.

## Uniporous Gustatory Sensilla (UGS)

These are typical sensilla chaetica, generally long, straight antennal setae (hairs) that stick out (Fig. 2a–b). These sensilla have a fluted setal shaft tapering from the base to the rounded uniporous tip (Fig. 2c). The cuticular wall is relatively thick. The UGS are present in both sexes and are either clustered at the apical antennomere or latero-ventrally in several antennomeres (Figs. 2, 3 a–c). The cellular components consist of three sheath cells (techogen, tormogen and trichogen) and five sensory neurons, 4 of which are chemoreceptors. The 4 dendrites reaching unbranched to the apical pore with the 5th one functioning as a mechanoreceptor (Fig. 3d). Therefore, we suggest that the UGS respond not only to chemicals acting on contact, but also respond to mechanical stimuli. These common ultrastructural features have been ascertained in *Trissolcus basalis* (Bin *et al.* 1989), *Amitus spiniferus* and *Encarsia asterobemisiae* (in preparation).

We suggested that sensilla with a similar external appearance and location, commonly reported in different taxa, can be referred to with different names, can be referred to as uniporous gustatory sensilla. Some examples are the thick walled pegs (Slifer 1969), sensilla chaetica (Miller 1972; Wibel 1984; Bin *et al.* 1989), and fluted basiconic sensilla (Norton and Vinson 1974a, 1974b; Navasero and Elzen 1991) described from various parasitic species.

## Multiporous Gustatory Sensilla (MGS)

These are present ventrally only in females and their shape, number and pattern per antennomere varies remarkably within different groups. The multiporous area is also variable in shape and size. In *Trissolcus basalis* the MGS appear as basiconic sensilla and occur in longitudinal pairs on several antennomeres, A7-A10, except the apical one, A11, which has only one (Fig. 4a). The cuticular apparatus consists of a short, conical peg inserted in a narrow shallow pit and terminating in an elongated sub-elliptical multiporous area with 7–8 transverse ridges grooved on the top. Each ridge consists of 4–7 lifetable lobes which cover a thin multiporous lamina (Fig. 5b). The multiporous area is generally covered with a secretion (Fig. 4b), from accessory glands (see below), which can be removed by a protease treatment (Fig. 4c). The cellular components consists of three well developed sheath cells enveloping a very high number of sensory neurons, about 420 (Fig. 5a). The perikaryons occupy most of the antennomere volume while outer dendritic segments, gradually tapering to the tip, end unbranched near the pores present on the multiporous area (Fig. 5b). In another scelionid, *Mantibaria anomala*, 3 or 4 MGS, with a conical shape and a smaller multiporous area innervated by 120 sensory neurons, are present on the apical antennomere (Fig. 4 d–e). No accessory glands are found in this species (in preparation).

In the platygastrid *Amitus spiniferus* the MGS are distributed in a similar way to *Trissolcus basalis* but in a smaller number. One is present on A8 and A10 and 2 on A9 (Fig. 4 f-g). However these are deprived of the accessory glands. Further, the multiporous area is smaller and only innervated by 220 sensory neurons (in preparation).

In *Trichogramma brassicae* there are about 20 MGS distributed on the distal half of the apical antennomere (Fig. 6a). Externally they resemble recurved sensilla trichoidea and are laterally flattened (Fig. 6b) with numerous pores located along the sharp outer margin of the distal half of the sensillum (Fig. 7). Each sensillum is inner-
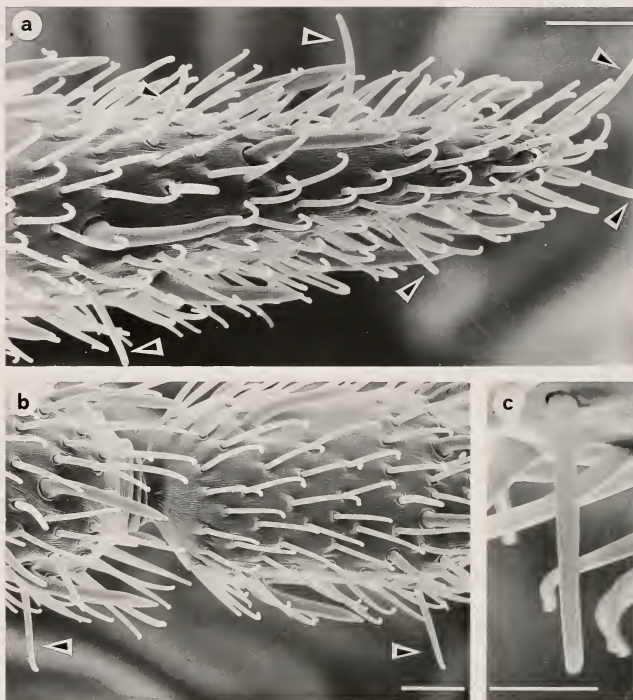
Fig. 2. Uniporous gustatory sensilla (arrows), an example in *Trissolcus basalis* male: a) clustered on apical antennomere, b) ventro-laterally located on other antennomeres, c) detail. (bars: a and b = 10 micron, c = 5 micron).

vated with 10 sensory neurons, with the outer dendritic segments running naked along the shaft lumen to reach the pores where some of them branch (Fig. 7).

In *Trichopria* sp. (probably *drosophilae*), A11 and A12 have about 20 and 40 MGS respectively, distributed in a large patch and interspersed with tactile hairs (Fig. 8a,

b). Each MGS is innervated by 5 sensory neurons. Only A12 presents a ventral accessory gland (in preparation).

## GLANDS

Antennal glands were first discovered in the antennae of male parasitoids (Dahms 1984, Bin and Vinson 1986; Pedata
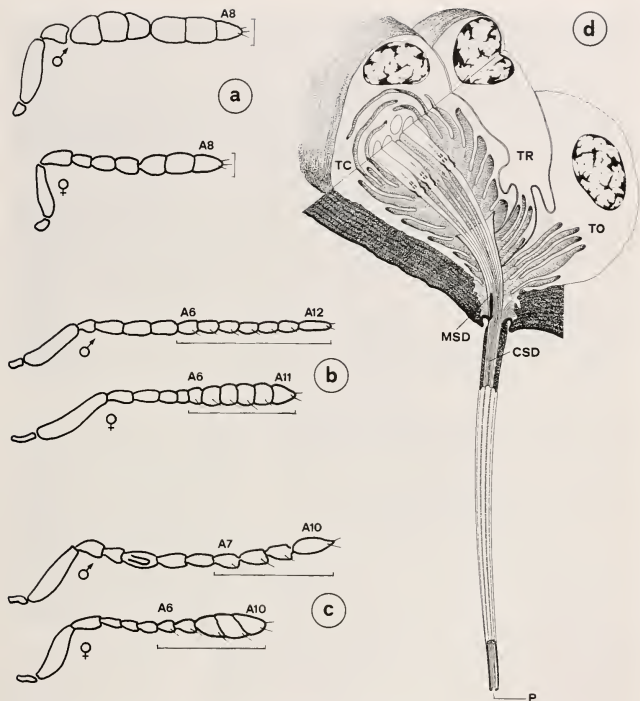
Fig. 3. Distribution of uniporous gustatory sensilla (arrows) on males and females of three different species showing some differences in location: a) *Encarsia asterobemisiae*, b) *Trissolcus basalis*, c) *Amitus spiniferus*. A diagram of a Uniporous Gustatory Sensillum based on data from *Trissolcus basalis* (d): CSD, chemosensory dendrites; MSD, mechanosensory dendrites; P, pore; TC, techogen cell; TO, tormogen cell; TR, trichogen cell. (Based on Bin *et al.*, 1989).

*et al.* 1993; Isidoro and Bin 1995) but have also been found in females (Bin *et al.* 1989). These glands occur in different locations and are thus classified accordingly. Some glands are associated with campaniform sensilla. Other glands are associated with multiporous gustatory sensilla and we

have considered them to be accessory glands to the MGS.

**Female Dorsal Glands (FDG)**

In female *Trissolcus basalis* shallow dorsal depressions are present on A7 to A11 (Fig. 10a, b). These depressions are the re-
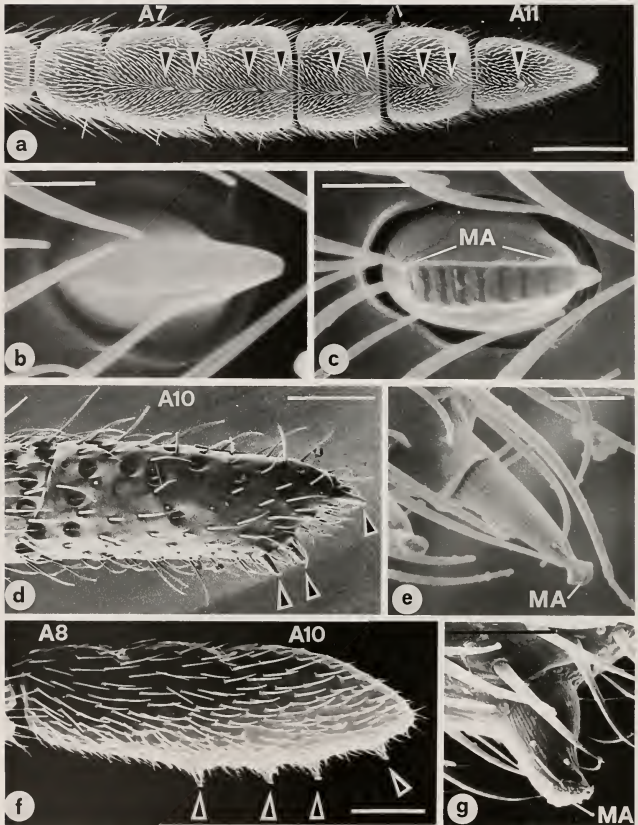
Fig. 4. Distribution of multiporous gustatory sensilla (arrows), in females of: a) *Trissolcus basalis*, ventral view; b) and c) single MGS before and after protease treatment respectively; d) and e) *Mantibaria anomala*, lateral view; f) and g) *Amitus spiniferus*, lateral view. MA, multiporous area. (bars: a = 50 micron, b and c = 2 micron, d and f = 25 micron, e and g = 5 micron).
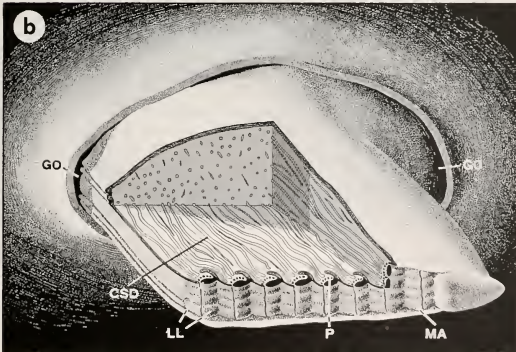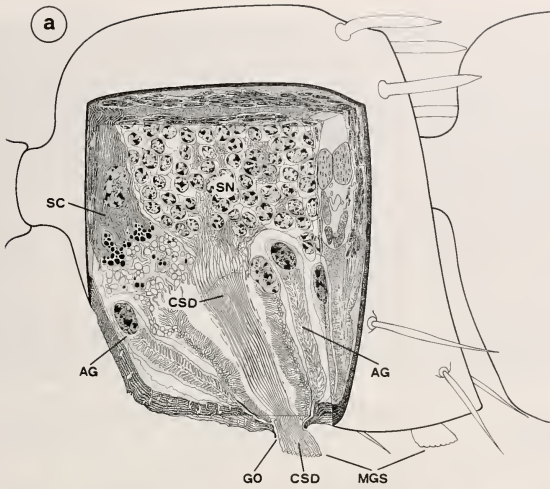
Fig. 5. Semischematic representation of multiporous gustatory sensilla (MGS) and associated accessory glands (AG) in *Trissolcus basalis*: a) internal view of a subapical antennomere, b) detail showing the multiporous area (MA). CSD, chemosensory dendrites; GO, glandular outlet; LL, liftable lobes; P, pores; SC, sheath cells. (Adapted from Bin *et al.*, 1989).

Fig. 6. Multiporous gustatory sensilla (some arrowed) of *Trichogramma brassicae* female: a) lateral view of apical antennomere, b) detail showing the multiporous area (MA). (bars: a = 25 micron, b = 5 micron).

lease sites of a series of extensive glands (Bin *et al.* 1989) forming a longitudinally elongated cluster of about 20 unicellular secretory units that correspond to class 1 gland cells of Noirot and Quennedey (1974, 1993) (Fig. 11a). The internal wall of the dorsal depression shows pores which correspond to the irregular outlets of the glands (Fig. 10c). The associated campaniform sensillum, visible from both an external and internal view (Fig. 10b, c) is innervated by a single sensory neuron whose dendrite terminates in a typical tubular body (Bin *et al.* 1989) (Fig. 11a).
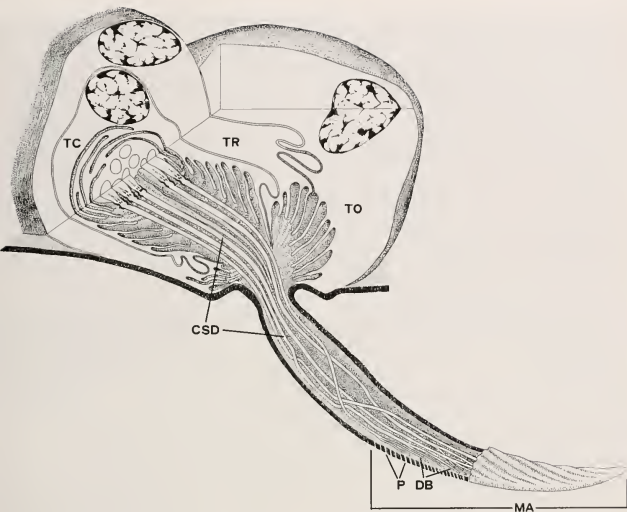
Fig. 7. Semischematic drawing of multiporous gustatory sensillum of *Trichogramma brassicae* female. CSD, chemosensory dendrites; DB, dendritic branches; MA, multiporous area; P, pores; TC, tecogen cell; TO, tormogen cell; TR, trichogen cell.

A similar type of gland is found in female *Trissolcus simoni*, but in this species the release sites are pits that occur on A4-A11 (Fig. 10d). Together with pits the campaniform sensilla are easily visible both externally (Fig. 10e) and internally (Fig. 10f). A dorsal gland in the antennae of *Amitus spiniferus* occurs in A8–A10, the claval segments being fused. This gland extends the length of the clava and occupies the dorsal half of the antennomeres (in preparation).

Another new case of these glands has been found in an aculeate parasitoid, the dryinid *Neodryinus typhlocybae*. In this species the antennomeres involved are A5 to A10. The glands belong to class 1 (in preparation). The conspicuous external structure is composed of 4 longitudinal deep grooves each incorporating a longitudinal lamina (Fig. 23a, b). These grooves have erroneously been thought to be sensilla and named rhinaria (Olmi 1984, 1994).

The function of the dorsal glands are not clear but, as described below, we suggest they play an important role in sex recognition.

## MGS Accessory Glands (AG)

These glands can be found associated with a single multiporous gustatory sensillum, as in *Trissolcus basalis*, or with a group of sensilla, as in *Trichopria* (probably *drosophilae*). In both situations the glands belong to type 1. In the first case there is at least a couple of glands per sen-
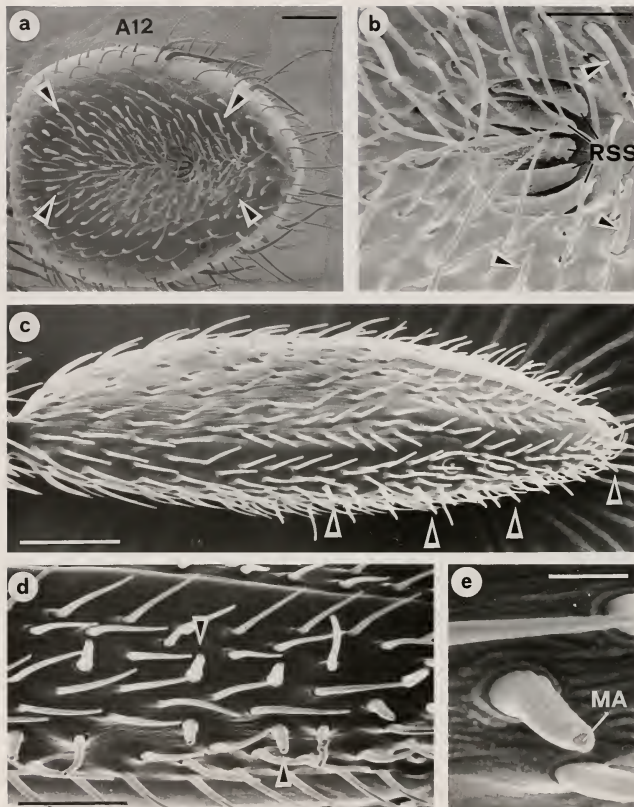
Fig. 8. Ventral view of apical antennomere in *Trichopria* (probably *drosophilae*) showing: a) area with MGS interspersed with trichoid sensilla (arrowed), b) detail with some MGS (arrowed) surrounding the release and spread structures (RSS). Suspected multiporous gustatory sensilla (some arrowed) of *Polynema striaticorne* female: lateral view (c) and ventral view (d) of apical antennomere; e) detail showing the possible multiporous area (MA). (bars: a and c = 25 micron, b and d = 10 micron, e = 2 micron).
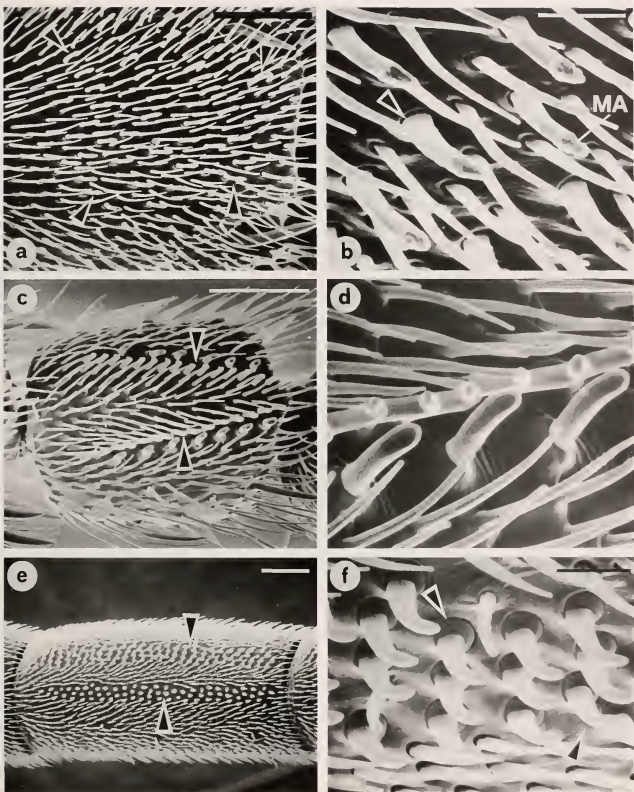
Fig. 9. Suspected multiporous gustatory sensilla (some arrowed) in ventral view of a-b) *Coptera occidentalis*, c-d) *Aphanogmus steinitzi*, e-f) *Neodryinus typhlocybae*. MA, possible mulitporous area. (bars: a, c and e = 25 micron, b = 10 micron, d and f = 5 micron).
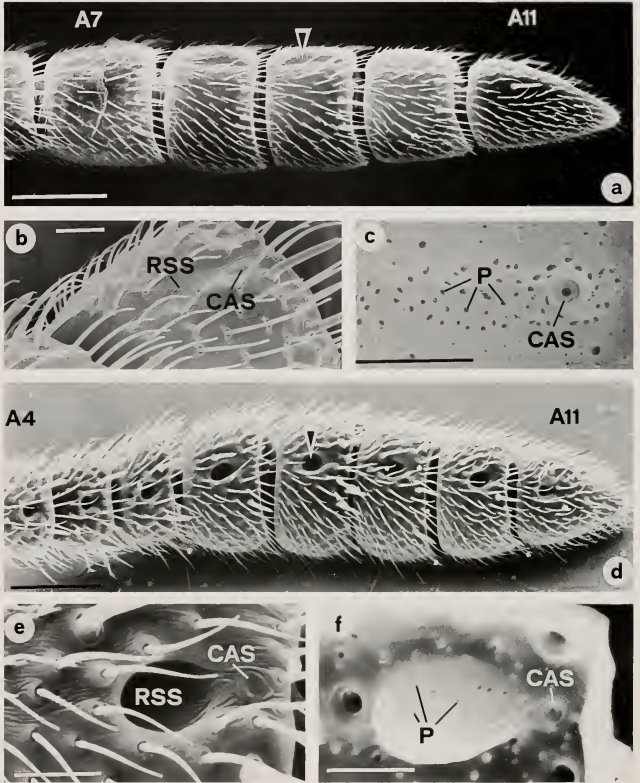
Fig. 10. Release and spread structures (RSS, one arrowed) of female dorsal glands in *Trissolcus basalis*: a) distribution in dorso-lateral view; b) details of external view with a campaniform sensillum (CAS) and (c) corresponding internal view . The same in *Trissolcus simoni* (d-f). P, pores. (bars: a and d = 50 micron, b, c, e and f = 10 micron).
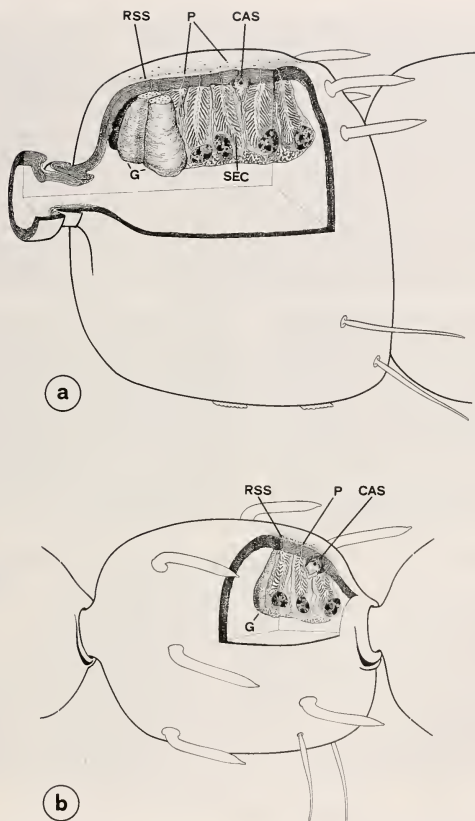
Fig. 11. Semischematic drawings of female (a) and male (b) dorsal glands of *Trissolcus basalis*. CAS, campaniform sensillum; G, gland; P, pores; RSS, release and spread structures; SEC, secretory cells. (Based on Bin et al., 1989).
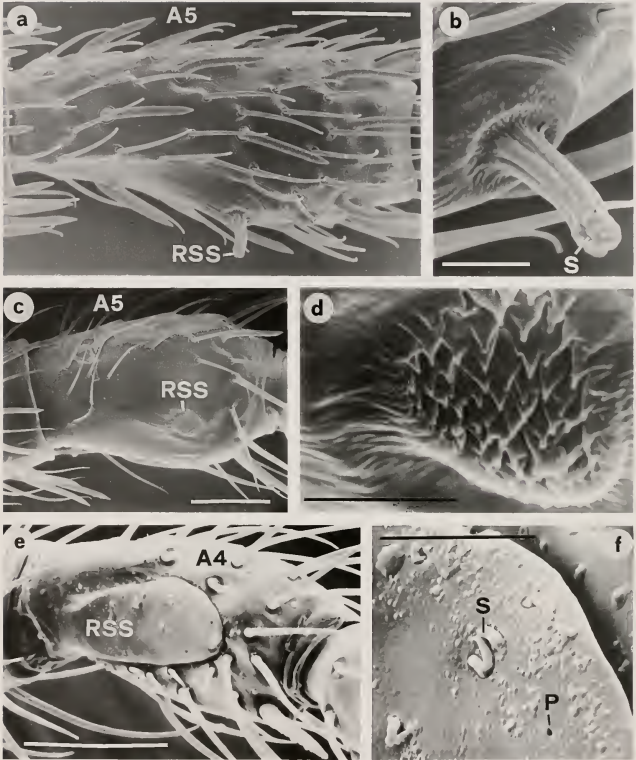
Fig. 12. Release and spread structures (RSS) of male ventral gland in: a-b) *Trissolcus basalis*; c-d) *Telenomus chloropus*. The same of male lateral gland (e-f) in *Amitus spiniferus*. S, secretion; P, pore. (bars: .a, c and e = 25 micron, b, d and f = 5 micron).

sillum having their outlets in the socket (Fig. 5) so that the secretion covers the multiporous area obscuring the cuticular ultrastructure (Fig. 4b) unless removed with proteolytic enzyme (Fig. 4c) (Bin *et al.* 1989). In the second case shown by *Trichopria* (probably *drosophilae* ) 5–6 glands open in the center of the apical antennom-
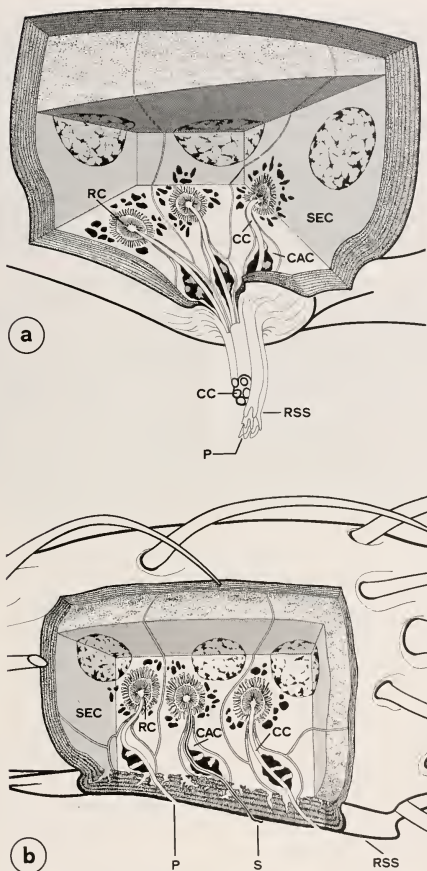
Fig. 13. Semischematic drawings of male ventral gland, lateral view, of *Trissolcus basalis* (a) and male lateral gland, dorsal view, of *Amitus spiniferus* (b). CAC, canal cell; CC, conducting canal; P, pore; RC, receiving canal; RSS, release and spread structure; SEC, secretory cell. (a: based on Bin & Vinson, 1986; b: based on Isidoro and Bin 1995).
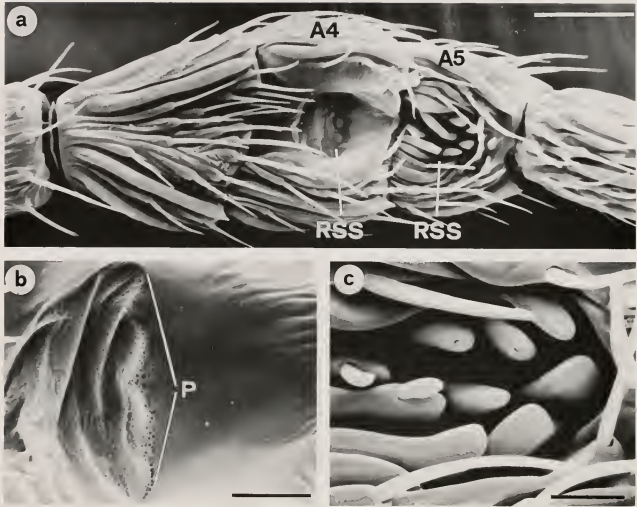
Fig. 14. Release and spread structures (RSS) of male ventral glands in *Encarsia asterobemisiae* (a) of different type in A4 (b) and A5 (c). P, pores. (bars: a = 25 micron, b and c = 5 micron).

ere (A12) (Fig. 8a, b) through 5–6 sub-conical porous structures located in a shallow depression surrounded and partially covered by MGS with setae (in preparation).

Although the role of the glands is not clear, a hypothesis is discussed in the section on "release and spread area".

## Male Dorsal Glands (MDG)

Male *Trissolcus basalis* have antennal glands located in the dorsal distal region of A6-A11 but no obvious cuticular structure appears with SEM observations. Only ultrastructural investigations show that the glands are of type 1 and small in size (Bin *et al.* 1989) as diagrammed in Fig. 11b. It also appears they are associated with a campaniform sensillum.

## Male Ventral and Lateral Glands (MVG and MLG)

These two types of glands may belong to the type 1 or 3, depending on the different taxa.

In the scelionid *Trissolcus basalis* the ventral gland on the modified A5 antennomere has an apparent release site consisting of a cylindrical peg, longitudinally fluted, and inserted in a shallow depression (Fig. 12a, b). The tip of the peg (the release site of the gland) when treated with protease shows 8–10 openings. Internally the gland consists of 8–10 isolated bicellular secretory units each formed by a secretory cell, corresponding to class 3 gland cells, and a canal cell forming the
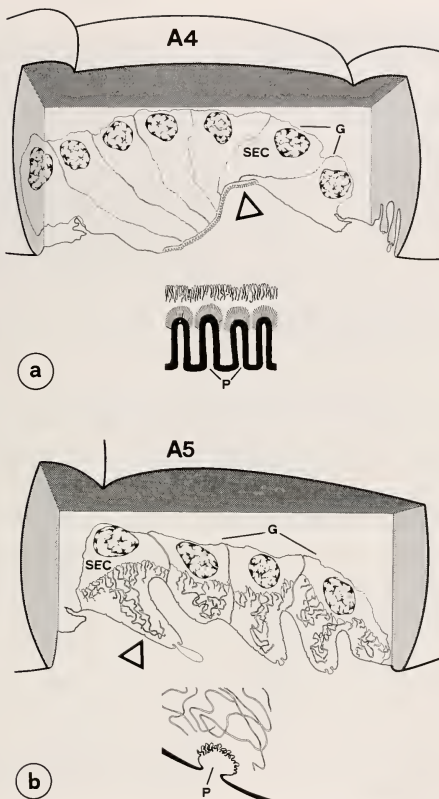
Fig. 15. Semischematic drawings of the two different types of male ventral glands in *Encarsia asterobemisiae*. Pores (arrows) of the two different release and spread structures in insets. G, glands; P, pores; SEC, secretory cell (based on Pedata *et al.* 1993).
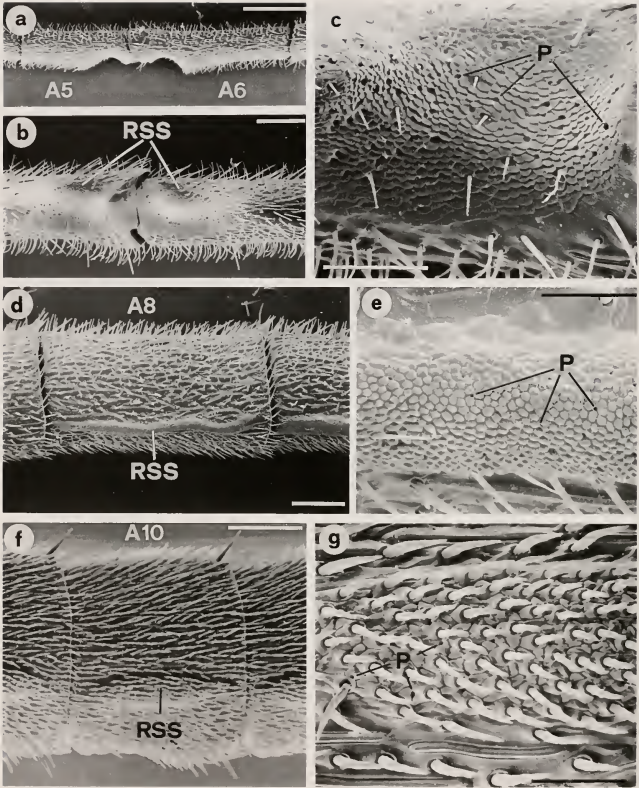
Fig. 16. Suspected release and spread structures (RSS) of male glands in some Ichneumonidae: a-c) *Cylloceria melancholica*; d-e) *Pimpla hypocondriaca*; f-g) *Ichneumon sarcitorius*. P, pores. (bars: a = 250 micron, b, d and f = 100 micron, c = 50 micron, e and g = 25 micron).
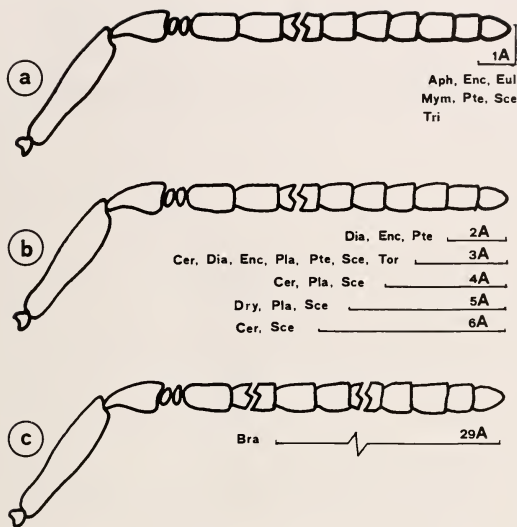
Fig. 17. Hypothetical female antenna with distribution of ascertained and supposed multiporous gustatory sensilla (MGS) in different taxa: a) apical and/or apico-ventral area, b) ventral area involving several antennomeres, c) ventral area involving many antennomeres. Aph, Aphelinidae; Bra, Braconidae; Cer, Ceraphron-idae; Dia, Diapriidae; Dry, Dryinidae; Enc, Encyrtidae; Eul, Eulophidae; Ich, Ichneumonidae; Mym, Mymar-idae; Pla, Platygastridae; Pte, Pteromalidae; Sce, Scelionidae; Tri, Trichogrammatidae; Tor, Torymidae.

conducting canal which connects the re-ceiving canal to the external glandular opening (Fig. 13a) (Bin and Vinson 1986).

The release site in not always an obvi-ous peg. For example on another scelionid the gland opens on the surface of the an-tennomere (Fig. 12d), but is even less ob-vious when covered by secretion (Fig. 12c). In the platygastrid *Amitus spiniferus* there is a lateral gland on modified A4 with an external release site in form of a glabrous elevated plate elliptical in shape and with about 20 scattered pores (12e, f). Internally, the gland consists of some 20 isolated bicellular secretory units similar

in structure to those observed in the male ventral gland of *Trissolcus basalis* (Fig. 13b) (Isidoro and Bin 1995).

In the aphelinid *Encarsia asterobemisiae* there are two ventral glands on modified A4 and A5 (Fig 14a). Externally the ventral side of A4 has a deep cavity with the bot-tom and the proximal wall perforated by numerous pores (Fig 14b), whereas the A5 has a concave area with 9 subconical cu-ticular projections (7 with a small spheri-cal structure on the tip and 2 with a spat-ulate structure) (Fig. 14 c). Internally, the two different release sites correspond to two integumentary glands, both belong-
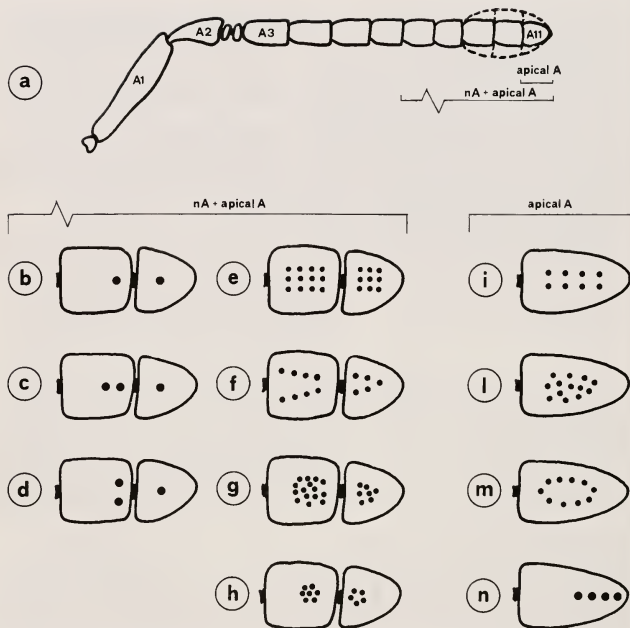
Fig. 18. Hypothetical female antenna (a) and distributional patterns of ascertained and supposed multiporous gustatory sensilla in different taxa: b) single, c) single and parallel pairs, d) single and transverse pairs, e) triple row, f) double row convergent, g) scattered, h) clustered, i) double row, l) scattered, m) elliptical, n) single row.

ing to the class 1 gland type, but with different cytological features (Fig. 15) (Pedata et al. 1993).

FUNCTIONAL AREAS AND THEIR POSSIBLE
BIOLOGICAL ROLE

The lack of anatomical studies of the antennal sensilla and other antennal structures or antennal regions has led to a presumption of a sensory function for these structures. Further, the diversity in the external morphology has resulted in a diversity of terms for these structures and regions. Thus, attempts to associate functions with receptor morphology have been predicated on an assumed sensory function. The realization that some of these structures are secretory and others are sensory along with common associations between these two, suggests a functional region may exist. We are here proposing a new terminology in the attempt to com-
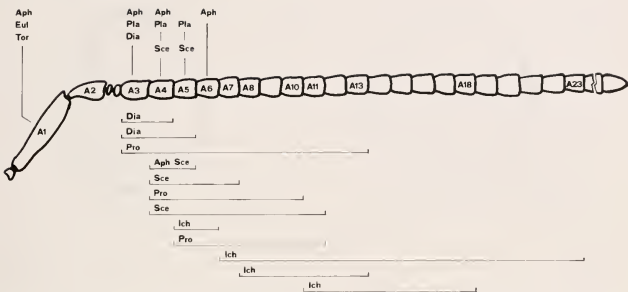
Fig. 19. Hypothetical male antenna with distribution of ascertained and supposed antennal glands in different taxa. Taxa having only one antennomere with gland are indicated above the antenna, those with more than one are reported below. Aph, Aphelinidae; Dia, Diapriidae; Eul, Eulophidae; Ich, Ichneumonidae; Pla, Platygastridae; Pro, Proctotrupidae; Sce, Scelionidae; Tor, Torymidae.

bine the new data illustrated above with the behavioral observations available from the literature.

### "Touch and Taste Area"

The occurrence of non-volatile chemicals perceived by the antennae which are important in host recognition have been described for a number of species of parasitoids (Vinson 1985, 1991). Similarly, non-volatile chemicals have been isolated from the braconid, *Cardiochiles nigriceps* Viereck, that are produced by females which only elicit sexual behavior in males on contact (Syvertsen *et al.* 1995). Thus, touch and "taste" appears to be important in both host and mate recognition.

The touch and taste area can be defined as an area of an antennomere or series of antennomeres that is associated with one or more gustatory sensilla. This definition includes both uniporous (UGS) and multiporous gustatory sensilla (MGS) which have to "touch" the active compound/s in order to "taste" the proper chemical stimuli. Further, the UGS, being equipped with a mechanoreceptor, can also perceive a mechanical stimulus while the MGS can-

not. The "area" is the portion of antennomere/s bearing one of this type of sensilla. Examples of "touch and taste areas" are documented here. In regards to UGS, this functional area can be found in both sexes. The functional area may be only the tip of the apical antennomere or may consist of the ventro-lateral side of several antennomeres. In contrast the touch and taste area involving the MGS are found only in females, either on the tip of the apical antennomere or ventrally on several antennomeres. These latter sensilla are, however, surrounded by numerous tactile trichoid sensilla, all oriented ("combed") towards the midline and the MGS, or they are interspersed with them.

Touch and taste areas involving UGS are present in *Encarsia asterobemisiae* (Fig. 3a), *Trissolcus basalis* (Fig. 3b), and *Amitus spiniferus* (Fig. 3c). Together the MGS, which lack mechanical receptivity, and the tactile sensilla form a touch and taste area as shown by MGS found in *Mantibaria anomala* (Fig. 4d–e; Fig. 18n), *Trissolcus basalis* (Fig. 4a–c; Fig. 18c), *Amitus spiniferus* (Fig. 4 f–g; Fig. 18c), *Trichogramma brassicae* (Fig. 6a; Fig. 18l) and *Coptera occiden-*
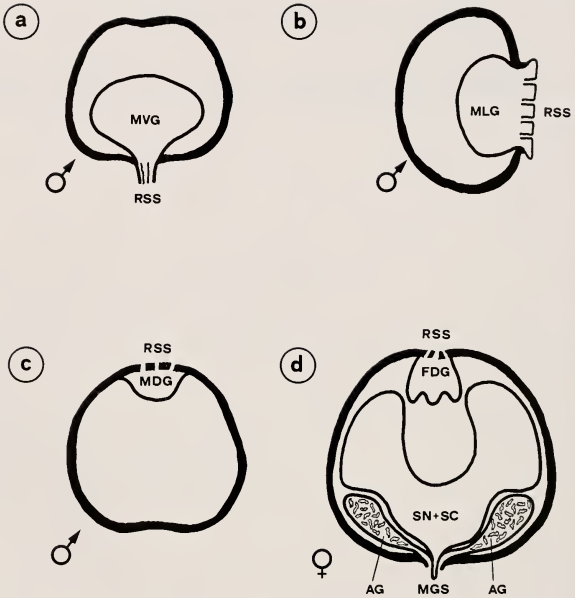
Fig. 20. Semischematic drawings of transverse sections of male (a, b, c) and female (d) antennomere showing localization and relative volume of glands and sensory neurons with sheath cells (SN + SC) of multiporous gustatory sensillum (MGS) (a, c, d: *Trissolcus basalis*; b: *Amitus spiniferus*). AG, accessory glands; FDG, female dorsal gland; MDG, male dorsal gland; MLG, male lateral gland; MVG, male ventral gland; RSS, release and spread structure.

*talis* (Fig. 9a–b; Fig. 18g). The evidence for a touch and taste area involving the MGS in the scelionid *Trissolcus basalis* and the platygastrid *Amitus spiniferus*, can conceivably be extended to the whole superfamily Platygastroidea. There are a number of authors who have focused on parts of the antennae, which we now refer to the "touch and taste area". Referring to these either as indefinite or as abrupt clava, or referring to a specific sensillar formula

(Bin 1981; Masner 1976; Masner and Huggert 1989), including the unique case of the genus *Nixonia* Msn. (Masner and Huggert 1989) (Fig. 18d). Further, we provide evidence (Fig. 18l) that the basiconic sensilla in *Trichogramma brassicae* are MGS forming a "touch and taste area" or "sole chercheuse" (= searching sole) proposed for *Trichogramma* species (Voegele *et al.* 1975; Olson and Andow 1993). In the diapriid *Trichopria* (probably *drosophilae*), a
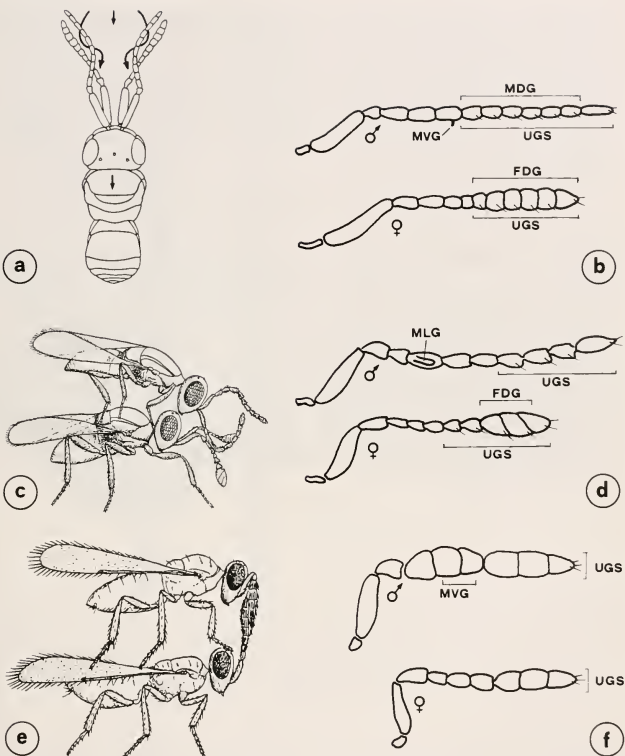
Fig. 21.   Suggested correlations between uniporous gustatory sensilla (UGS) and glands in sexual recognition. Precopulatory phase in a) *Trissolcus basalis*, c) *Amitus vesuvianus*, e) *Encarsia asterobemisiae*. Semischematic drawings of male and female antennae in *T. basalis* (b), *Amitus spiniferus* (d), and *E. asterobemisiae* (f). FDG, female dorsal gland; MDG, male dorsal gland; MLG, male lateral gland; MVG, male ventral gland. (c: from Viggiani and Battaglia, 1983a; e: from Viggiani e Battaglia, 1983b).
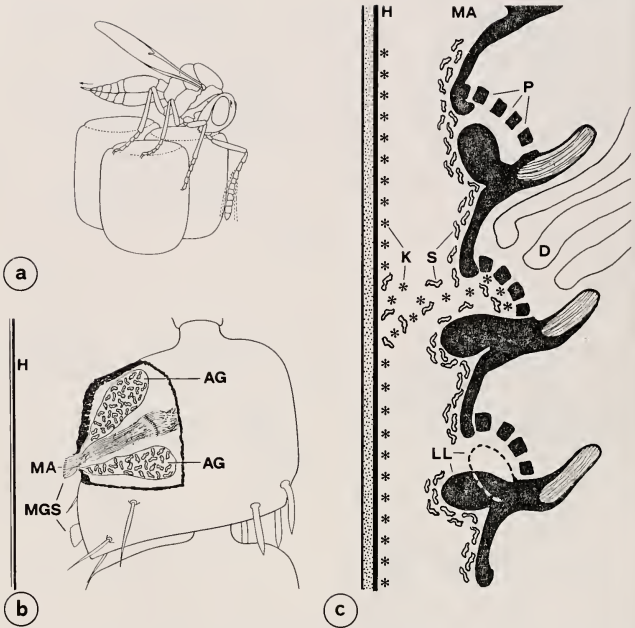
Fig. 22. Possible role of multiporous gustatory sensilla (MGS) and accessory glands (AG) in host recognition of *Trissolcus basalis*: a) host examination by antennal drumming and rubbing; b) semischematic detail of host egg (H) and antennomere with MGS and AG; c) semischematic detail of host and multiporous area (MA) of MGS. D, dendrites; H, host; K, kairomone; LL, liftable lobe; P, pores; S, secretion.

group of MGS interspersed with tactile setae defines a "touch and taste area" in the two apical antennomeres of a three segmented clava (unpublished).

Several other examples of distinct areas with characteristic sensilla have been reported in females of several parasitoid families. These could fit the definition of "touch and taste area" when anatomical studies of the sensilla are available. All the traditionally described clavomeres and

probably many of the non-incrassate antennomeres may exhibit a "touch and taste area" ventrally or ventro-laterally. Dessart (1994) proposed the term "thigmochore" or touching area for a region of the antennae of ceraphronids distinguished by an area with trichoidea and basiconica sensilla, "thigmomere" for any flagellomere provided with such an area, and "thigmus" for the continuous or discontinuous antennal segments bearing
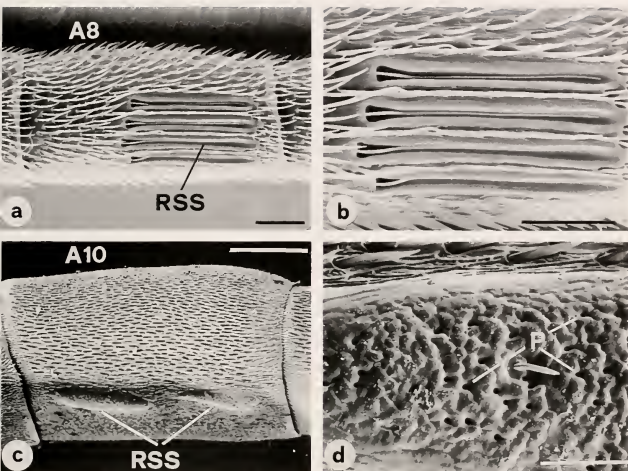
Fig. 23. Dorsal view of female antennomere 8 (A8) showing the release and spread structures (RSS) of dorsal glands in *Neodryinus typhlocybae* (a, b). Ventral view of male antennomere 10 (A10) with a couple of release and spread structures (RSS) in *Vespa crabro* (bars: a, b, and d = 25 microns, c = 250 microns).

thigmomeres. However, the presence of gustatory sensilla important in the detection of contact chemical cues (Vinson 1991) suggests a taste function as well. Some other possible examples of a "touch and taste area" involving gustatory and tactile sensilla include the following. In the mymarid *Polynema striaticorne* the clava exhibits a double row of blunt tip basiconic sensilla which likely have a multiporous tip (Fig. 8c-e, 18i). In Pteromalidae the clava has often an area of finer or at least different pilosity, usually collapsing in dry specimens, called the "micropilosity area" (Graham 1969; Boucek 1988). In some pteromalids (Miller 1972) the micropilosity area can be defined by thickwalled chemoreceptors. For some aphelinids the term "claval sensorial complex"

has been proposed, suggesting a host or mate recognition function (Polaszek and Hayat 1992). In some encyrtids the "sensory part of clava" is indicated by an area of micropilosity or microtubules or a sieve-plate structure which may be limited to the extreme apex of the antennae or extended almost to the base (Noyes and Hayat 1994). In other encyrtids the tip of the antenna is flattened and bears sensilla located in an elliptical pattern (Weseloh 1972; Domenichini 1977–78) (Fig. 18m). A torymid has patches composed of several fluted basiconic sensilla terminating apically in a small bulb-like structure (Domenichini 1977–78) which could be multiporous gustatory sensilla. These basiconica sensilla are likely multiporous gustatory sensilla arranged in different

patterns, triple row, double convergent rows, large patches (Fig. 18e,f,g) and at least in one case (Fig. 9c,d) could be of two different types. In the dryinid *Neodryinus typhlocybae* the ventral side of the 6 distal slightly thickened antennomeres presents short apically bent and flattened basiconic sensilla located in two longitudinal parallel bands, each composed of two-three rows (Fig. 9e, f). These could be multiporous gustatory sensilla (in preparation). Even the braconid *C. nigriceps* has fluted bent-tipped basiconic sensilla on the apical antennomere and the preceding 28, all appearing to contact the substrate during host searching (Norton and Vinson 1974a, 1974b).

Ascertained and suspected "touch and taste areas" are summarized in Fig. 17 which shows how the antennomeres involved may greatly vary in number between and within the groups, and are concentrated in the distal portion of the antenna. The functions of the "touch and taste areas" are likely correlated with intra- or interspecific communication, i.e. sexual or host recognition and discrimination, respectively.

## "Release and Spread Area"

This term suggests a double function for some cuticular structures which, while they "release" the gland secretion through pores, also may "spread" the secretion onto the proper sensilla or surface, or at least make contact with them. The "area" refers to single or numerous antennomeres, modified or unmodified, bearing any type of a "release and spread structure" (RSS), apparent or inconspicuous. The location of RSS reflects that of the respective glands, i.e. dorsal, ventral or lateral (Fig. 20a–d). All the glands listed in the previous section have a more or less characteristic RSS, including the special case of accessory glands (AG) which are associated with the MGS in some species (Fig. 20d).

The RSS connected with female dorsal glands (FDG) appear as shallow depressions in *Trissolcus basalis*, from A7 to a11 (Fig. 10a–b), or as deep pits in *Trissolcus simoni*, from A4 to A11 (Fig. 10d–e). The RSS are inconspicuous on A8-A10 of *Amitus spiniferus*. In an internal view of RSS in both species of *Trissolcus* the pores that penetrate the cuticular wall become apparent together with an opening associated with the campaniform sensillum (CAS) (Fig. 10b–c, e–f; 11a).

The release site of MGS accessory glands (AG) in *Trissolcus basalis*, is located in the sensillum socket (Fig. 5a–b; 20d). It seems logical that the spreading function be performed by the multiporous area at the tip of the sensillum which, in fact, appears to be covered by abundant secretion (Fig. 4b). What the general situation is within a family or superfamily, cannot be determined as yet since the scelionid *Telenomus busseolae* has an AG, whereas we have no evidence of such a gland in another scelionid, *Mantibaria anomala*, or the platygastrid *Amitus spiniferus* (in preparation). Therefore, the presence of MGS does not necessarily imply the existence of accessory glands.

The inconspicuous RSS of the male dorsal glands (MDG) in *Trissolcus basalis*, the only species for which such structures in males have been described so far (Bin *et al.* 1989), does not differ from the surrounding sculpture which includes the associated campaniform sensillum (CAS) (Fig. 11b).

In contrast, a great variety of RSS have been described for the male ventral (MVG) and lateral (MLG) glands, having been noticed for their appearance, but until recently (Dahms 1984, Bin and Vinson 1986, Bin and Isidora 1995, Pedata *et al.* 1995) confused with sensory organs. The RSS are often associated with variously modified antennomeres but also occur on unmodified ones.

Among the scelionids a number of species have a single modified antennomere, A5, for a which a gland and a peg-like release structure has been described in one

species (Bin and Vinson 1986). All the others, whether having single or multiple modified antennomeres, (Waterston 1923; Ogloblin 1930; Masner 1976, 1980; Galloway and Austin 1984; Villa and Mineo 1990a, 1990b), also have specialized structures such as carine (keels), tyloids, plates, or pegs, which can be suspected to be release and spread structures.

In the aphelinids a variety of RSS may exist and, as shown (Figs 14, 15), may even differ on different antennomeres of the same species. In some species specialized structures have been found on A1 or other antennomeres that appear as lamellar projections (Viggiani et al. 1986) or conical processes (Viggiani and Ren 1991), short setae or pegs on A3 or A4 (Viggiani 1985, 1987), or a ventral plate bearing numerous minute setae on A6 (Rosen and DeBach 1979).

In males of many species, "sexually" modified antennomeres have been reported (see below).

In diapriids a modified antennomere with a longitudinal carina with a tooth or a pointed tyloid, can be found on A3, A4 or A5 depending on the subfamily. In Belytinae a modified antennomere can be found on A3 or, with only one exception, on A4 (Nixon 1957; Masner 1993). In Ambositrinae a modified antennomere can be found as A3 and A4, but sometimes also A5 (Naumann 1987; Masner 1993) and in Diapriinae A4 (Masner 1991) or a few cases occur with A3 and A4 (Silvestri 1913, Nixon 1957; Huggert and Masner 1983; Early and Naumann 1990). A doubtful case is a species of Diapriinae having A1 to A3 remarkably modified (Baudoin 1962).

In eulophids a glandular release and spread site is documented in by Dahms (1984). Another spread and release site is suspected in Aprostocetus (=Tetrastichus) hagenowii because of the presence of a shallow trench at the center of A1 (Takahashi and Sugai 1982).

In platygastrids the only documented

case of a gland refers to the elevated lateral plate of A4 (Isidoro and Bin 1995). In other members of the family the secretory function can be suspected when the antennomeres are strongly bent ventrally or are much longer than the others, such modifications also occurring on A3 or A5. The specialized structures can be plates (MacGown 1979), or longitudinal sharp ventral carina which in some cases end in a subapical tooth (Masner and Huggert 1989).

In proctotrupids, the species of a genus are nearly always provided with patches of specialised antennal structures (Nixon 1938) some of which have been called tyloids. These appear as slightly raised elliptical areas that may be hairless, polished or minutely punctate and vary in size depending on the length of the segments. They may involve several antennomeres up to the apical one (Townes and Townes 1981). In ichneumonids, as illustrated in Fig. 16, tyloids usually appear and vary in form, such as a longitudinal prominence (Richards 1956), an elliptic or linear raised area on the outer side of each of several antennomeres near the mid-length of the flagellum (Townes 1969), or as a porous keel (Frilli 1974). These tyloids may also be gland release structures.

In two torymid species A1 is broadened and strongly arched, with the ventral surface covered with small pores. This area of A1 appears to come into contact with the female flagella during courtship (Goodpasture 1975).

Besides the examples described above, there are a few others which are questionable because the antennomere is modified, but there is no obvious specialized structure. Examples of this situation occur in two groups; the Eucoilidae with A3 and/or A4 bent, the outer side flattened proximally and more or less swollen distally (Nordlander 1980), and the Heloridae with the posterior surface of A5 sinuate and smooth (Naumann 1983).

Based on identified RSS and those sus-

pected to be RSS, due to their morphology and location, we have developed a map (Fig. 19) of the location of RSS on a hypothetical male antenna. As can be seen on the map, the RSS may range from the scape, A1, to the most apical antennomere with a concentration in the proximal half of the antenna. The suspected secretory function may only occur in A1 in the Chalcidoidea (Aphelinidae, Eulophidae, Torymidae). These RSS may occur much more frequently in A3 to A5 in all the Superfamilies regardless of the antennomere number. However, the glands extend from A6 to several others in Scelionidae, Proctotrupidae and Ichneumonidae. In no case does A2 play this role. Multiple modified antennomeres with RSS may have a different functional significance or may simply be a multiplication of the same functional structure, possibly to allow for the enhancement of the stimulation or to allow for the induction of a more rapid response. An example of the first case is that of A4 and A5 in *E. asterobemisiae* (Pedata *et al.* 1995) which have different specialized structures associated with different glands which may play different roles in some complex behavior. The second seems to be the situation of some Scelionidae, Proctotrupoidea and Ichneumonidae because the repeated specialized RSS structures appear to be the same.

The term "sex segment" was proposed for the modified antennomere/s on the basis of their speculated involvement in mating behavior of scelionids (Masner 1976). Evidence of a role in mating behavior was later provided by Bin *et al.* (1988) for *Trissolcus basalis*. A similar term, male-sex antennomere (MSA) (Isidoro and Bin 1995), has also been used in a platygastrid being determined by ultrastructural evidence and some behavioral observations. The presence of modified antennomeres with release and spread structure (RSS) in males of various parasitoid groups strongly suggest a sexual recognition function. However, similar structure in females

could function in either sexual recognition or host recognition, or both.

**Sexual Recognition**

All the documented cases listed above indicate that the "UGS touch and taste area", located apically or latero-ventrally, could be used for sexual recognition in conjunction with the female dorsal glands and male ventral or lateral glands and associated "release and spread areas".

The diversity of gland structure and location suggests a strong selection pressure towards a unique antennal glandular system in each species. It has been long recognized that the elaborate courtship behaviors in many parasitoid hymenoptera are very effective reproductive isolation mechanisms (Barrass 1979; van de Assem 1986, 1996). However, it is difficult to use a complex behavioral sequence involving two individuals as a taxonomic tool. The use of the glands may provide a key to reproductive isolation mechanisms in these insects. Further, the UGS pattern may also play a role in the sexual isolation. The secretion, if important in sex recognition, must be perceived by the opposite sex. Since the secretions appear to be non-volatile, as evidenced by the need to remove high molecular weight lipids and proteins to reveal details of the surface ultrastructure of many of these glands, and the presence of visible secretions (Fig. 12), they must be detected by a gustatory type of sensilla. Thus, the placement of the uniporous gustatory sensilla and the glands should reflect the behavior. Although details of the sexual recognition behavior of the parasitic Hymenoptera that consider the positions of the glands and sensilla have not been examined, with the exception of information concerning *Trissolcus basalis* (Bin *et al.* 1988; Bin and Vinson, unpub.), we suggest that such information could demonstrate the importance of the glands, sensilla, and behavior as a reproductive isolation mechanism. In *Trissolcus basalis*, males mount the female and en-

gage in elaborate antennal interactions (Fig. 21a) where the antennae of the male initially drums the female antennae. This places the male uniporous sensilla in contact with the female dorsal glands. As the antennation proceeds, the antennae of the male appears to coil partly around the antennae of the female, usually from the medial side (Fig. 21a). The male then moves back slightly, resulting in the sliding of the males antennae segment A5, along the inner lateral edge of segments A11 to A6 of the female where uniporous sensilla are located. Whether these glands and sensilla are involved in sexual recognition remains to be ascertained.

Some behavioral observations on *Amitus vesuvianus* and *A. rugosus* have shown that the male A4, having a lateral plate functioning as a release and spread structure very similar to that of *A. spiniferus* (Fig. 21d) (Isidoro and Bin 1995), touches the median side of the basal segments of the female funicle during courtship and mating (Fig. 21c) (Viggiani and Battaglia 1983a, 1983b).

Another example is provided by *E. asterobemisiae* where the behavior has been described by Viggiani (1980) (Fig. 21e). During the elaborate antennal interaction involved in sexual recognition, the reported glands and uniporous gustatory sensilla of the male seem to be appropriately positioned with the uniporous gustatory sensilla of the female. However, the role of uniporous gustatory sensilla of the male is uncertain because it is unknown whether a gland is present in these antennomeres of the female.

We suggest that correlating the location of secretory areas of the antennae with that of the uniporous gustatory sensilla, entering into contact during courtship, may provide valuable keys to some species specific sensilla and gland patterns. These aspects do not seem to have been considered in other groups of parasitoids (van den Assem 1996).

## Host Recognition

The "MGS touch and taste area", which typically occurs ventrally, ventro-laterally or apically, could be a common feature of parasitoids. Such an area, consisting of MGS, mechanoreceptive sensilla and in some cases UGS and accessory glands, could be functionally responsible for host recognition and discrimination since MGS and possibly UGS could be capable to respond to host recognition kairomone and host marking pheromone.

At least in one case, that of *Trissolcus basalis*, it can be speculated that the accessory gland secretion may be important in the host recognition process (Fig. 22). Bin *et al.* (1993) reported that host eggs removed from the ovary prior to the addition of an adhesive were not recognized. However, once the adhesive layer was added to the egg chorion, the parasitoid responded (Fig. 22a). Using glass beads of similar size to host eggs, Bin *et al.* (1993) reported no response, but if the adhesive was added, females responded. Further, females only responded when the adhesive was present on a curved surface. The results suggest the adhesive contains a kairomone to which the female parasitoid responds only when encountered on a curved surface (Bin *et al.* 1993). Further, the adhesive was found to be composed of a slightly acidic muco-polysaccharide with some protein. Thus, the adhesive is very complex. Although we do not know what specific compound or component of the adhesive is responsible for the recognition of the object as a host, the glandular secretion of the antennae of the parasitoid may play an important role in this response (Fig. 22b). Several possible scenarios include the dissolving of the adhesive by the secretion releasing the recognition cue, enzymatic degradation of the adhesive that releases or produces the recognition cue, or the secretion may act as some sort of receptor protein (Fig. 22c).

## CONCLUSIONS

Antennal gustatory sensilla and several types of glands, have been documented in a relatively few species of parasitoid Hymenoptera, but we suggest, based on locations and external features, that such sensory and secretory structures may be common. While these sensory and secretory structures appear to differ in detailed structure, shape, size, number, location and distribution; there are similarities and patterns that indicate a common function.

The presence of such organs has also been determined in Aculeata, such as the multiporous gustatory sensilla and female dorsal glands in the Dryinidae (Fig. 23a, b) and male ventral "tyloids" with conspicuous pores, likely indicating a releasing role, in *Vespa crabro* (L.) (Fig. 23c, d). In addition, cuticular structures possibly playing a secretory role, based on the presence of evident pores, occur in males of several parasitoid families (Sapygidae, Tiphiidae, Mutillidae, Pompilidae, Sphecidae) and non parasitoid hymenopterans (Eumenidae, Andrenidae, Anthophoridae) (Pagliano *et al.* unpublished).

Whether sensilla and glands are interactive structures for sex communication or play a role in host recognition (a kind of a "lock and key system") are hypotheses which still need confirmation. It is our hope to stimulate others to examine the antennae of the hymenoptera, not just as a sensory receiving organ, but as an organ that can be involved in the release of secretions. While the role of these secretions is speculative, we suggest they may be involved in sexual communication and in a few cases along with the gustatory sensilla, aid in host recognition. Assuming that the secretions are involved in sexual communication and the gustatory sensilla are involved in either sexual communication, host recognition, or both; mapping of these particular structures may provide for some taxonomic advance. Consideration of the glandular function of the an-

tennae and the presence of gustatory sensilla along with additional anatomical studies and behavioral observations focused on these structures may help to reinterpret antennal function, define homologies, unify terminology and provide additional information regarding phylogeny.

## ACKNOWLEDGMENTS

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# Nesting Behavior and Nest Distributions of *Ammophila gracilis* Lepeletier (Hymenoptera: Sphecidae) in Brazil

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*Abstract.*—*Ammophila gracilis* is a mass provisioner, supplying an egg with 1–2 geometrid caterpillars over 1–2 days before final nest closure. Nesting of marked wasps was observed at two sites in Belo Horizonte, Minas Gerais, Brazil. Nests at the more homogeneous site (n=54), an open dirt road, had a clumped distribution, compared to those at the other site (n=30) which consisted of a series of small patchy clearings. Adult wasps lived up to 84 days. Development averaged 56±10 days. Seven nests were destroyed by miltogrammine flies (*Metopia* n. sp. nr. *sinipalpis*). Ant predation was suspected as the major cause of mortality for 59 nests that did not yield adult wasps or parasites. A distinctive "crouching" behavior displayed by nesting females when miltogrammine flies were detected is described for the first time.

## INTRODUCTION

Sphecids in the genus *Ammophila* Kirby are all ground-nesting wasps that capture prey, especially naked lepidopterous caterpillars and symphytan larvae, to provision each nest where a single larva develops (Evans 1959; Powell 1964; Bohart and Menke 1976). However, larval weevils have been recorded as prey for *A. azteca* Cameron (Evans 1965). The complexity of nesting behaviors is noteworthy in this genus (Evans and West-Eberhard 1970; Tinbergen 1974; Field 1989), and is among the most diverse in the Sphecidae. The importance of ethological studies to the systematics of the group was demonstrated by Baerends (1941) and Adriaanse (1947), who discussed the inter- and intra-specific nesting behavior, and Rosenheim (1987), who also discussed the importance of prey-nest sequences, though Weaving (1989) stressed that prey-nest sequences in *Ammophila* do not always reflect the systematic relationships supported by morphology.

Members of *Ammophila* display a wide range of nesting tactics (discussed by Evans 1959; Powell 1964; Bohart and Menke 1976; Parker *et al.* 1981), including mass provisioning, in which one to a few caterpillars are put into a single nest over a period of 1–2 days; delayed provisioning, in which the last prey item is provided after egg eclosion; and progressive provisioning, in which they continue to reopen nests to provide food through much of larval life. The progressive-provisioning members, such as *A. harti* (Fernald), may maintain several nests in different developmental stages at one time (Baerends 1941; Evans 1965; Tsuneki 1968; Hager and Kurczewski 1986). Also, as Weaving (1989) pointed out, many mass provisioning species can be facultatively delayed provisioners due to inclement weather. Krombein (1984) discussed the general provisioning tactics for several species, including *A. laevigata* Smith (a mass provisioner of several prey items per nest) and *A. atripes* Smith (a mass provisioner of one large prey item per nest). *Ammophila* are

also noted for tool use, especially for using a pebble in the mandibles to push down and pack soil into their completed nests (Peckham and Peckham 1898; Evans 1959; Powell 1964; Tsuneki 1968). A classic account of nest building and provisioning in *Ammophila* and other wasps, including numerous outstanding, informative photographs, is provided by Olberg (1959). Many of the behaviors discussed in the present work are also illustrated with photographs for other *Ammophila* species in Olberg (1959).

We observed the nesting behavior of female *A. gracilis* Lepeletier, gathering information about their general habits of searching and nest construction, provisioning and nest closure, interactions with other insects, and nest distributions at two sites on the Pampulla campus of the Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil.

## MATERIALS AND METHODS

The first site, which we will call "Prefeitura," was a 150 m long and 6–10 m wide, homogeneous, compact sand and dirt road (Fig. 1A) within a 3 hectare plot of land containing vegetation in secondary succession. The second study area, which we will call "Estação Ecológica," was a long trail with a series of small, patchy clearings (Fig. 1B), all within a 156 hectare research facility of 2nd growth vegetation. Details of the vegetation of Estação Ecológica are discussed by Martins and Almeida (1994) and Martins and Antonini (1994). Both sites had dense, grassy and shrubby vegetation along the edges. *Ammophila gracilis* was commonly encountered at both of these sites, at which we logged over 100 hours of observations at each from April to December 1993.

We spent the first few weeks making preliminary observations and marking and measuring female *A. gracilis*. They were hand netted and worked into a matchbox such that only their head and

upper surface of the thorax were exposed (see Fig. 9 of Martins and Pimenta 1993). Head and thorax widths were measured, and each wasp was marked on the mesothorax with three dots of acrylic, fast-drying paint, in a unique color combination. It was carefully noted where each was originally captured, and any subsequent sightings were noted as to exact location and date. Fifty-four wasps were captured and marked.

We carefully recorded female activities, including searching and nest building, prey handling and nest provisioning, nest plugging and camouflaging, breaks for taking nectar from flowers, and any interactions with other insects. In addition, we marked 84 nests (54 at Prefeitura, and 30 at Estação Ecológica) to identify the individual wasp and the date of her nest completion.

Upon seeing a wasp with prey, we followed to her nest. After the nest was finally provisioned and plugged, we placed a glass chip over the entrance (after Weaving 1989). After the chip remained unmoved for over a week, indicating that she probably has not returned and reexcavated the nest, we secured a marked plastic cup over the nest to capture whatever emerged.

During ongoing studies of various ground-nesting wasps and bees at the two sites (e.g. Martins and Almeida 1994; Martins and Antonini 1994), *A. gracilis* has been active during the period of February through September. However, they have been noticeably absent during the rainy season of October through January, though the nature of this apparent dormancy remains a mystery.

All values presented are expressed as the mean ± standard deviation. Voucher specimens of *A. gracilis* have been placed in the "Laboratório de Ecologia e Comportamento de Insetos" at UFMG, Belo Horizonte, Minas Gerais, Brazil, and in the Illinois Natural History Survey, Urbana, Illinois, USA. Voucher specimens of the

Fig. 1.   A-B. Nesting sites, A. "Prefeitura," showing the homogeneous nature of the area, B. "Estação Ecológica," showing the heterogeneous, patchy nature of the area.

*Metopia* species (Diptera: Sarcophagidae: Miltogramminae) have been placed in the Swedish Museum of Natural History, Stockholm, Sweden. The nest distributions underwent nearest neighbor analyses in one dimension (after Boots and Getis 1988), using each nest as a point along a line. The nesting sites were linear in nature, and so were compressed longitudinally so as to be reduced to one dimen-

sional lines. To test whether our distributions were different from random, we calculated a z-value based on the S-statistic suggested by Durbin (1965) and compared it with the normal.

RESULTS AND DISCUSSION

The mean head width and thorax width of the marked *A. gracilis* was $3.33 \pm 0.29$ mm and $2.68 \pm 0.25$ mm, respectively
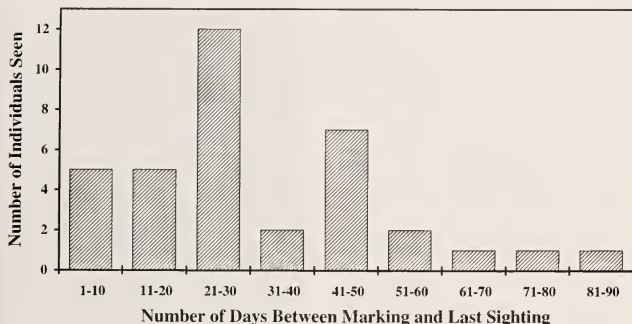
Fig. 2. Histogram representing the minimum longevities of the individual, marked *Ammophila gracilis* females.

(n=53), with no differences between the sites.

*Ammophila gracilis* is a mass provisioner, always supplying 1 or 2 geometrid caterpillars (Lepidoptera: Geometridae) to a nest over a 1–2 day period before permanent closure. Other species are known to use a variety of prey, such as *A. aberti* Haldeman, which prey on members of 14 genera in five families of Lepidoptera (Parker *et al.* 1980), and *A. harti*, which uses at least 16 genera in seven families (Hager and Kurczewski 1986).

Marked individuals were never observed far from where they were initially captured. At Prefeitura, individuals were only seen within about 10–20 m of their original marking site. At Estação Ecológica, they were never observed to move between clearings, and they were only seen in the same general area as they were originally marked in a given clearing. As in *A. harti* (Hager and Kurczewski 1986), marked *A. gracilis* females each constructed their own nests within this same area. However, each individual wasp was not seen every day, and their activity on those days is unknown, but of interest. The

wasps were typically active only during sunny periods of the day, with little or no activity on cloudy days.

The adult life span of *A. gracilis* is considerably longer than for any other *Ammophila* species recorded. The minimum longevity histogram (Fig. 2) represents the longest period of time between our initial marking and last sighting of an individual, with 84 days being the longest interval. Eighteen individuals were never seen after the initial marking (not shown in Fig. 2).

## Nest Digging

The general nesting behavior was similar between the study sites. Typically, while searching, the female wasp would not act aggressively towards other insects. She usually concentrated her search in sandy patches and along cracks of more compact ground, and would often start digging in several different spots before finally settling in on one, similar to that of its close relative (another Ammophilini), *Podalonia robusta* (Cresson) (Kurczewski *et al.* 1992). On most occasions she would use pebbles and sand to rebury unsatisfactory holes, and would occasionally

abandon nearly completed nests, as was also seen in *A. sabulosa* (L.) (Field 1989). Interestingly, on one occasion, an *A. gracilis* female was observed digging two nests simultaneously, each a few centimeters apart. This was probably reminiscent of the false burrows discussed by Evans (1966a), where more than one burrow is simultaneously constructed in a possible effort to mislead parasites.

Once a suitable spot was found, she would begin cutting soil with her large mandibles, flying out of the hole and throwing each load of soil about one-half meter from the hole, in all directions. She did, however, consistently enter the hole from a single direction. As she dug deeper (to approximately thorax depth), she would start flying out of the hole in a single direction, about 45° to one side of her entrance direction, throwing soil farther from the hole each time, with a maximum distance of about 1.5–2.0 m. This behavior of flying loads of soil away from the nest was also reported, and nicely illustrated with photographs, for *A. pubescens* Courtis and other sphecids (Olberg 1959). Completed nests averaged 21.6±2.0 mm deep, with an entrance diameter of 6.4±0.8 mm (n=18).

During the entire process she would regularly stop and fly into the nearby vegetation to take nectar from any of several plant species, including *Elephantopus mollis* Humboldt, Bonpland, and Kunth (Asteraceae), *Vernonia polyanthes* (Sprengel) Lessing (Asteraceae), *Bredemeyera floribunda* Willdenow (Apocynaceae), *Mitricarpus hirtus* (L.) DeCandolle (Rubiaceae), *Waltheria indica* L. (Sterculiaceae), and a *Sida* sp. (Malvaceae). These share the characteristic of possessing small flowers.

## Interactions With Other Insects

While digging, female *A. gracilis* often had encounters with other insects. An ant crossing her nest building area was responded to aggressively, by attacking and hovering above, nipping at the ant until it

left. She would often carry the ant into the air, dropping it a few cm away, as was also observed for *A. dysmica* (Rosenheim 1987). When she encountered a female conspecific, or another ground-nesting wasp, which were common to the area, she would attack it aggressively, driving it away in a similar fashion as with ants.

The case of perching satellite flies (Diptera: Sarcophagidae: Miltogramminae), was rather interesting, and warrants further investigation. When a fly or flies were perching near her nest, she would often stop nesting activities and freeze. This has been aptly described as "freeze-stops" in some other sphecid wasps (Alcock 1975; Spofford *et al.* 1986), and was mentioned for *A. harti* (Hager and Kurczewski 1985). The wasp would also crouch low to the ground with her legs spread wide, remaining in this position until the flies left. This is described here as "crouching" behavior. Sometimes, however, she would attack the parasites, temporarily driving them from her nesting area. Despite such efforts, parasitism of the nests was at least 8.3% by these flies.

## Provisioning and Nest Closure

Once the nest was complete, she would search for a plug to form a temporary closure. In searching for a plug, she would pick up and manipulate numerous pebbles in her mandibles, often dropping them without trying them in the hole before finally finding a suitable one, which was also observed in *A. aberti* (Powell 1964). Then she would plug the hole and pile several (mean: 6.25±1.50; n=4) more smaller pebbles on top, finally shoveling sand over the entrance. Once so plugged, she would fly off and disappear, usually not to return for over an hour or two, and sometimes not until the next day. On several occasions, we observed females moving to tall grass and running their mandibles up and down the blades, as if cleaning the mouthparts.

Eventually, she could be seen dragging,

Fig. 3. Egg of *Ammophila gracilis* on the first abdominal segments of the prey caterpillar.

or taking short hopping flights with, a paralyzed caterpillar, which she had grasped in her mandibles by its thorax, usually venter up, as has also been observed for several *Ammophila* species (Powell 1964; Tsuneki 1968). Then she would find her plugged hole, drop the caterpillar nearby, and unplug the nest. At both sites, ants would occasionally carry off the prey if left for more than a few minutes. Rosenheim (1989) observed that over 5% of prey items of *A. dysmica* were stolen by ants. After inspecting the nest, she would back down the hole, dragging the caterpillar down head first, and would remain inside for 1–3 minutes before exiting, presumably laying an egg on the lateral part of the first few segments of the prey's abdomen (Fig. 3), or on the second or third thoracic segment.

Then she searched out a new plug, or occasionally used the old one, to close the nest. If the first caterpillar was a large one (e.g., 2× her own body size), she would put a permanent closure on the nest. If it

were smaller, such that she needed to find another prey item, she would make another temporary closure, as described above. The mean caterpillar size (n=9), including prey from both one- and two-caterpillar nests, was 30.4±10.8 mm long, and 3.9±0.9 mm body width. For permanent closure, she would set the plug deeper into the hole, then adding smaller pebbles (mean: 12.50±1.29; n=4) before shoveling in sand and packing it tight, using her head and mandibles, or a pebble grasped in her mandibles, to push. A typical sequence would be: add plug, then seven pebbles, then shovel in some sand, then add two pebbles and a small stick, then shovel in some more sand, then add five pebbles, then finish by shoveling in sand. Once filled in with pebbles and sand, she would carefully camouflage the area by moving sand, pebbles, and small sticks around the entrance, even rearranging pebbles and sticks up to 0.5 m from the nest entrance.

## Mortality and Emergence Patterns

Of those *A. gracilis* that emerged from both sites (n=12), the mean time period spent underground after nest closure was 56.30±10.14 days. Although the range was quite wide (37 days), there was no correlation between days spent underground and the date. In fact, the individuals with the shortest (35 days) and longest (72 days) times were initially buried within four days of each other. An additional six pupae were excavated from their nests prior to adult emergence.

Of the remaining 66 nests that did not have *A. gracilis* emergence or pupae, seven nests were found to have been successfully parasitized by members of an undescribed species of *Metopia* (*Allenicia*) Townsend (near *M. sinipalpis* Allen) (Diptera: Sarcophagidae: Miltogramminae) (T. Pape, pers. comm.). Each of these nests produced from one to ten flies within 35.75±4.99 days after nest closure. After excavation, some prey items were ob-

served to have up to 15 parasite eggs clustered over the caterpillar's head capsule or first thoracic segment. No other parasites were recovered from nests of *A. gracilis* in this study, although there were numerous digger wasp and bee parasites (especially Diptera: Bombyliidae, and Hymenoptera: Chrysididae, Mutillidae, and Leucospidae) present at each site. We can only speculate about the remaining mortality factors, which were responsible for the non-emergence of 59 of the 84 total nests. We suspect that there is extremely high ant predation, as all of these nests were excavated to yield no remains whatsoever. Rosenheim (1987) observed that ants would also prey on nest contents after final nest closure in *A. dysmica*. Therefore, we do not know the true rate of miltogrammine fly parasitism, as these nests could also have been removed by ants. Assuming nests with flies were destroyed by ants at the same rate as those with wasps, fly parasitism could have been as high as 28%.

On only one occasion did we observe the results (but not the event itself, unfortunately) of physical removal of a prey item after nest closure. Within one day after an observed final nest closure, we found the nest unplugged with the paralyzed caterpillar beside the entrance, with no *A. gracilis* egg attached. This removal of prey may have been by a conspecific, as has been observed, for example, in *A. sabulosa* (Field 1989), *A. dysmica* (Rosenheim 1987), and *A. aberti* (Parker *et al.* 1980).

Interestingly, the total mortality for *A. gracilis* was quite high compared to other published accounts of *Ammophila* species. The total mortality for both study sites was 78.6% (66 of 84 nests), with Prefeitura mortality at 72.3%, and Estação Ecológica mortality at 90%. Mortality rates for other species include: 52.5% for *A. dysmica* (Rosenheim 1987); 51.7% for *A. harti* (Hager and Kurczewski 1986); and 33% for *A. sabulosa* (Field 1989). Outside of *Ammophila*,

the mortality of another sphecid, *Tachysphex terminatus* (Smith), due to miltogrammine fly parasitism alone, was 30.6–57.9%, depending upon nesting site (Spofford *et al.* 1986). Only 10.6% of the mortality of *A. gracilis* could be explained by miltogrammine fly parasitism, although the actual rate of parasitism is probably considerably higher if ant predation of closed nests is great.

## Nest Distributions

For our nearest neighbor analyses, using Durbin's S-statistic (Durbin 1965), we concluded that the distribution of *A. gracilis* nests was clumped at Prefeitura. The calculation of the S-statistic for the Prefeitura nests yielded a z-value of $-2.406$. Because this calculated value of $z$ is negative and the value obtained from the tables of the normal distribution is smaller than 0.05 (P=0.016), the $H_o$ (that the distribution of nests is random) is rejected in favor of one indicating a clumped distribution of points along the line. Regarding the distribution of nests at Estação Ecológica (using only the most heavily nested clearing, at the beginning of the series of patchy clearings), we found that we could not reject $H_o$. The calculation of the S-statistic yielded a z-value of $-1.027$. The value obtained from the tables of the normal distribution is larger than 0.05 (P=0.306), indicating the distribution cannot be considered different from random. This could possibly be explained by the smaller sample size, or it may be a real difference in the distributional patterns between the two sites.

If the differences in nest distributions between the sites are real, they can be accounted for. It is possible that there is a differential parasite and predator pressure, causing more clumping and aggregation at the Prefeitura site, but more data is needed to support this. If that is the case, there may be less pressure on *A. gracilis* in the very diverse, patchy areas of Estação Ecológica, where they could be

more difficult to find by searching, generalized parasites. Prefeitura is a very large, open, and homogeneous site, with numerous other ground-nesting wasps continuously present. This, coupled with the numerous parasites could pressure the wasps into small aggregations, affording them at least some protection by sheer numbers, as a type of "selfish herd" response (Hamilton 1971; Wcislo 1984), where the probability of nest parasitism decreases with increasing nest density. However, it has also been proposed that parasite pressure may act against the formation of nesting aggregations, and in favor of delayed nest provisioning (Rosenheim 1989) or progressive provisioning (Evans 1966b; Hager and Kurczewski 1985).

## ACKNOWLEDGMENTS

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# Biology of *Tricholabiodes* Radoszkowski in Southern Africa, with a New Synonymy and Review of Recent Biological Literature (Hymenoptera: Mutillidae)

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*Abstract.*—Papers dealing with the biology of Mutillidae since the last survey (Brothers 1989) are cited. *Tricholabiodes* Radoszkowski is the only genus of nocturnal Mutillidae recorded from southern Africa. Aspects of the biology of three species, *T. thisbe* (Péringuey) (= *T. carinifera* Bischoff **syn. nov.**), *T. livida* André and *T. imbellis* (André) (grooming), are described, based on field and laboratory observations in South Africa and Namibia. The following aspects are discussed: habitat, times of activity, predators and defence, mating, stridulation (during distress, copulation and as apparent communication) and grooming. This is the first account of the biology of any species in the genus.

## INTRODUCTION

Although the Mutillidae comprises about 8000 species of sexually dimorphic wasps (female always wingless and male almost always winged), knowledge of their basic biology is very limited. Of the more than 200 papers dealing with mutillid biology, host-parasite relationships or life-history information, fewer than 20 report detailed studies of their biology (Brothers 1972, 1975, 1989). Since the last paper cited, the following papers have appeared: a review of mutillid adaptations (Deyrup 1988); information on water loss in *Dasylabris* sp. (Zachariassen *et al.* 1988); biological information on *Dasymutilla pyrrhus* (Fox) (Manley & Deyrup 1989), *D. scaevola* (Blake) (Hook & Evans 1991) and *Pseudomethoca* species (Krombein 1992); details on copulation of *Myrmilla calva* f. *distincta* (Lepeletier) and *Myrmilla erythrocephala* f. *bison* (Costa) (Monastra 1989); seasonal flight activities of species of *Ephuta* Say, *Photomorphus* Viereck, *Pseudomethoca* Ashmead, *Sphaeropthalma* Blake and *Timulla* Ashmead (Deyrup & Manley 1990); observations on host associations

(e.g., Callan 1991, 1993, Krombein 1991, Riddick 1991, Brothers 1994, Yanega 1994, Weaving 1994, 1995, Neff & Rozen 1995); the effects of urbanization on Mutillidae (Gayubo & Torres 1989); and sex associations and mating behaviour (Cambra & Quintero 1993, Quintero & Cambra 1994).

*Tricholabiodes* (Sphaeropthalminae, Dasylabrini), one of several genera of nocturnal mutillid wasps, is restricted to the arid and semi-arid regions of Africa and the Palaearctic. Its distribution in southern Africa includes all four desertic biomes: Nama Karoo, Succulent Karoo, Desert and arid parts of Savanna, which represent more than half of the area of the subcontinent, covering the western coastal belt between 12°S and 33°S and extending into the Kalahari basin and central Karoo plateau as far as about 26°E (Lovegrove 1993; Rutherford & Westfall 1994). This paper provides the first account of aspects of the biology of any species of the genus.

Specimens of *Tricholabiodes* are 3–12 mm long, with the mesosoma completely testaceous; males have large ocelli, hyaline wings with the forewings infuscated dis-

tally and a sparsely setose petiolate metasoma; females have the metasoma petiolate to sessile. Three species, *T. thisbe* (♂ & ♀), *T. livida* (♂ & ♀) and *T. imbellis* (♂), are treated (figs. 1–5). Identifications of males were made by comparison of voucher specimens with the holotypes or lectotypes, and of females by direct observation of sex associations (see below). As a consequence of such observations, the following new synonymy was established: *T. thisbe* (Péringuey 1898) (based on males only) = *T. carinifera* Bischoff 1920 (based on female only), **syn. nov.**, male observed *in copula* with female. (The female was identified by reference to the original description with which it agrees well; this is the only female found in southern Africa which has the very characteristic strong longitudinal ridges on the second metasomal tergum.) The genus is currently being revised by Bayliss & Brothers, and taxonomic details will be published later.

MATERIALS AND METHODS

Field observations were made during January to March 1995 and in January 1996 in the south-central and northwestern regions of South Africa, and in central Namibia; laboratory and field observations were made at Gobabeb Research Station, Namibia. In the field, a lighted dome (Oberprieler 1984) (with three centrally placed fluorescent tubes emitting a mixture of white and ultraviolet light and powered by a 12V battery) was used for attracting males which were then collected by hand. Females were caught by searching the ground using a flashlight, looking for signs of movement, or by excavating burrows. Field observations of behaviour were made with a red filter over the flashlight.

Live adults, brought into the laboratory for observations on communication, stridulation, mating, grooming and feeding, were kept in small vials or petri dishes (diameter 90 mm, height 20 mm) with the bottom lined with paper towel to provide

a rough substrate, in a dark cupboard, simulating conditions in natural refuges. A Wild M5 stereo microscope, using white light from a desk lamp, was utilised for laboratory observations at irregular intervals during the day and at night. Details on mating were obtained by placing two adults of opposite sex in the same petri dish. If no interactions (including stridulation or rubbing of antennae) occurred between them after several minutes, they were separated. The same two individuals were never placed together more than once, unless interactive behaviour between them had previously occurred. Grooming has not previously been described in mutillids, so grooming behaviour was noted in the field and the laboratory whenever seen, and detailed experimental observations were carried out after covering the body with flour. Observations (a total of at least 50) involved several specimens of all three species and the full repertoire of cleaning activities was seen in about 5 individuals of *T. thisbe* (including 1 female) and 8 of *T. imbellis*. The terminology used in the accounts of grooming is from Basibuyuk and Quicke (in litt.).

The accounts below apply to *T. thisbe* and *T. livida* unless otherwise stated.

RESULTS AND DISCUSSION

**Habitat and Activity Patterns**

Females are commonly associated with dry river beds, walking or running on the banks or in the adjacent loose vegetation. They walk slowly over hard compact soil, probing cracks and crevices with their antennae and regularly entering and leaving burrows. On loose sandy soil they move quickly without appearing to search. (Ferguson (1962) observed similar behaviour in females of the nocturnal subgenus *Photopsis* Blake.) When inactive, they hide in pre-existing burrows. Females were seen emerging from burrows with entrances opening on the vertical faces of banks of

Figs. 1–5. *Tricholabiodes* spp. 1, *T. thisbe*, ♂, lateral view. 2, *T. thisbe*, ♀, dorsal view. 3, *T. livida*, ♂, lateral view. 4, *T. livida*, ♀, dorsal view. 5, *T. imbellis*, ♂, lateral view. Scales = 3 mm.

compact soil and they were occasionally found when such burrows were excavated during the day.

Where the males reside during the day is unknown. At night, they were often seen entering and leaving small circular burrows but were never found residing in the burrows. Burrows and crevices that males were seen entering the previous night were excavated several hours later, but no males were found. They could not be found in the surrounding vegetation along the riverbanks, under rocks, nor in neighbouring crevices or burrows. Males are hesitant to fly and prefer running with the wings folded above the metasoma. They fly in hops, landing every several metres. On cold (<20°C) evenings males were not seen, while on warm evenings, even with light drizzle, they were frequently found.

Based on specimen labels, individuals

of all southern African species of *Tricho-labiodes* have been most frequently collected (and are probably most active) during the summer months (November to March); they are seldom active during early spring and late autumn, and never during winter (June to August). Although most species are strictly nocturnal, females of *T. thisbe* were sometimes observed active up to two hours before sunset. Since Nonveiller (1963) hypothesized that mutillids are generally stenothermic and thermophilic, these females may not be avoiding light, but are rather being active during optimum conditions of temperature, which usually occur only after sunset but on cool overcast days could occur several hours before sunset.

Females are not influenced by a stationary light. If a female enters the area illuminated by such a light, she continues her activities as if the light were not present. In contrast, females of *Photopsis* are positively phototropic (Ferguson 1962), and they usually approach the light in a semi-direct path, then move away into a shadow and remain motionless. Females of *Tricholabiodes* are startled by moving lights and either remain motionless for some time thereafter or show escape reactions.

Males could be collected only by attracting them to light; they have seldom been caught in malaise traps. It is thus probable that they are strictly nocturnal. Upon arriving at a light, they immediately entered the brighter inner circle of light before moving away and grooming themselves in the dimmer outer circle. The umbrella used in the light trap was divided into brown and white segments, with the white areas brighter than the brown. The males never rested on the white areas.

## Predators and Defence

Females of *Tricholabiodes* appear to have relatively few enemies. Vertebrates were not observed eating them and they were ignored by invertebrates such as ants. The escape reaction used by the females in re-

sponse to disturbance tends to be species specific. When disturbed, females of *T. thisbe* entered the nearest convenient hole or crevice, but females of *T. livida* started burrowing. Female mutillids generally have a strongly sclerotized exoskeleton, especially the mesosoma which is robust. They also have potent stings and can bite (Masters 1979). When grasped, a female often stridulates and attempts to sting. A predator may thus become innately aware that sound and defence, i.e. sting, are often associated, and stridulation may aid predators in recognizing well defended mutillids in consequent encounters (Edmunds 1974).

Males of *Tricholabiodes* were seen being attacked and eaten by toads, birds (nightjar) and bats, and several species of ants. If attacked, males of *Tricholabiodes* stridulate and attempt to escape by flying or running. Stridulation is accompanied by opening and closing of the mandibles and flexing of the metasoma under the mesosoma, resembling the stinging motions of the female. Male mutillids are usually poorly protected against predators. If grasped, however, a male may administer a slight prick to a potential predator with the sharp parameres of the genitalia (Masters 1979). Masters (1979) further hypothesized that stridulation may also startle an attacker, thereby increasing the likelihood of escape by the mutillid, and noted that, in insects generally, stridulation is frequently coupled with other defences such as distasteful or noxious secretions. The stridulation and stinging motions of the male may thus trick the predator into assuming that he is well defended.

## Mating

*Tricholabiodes thisbe.*—When a male and a female were confined to a petri dish after having been kept in separate vials (n = 3 pairs), they initially tried to escape. The male acted in an excited manner by attempting to fly and run randomly. Within a few seconds the members of the pair met
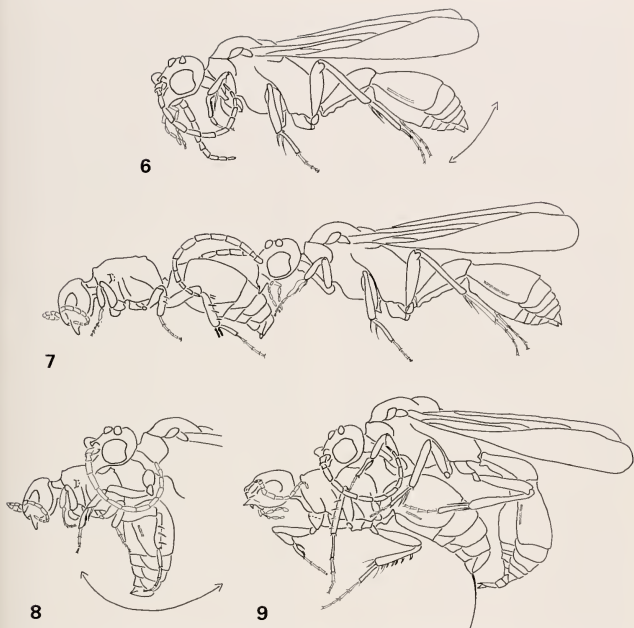
Figs. 6–9. *Tricholabiodes thisbe*, mating behaviour, diagrammatic. 6, antennal and metasomal movements of ♂ when sensing ♀. 7, antennal vibration by ♂ when contacting ♀. 8, ♀ resisting mounting attempt by ♂. 9, mating posture immediately before copulation.

at least once and whenever they met head-on neither member showed avoidance reactions. This is contrary to Ferguson's (1962) observations on *Photopsis* where he noted that whenever the two sexes met head-on both instantly showed avoidance or escape reactions by moving away in different directions. In *T. thisbe*, a male avoided a female only if she passed him from behind. Initially, when meeting, the male's antennae flickered continuously and his metasoma vibrated against the

base of the petri dish (fig. 6). His antennae then began to vibrate rapidly over the body of the female (fig. 7), and within seconds he attempted to mount her. The female resisted by stridulating strongly, flexing her metasoma so that the ventral surface touched her coxae (fig. 8), and used her mandibles to pry herself loose from him if he had not grasped her successfully.

The male grasped the female laterally at the mid length of the mesosoma with his

mandibles, and twisted his body so that both were lying on their sides. Her body was slightly arched with legs tucked under the mesosoma. His middle pair of legs rested laterally on her metapleuron, while the hind pair lay on the second tergum, near the felt line. Once the female was securely grasped, the male partly extruded his genitalia (fig. 9) and began prodding her genital opening at about one prod per second. At this point the female started stridulating softly. The duration of the prodding varied before copulation occurred, lasting about 5–15 seconds. Genital union lasted 10–15 seconds, during which her ovipositor was partly extruded, although the pair sometimes remained in the copulatory position for up to seven minutes. Immediately after genital union, the male released his hold and the pair separated. The way in which the apical segments were joined and the details of genitalic attachment could not be studied under the microscope as the slightest disturbance caused the pair to separate.

The entire copulation process occurred on the ground; no attempt was made by the male to fly with the female nor did the female, once firmly grasped by the male, try to dislodge him. Nonveiller (1963) stated that among individuals of similar size, mating takes place on the ground for it is not possible for the male to fly freely with the female. He observed *Smicromyrme jovanovici* Nonveiller mating in a position similar to that of *T. thisbe*, as does *Dasymutilla foxi* (Cockerell) (Spangler & Manley 1978). *Pseudomethoca frigida* (Smith), in contrast, mates with the female standing and the male above her (Brothers 1972).

For several minutes after copulation, the female partly extruded and withdrew her sting every few seconds. Brothers (1972) suggested that these pumping movements may aid movement of the sperm into the spermatheca. The male withdrew his genitalia before settling down to groom himself. After several minutes, he often again mounted the female but the encounter

lasted only several seconds and never more than a minute, and actual copulation was never repeated. Subsequent encounters between the male and female were of shorter duration than the previous ones. The attractiveness of a mated female diminishes rapidly after mating, as has been observed in other species (Brothers, 1972). On one occasion a different male attempted to mount the already mated female and he spent several seconds prodding her with his genitalia before ceasing his activities.

*Tricholabiodes livida.*—Mating in *T. livida* (n = 2 pairs) is similar to that in *T. thisbe* except for a few details. The male grasped the female more towards the anterior margin of the scutum with his mandibles and used all three pairs of legs to hold the female firmly once the pair was lying on their sides. The female then arched her metasoma forward, directing it between her legs, before copulation occurred. The male thus also curved his metasoma far forward. This position was probably adopted because the female was relatively much smaller than the male (compared with *T. thisbe*). Additional observations of mating in *T. livida* are needed to verify the consistency of the arching of the metasoma. No subsequent matings by other males with the already mated female were observed. Similarly, the mated female lost all attractiveness to neighbouring males.

## Stridulation

Stridulation in mutillids has been assigned various functions in the past, including that of intraspecific (Mickel 1928) and interspecific signalling (Masters 1979), but little or no hard evidence has been provided to support most of the suggested functions. During the present studies, stridulation by males and females of *Tricholabiodes* was observed during periods of distress, during copulation and as an apparent calling device. Sounds made while a wasp is on the ground could probably be sensed by others as vibrations through

the tarsi, but how individuals sense sounds produced by others during flight is unknown. Neither sex has any obvious specialized structures for sensing these vibrations.

*Distress.*—When grasped, both sexes stridulate vehemently. The sounds produced are loud, continuous and of long duration. They may function to startle predators and warn of possible stinging, as has been shown for other mutillids by Masters (1979).

*During copulation.*—The female stridulates as the male prods her genital opening with his genitalia. The sounds produced are loud and rhythmic. They are not as intense or continuous as those produced during distress, and their function is unknown. Reciprocal calling, whether by "honking" (vibration of the mesosoma and wings using the flight muscles) or stridulation, by the male during copulation was not observed, unlike the situation in *D. foxi* (Spangler & Manley 1978).

*Apparent calling: Communication.*—Males grouped together (3 in a petri dish) communicated by slow, barely audible stridulation (heard on 4 separate occasions over about one hour each when the laboratory was quiet). The sounds produced were not as intense as those made during periods of distress and were of short duration (≤ 2 seconds). Individuals did not stridulate simultaneously but sequentially. While stridulating they remained stationary with the metasomal sterna resting on the ground. Within an hour, 'conversations' between individuals occurred 20–30 times. The function of these calls is unknown.

*Apparent calling: Courtship.*—On at least 2 occasions, between about 21:00 and 22:00, males of *T. thisbe*, while flying, were heard stridulating in an area where females were known to be most common (confirmed by later investigation). These sounds were loud, audible up to several metres away, and of a continuous long duration. It is assumed that they had some

function in communication between the sexes. Sounds have an advantage over visual signals for nocturnal animals (Masters 1979), since visual signals are ineffective at night, whether intraspecifically or interspecifically. This could also explain why nocturnal mutillids, including *Tricholabiodes*, are dull coloured without the bright patterns commonly seen in diurnal species.

## Grooming

There are no differences in cleaning techniques between the species observed (except for one detail involving the antennae) and none between the sexes (except for the wings). If it is extremely dirty an individual first cleans the posterior part of the body partially, otherwise grooming proceeds anteroposteriorly.

*Head.*—The antennae are cleaned first, using the antennal cleaners of the ipsilateral forelegs. All species display either single- or, more commonly, double-antenna scraping (the cleaning of only one or both antennae at the same time respectively). During cleaning, the leg is lifted over the antenna which is placed in and pulled through the antennal cleaner by tilting the head backwards and simultaneously moving the leg away from the head. Individuals of *T. thisbe* and *T. livida* first clean the antennae distally then sequentially more proximally by cleaning a longer section each time the antenna is pulled through, using short rapid strokes. In contrast, individuals of *T. imbellis* pull the entire antenna slowly through the antennal cleaner 3–4 times. The ipsilateral middle leg cleans the foreleg after several strokes of the antenna through the antennal cleaner. The surface of the head is combed posteroanteriorly, using both fore legs simultaneously, the basitarsi and calcaria acting as combs or brushes. The calcaria also clean the mandibles. The fore leg, after several sweeps of the head, is cleaned by one or both middle leg(s).

*Body.*—Cleaning of the dorsal surface of

the mesosoma was not seen. The fore legs, reflected back and bent at the femoro-tibial joint, rub the tarsi, tibiae and calcaria along the mesopleura using short rapid movements. The calcar is angled away from the basitarsus. The calcaria and basitarsi clean the sterna. After several sweeps of the mesosoma, the forelegs are cleaned. The metasoma is cleaned using the hind legs, either individually or simultaneously. An individual balances on its front two pairs of legs, with wings folded dorsally, with the entire body slightly dorsally arched, while the hind legs rub along the metasoma, using the basitarsi and spurs. The longer tibial spur is angled away from the tibia. The sides are groomed first, followed by the dorsal surface and then the sterna.

*Legs.*—The legs are cleaned sequentially, anterior to posterior. A foreleg is cleaned either by the ipsilateral middle leg or both middle legs simultaneously. In the former, both fore and middle legs rub against each other or the fore leg may pass between the spurs and basitarsus of the middle leg; in the latter, the fore leg passes behind the ipsi- or contralateral middle leg spurs or is placed between the basitarsi of both middle legs which rub against it. In *T. thisbe* and *T. livida* at least, the fore leg is not pulled past the tibial spurs in one quick motion but is cleaned first distally, and then sequentially more proximally, as for the antennae. The middle legs are groomed separately using the tibial spurs and basitarsi of both hind legs. Only in exceptional circumstances, where the middle leg is very dirty, does the other middle leg aid the hind legs in cleaning it. One hind leg combs and rubs the other hind leg, using the basitarsis and tibial spurs. This action is then reciprocated for the other hind leg.

*Wings.*—The left and right wings, like the antennae, are cleaned either separately or simultaneously, using the tibiae and basitarsi of the hind legs; the fore wings are cleaned before the hind wings. They

are not cleaned in their normal resting position, but are orientated ventrolateral to the metasoma. When cleaning the dorsal surface, the fore wing has the costal margin ventrally oriented and the dorsal surface facing outwards. The metatibia and metabasitarsus, remaining outside the wing, slowly comb the wing. After 3–4 strokes of the wing the hind leg is cleaned. The posterior margin of the fore wing is cleaned once the dorsal surface has been combed; it is gripped and pulled between the spurs and the basitarsus. Thereafter, the fore wing is orientated so that the costal margin is dorsally placed, the ventral surface faces outwards, and the hind wing lies obliquely lateral to and slightly below the fore wing. The ventral surface of the fore wing is cleaned similarly to the dorsal surface, the leg being between the fore and hind wings. The hind wing is cleaned in a sequence similar to the fore wing, the latter being adjusted in position to permit access to the former. When the wings of both sides are being cleaned simultaneously, the animal balances on its front and middle legs, and when cleaning the wings separately, the wasp shifts its weight, arching the mesosoma away and the metasoma towards the wing that is being cleaned.

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# Microscopic Observations of the Digestion Condition of Pollen Grains in the Midgut of Stingless Bee Larvae

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*Abstract.*—The present paper presents results on the observations of the mechanisms of pollen digestion by larvae of stingless bees. The midgut content was observed with a transmission electron microscope. The morphological results suggest that pollen digestion in larvae can be a complex mechanism, which involves physical and chemical changes in the pollen cover by enzymatic action that may be allow some digestive enzymes to enter inside the pollen grains. Later, the intine may be ruptured as a response to the changes in the osmotic pressure, releasing the protoplasm for further digestion.

## INTRODUCTION

The stingless bees, like other pollenophagous insects, are important pollinators of plants. Pollen is the major source of proteins, lipids and vitamins for both adults and larvae. Relatively little is known about how pollen grains are digested in the digestive tract of the bees.

In adult bees, there are many probable strategies used to digest pollen grains. Some authors have suggested that adult bees can break the pollen grains by chewing them, or by proventriculus action (Morton 1950, Snodgrass 1956, Von Planta 1985). On the other hand, Martinho (1975), Kroon *et al.* (1984) and Velthuis (1992) have pointed out that pollen grains can be digested only after an osmotic shock that takes place inside the digestive tract that causes the release of its content. However, Cruz-Landim (1985) and Cruz-Landim and Serrão (1994) suggested that digestion occurs before the content extrusion, therefore still inside the covers. Klungness and Peng (1984a, 1984b) suggested that pollen digestion can occur by different mechanisms, which depends on the species of pollen.

Data about digestion of pollen grains by the larvae are not available. Since all previous studies were made with adult bees, this study was conducted to investigate the digestion condition of pollen grains ingested by larvae of two species of stingless bees.

## MATERIAL AND METHODS

Larvae were obtained from worker brood cells of the colonies of *Scaptotrigona postica* Latreille, 1807 and *Trigona spinipes* (Fabricius, 1794).

The digestive tracts of the larvae were removed into buffered saline solution for insects, and the midguts were isolated. The pieces were fixed in 2.5% glutaraldehyde in 0.1M Na cacodylate buffer at pH 7.2, washed twice in the buffer, post-fixed in 1% osmium tetroxide in the same buffer, dehydrated in a series of increasing concentrations of ethyl alcohol, and embedded in Epon-Araldite resin, following usual procedures. Thin sections cut with glass knives were stained with uranyl acetate and lead citrate, and examined in a Zeiss EM9S2 electron microscope.

## RESULTS

At the anterior midgut of the larvae, the walls and protoplasm of pollen grains ap-

peared to be largely intact (Fig. 1). By the time the pollen reaches the posterior midgut, their contents were disorganized and gradually removed through the germination pores mostly without rupture of the pollen wall, forming an electron-lucent periphery (Figs. 2, 3).

Some pollen grains were seen with their contents disorganized and retracted in the center, leaving a clear ring around it (Fig. 4). In addition, material similar to the content of pollen grains were seen outside of them and appeared to be formed by many lipid droplets surrounded by electron dense material (Fig. 5). Broken pollen grains are rarely seen inside the midgut of the larvae.

## DISCUSSION

The absence of broken pollen grains in the larval midgut is an expected result, because larvae do not have strong mandibles or a proventriculus bulb, which break some pollen grains as pointed out by Morton (1950), Snodgrass (1956) and Von Planta (1985) for adult bees. The presence of pollen grains with their walls intact and with disorganized content suggest that pollen grains can be useful to larvae without their walls being broken. Similar results were observed in adult stingless bees by Cruz-Landim (1985) and Cruz-Landim and Serrão (1994).

Kroon et al. (1974) and Martinho (1975) have pointed out that since pollen grains are immersed in honey or nectar in the crop of the adult worker, the concentration of sugar of the pollen grains is altered. When these pollen grains enter the midgut, where sugar concentration is lower, they absorb water osmotically, so that the protoplasm is forced to protrude through the germination pores. Larvae do not have a crop where pollen and honey could be mixed inside the gut. The provisions of food for them are placed by nurse workers into the brood cells in layers consisting of (from bottom to top) by pollen, a mixture of honey and pollen, and

glandular secretion (Sakagami et al. 1965, Sakagami and Zucchi 1966). Therefore, the mixture of pollen and honey is made in the brood cell. However our results never show protoplasm extrusion of the pollen grains in the anterior midgut. Therefore the model for pollen digestion suggested by Kroon et al. (1974) and Martinho (1975) for adult workers, above mentioned, has not morphological support to occurs in larvae.

On the other hand, pollen grains in the middle and posterior midgut have the protoplasm released through the germination pore. Similar results were presented for adult Apis mellifera Linnaeus by Klungness and Peng (1984a) and Peng et al. (1986). These authors suggested the occurrence of enzymatic degradation of pectic acid and hemicellulose of the exine in the germination pores where the pollen wall is thin. As a result of these changes, the protein constituents of the intine are exposed to the digestive protease, causing the protoplasm extrusion. However, our morphological results show that before protoplasm extrusion, it is disorganized, suggesting that digestion begins inside the pollen wall, perhaps by action of enzymes that enter the grain through the permeable wall, as suggested to occurs in adult workers by Cruz-Landim (1985) and Cruz-Landim and Serrão (1994) or by pollen protease as thought by Grogan and Hunt (1979).

Therefore, we suggest that pollen digestion in stingless bee larvae can be a complex mechanism, which involves physical and chemical changes in the pollen cover by enzymatic action, which would permit that digestive enzymes enter into the pollen grains. Later, the intine may be ruptured, as a response to the changes of osmotic pressure, releasing the protoplasm for further digestion.

Presence of material similar to pollen grains but outside of them has been reported by Klungness and Peng (1984b) and Peng et al. (1986) as being of pollenkitt
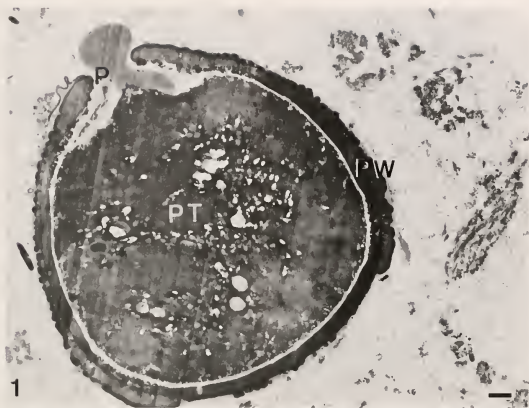
Figs. 1–2. Fig. 1, *Trigona spinipes*. Pollen grains inside of the anterior midgut showing the pollen wall largely intact (PW). P—germination pore, PT—protoplasm. Bar = 1 μm. Fig. 2, *Scaptotrigona postica*. Pollen grain inside of the posterior midgut showing disorganized protoplasm (PT) removed through the germination pore (P), forming a clear ring (EP). PW—pollen wall. Bar = 1 μm.
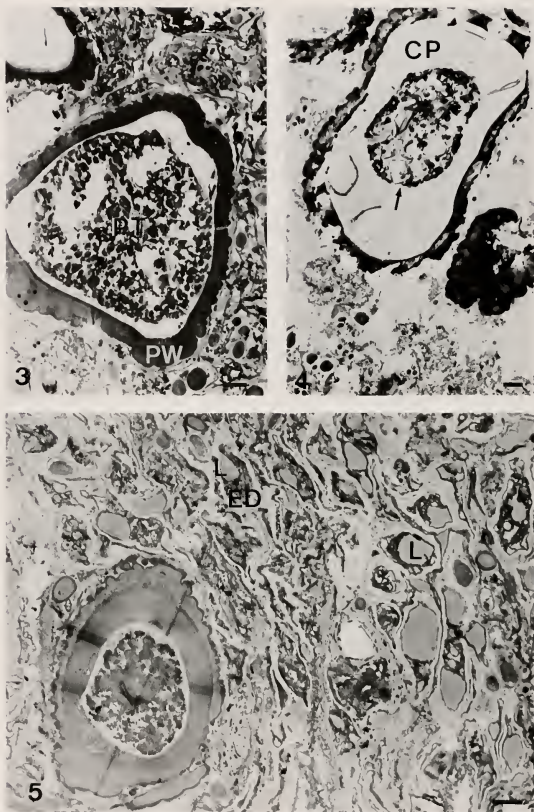
Figs. 3–5. Fig. 3, *Scaptotrigona postica*. Pollen grain inside of the posterior midgut showing disorganized protoplasm (PT) without extrusion. PW—pollen wall. Bar = 1 μm. Fig. 4, *Trigona spinipes*. pollen grain inside the posterior midgut showing disorganized protoplasm retracted in the center (arrow) leaving a clear peripheric space (CP). Bar = 1 μm. Fig. 5, *Trigona spinipes*. Material released by the pollen grains, showing lipid-like droplets (L) surrounded by electron dense material (ED). Bar = 1 μm.

origin. The pollenkitt is a protein- and lipid-rich layer that coats some species of pollen. Because the species of pollen grains present in the midgut of the stingless bees studied here could not be determined in order to know if they have or not pollenkitt, the origin of material outside of the pollen grains although undetermined, is though to be, at least partially resultant of pollen protoplasm extrusion.

Pollen grains with their content disorganized and retracted at the center have been also observed in adult bees by Cruz-Landim (1985), Klungness and Peng (1984b) and Cruz-Landim and Serrão (1994). As suggested by Klungness and Peng (1984b) pollen grains with these conditions have a wall composed primarily of cellulose and sporopollinin. Presumably, these species of pollen would be of less nutritive value to the bee. This is in agreement with Maurizio (1954) who observed that pollen of different species has different nutritional value to the worker of *Apis mellifera*.

Further, we believe that the larvae must profit from the ingested pollen, because of it lasting in the midgut during all larval life, given it needs a long time to be digested.

## ACKNOWLEDGMENTS

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# Bacteria Present in the Intestinal Tract of *Melipona quadrifasciata anthidioides* Lepeletier (Hymenoptera, Apidae, Meliponinae)

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*Abstract.*—Scanning and transmission electron microscopy were used to study the microbial flora present in the gut of a Brazilian stingless bee, *Melipona quadrifasciata anthidioides* Lepeletier (Hymenoptera, Apidae). At least 5 bacterial morphotypes were found, but only the flora present in the hindgut maintain relationships with the food and the epithelial wall, indicating that it is autocthonous.

## INTRODUCTION

The association of microorganisms with the intestinal tracts of insects is varied and widespread (Buchner, 1965; McBee, 1977; Breznak and Pankratz, 1977; Bignell et al., 1980; Bignell, 1983; Cruz-Landim and Costa-Leonardo, 1995 ab; Oliveira et al. 1995). In bees, the presence of bacteria in the gut or association with the digestion of food, has been reported by several authors (White, 1921; Kluge, 1963; Trienko, 1965; Giordani and Scardovi, 1970; Machado, 1971; Cruz-Landim, 1972, 1990; Gilliam and Prest, 1987; Gilliam et al., 1988).

It has long been recognized that the gut microbiota plays a significant role in digestion. However, the reports of insect-microbe associations usually describe populations in the hindgut where the bulk of digestion has already been completed. Colonization of the midgut is much less common and is generally restricted to insects without a peritrophic membrane (Bignell et al., 1980; Caetano e Cruz-Landim, 1985).

Most microorganisms found in the insect gut exist freely in the lumen, but others attach themselves to the intima (Strambi and Zybberberg, 1967; Cruz-Landim, 1972; Fogelsong et al., 1975; Breznak and Pankratz, 1977; Bracke et al., 1979; Bignel et al., 1979; Bayon, 1981; Caetano e Cruz-Landim, 1985). Bacterial attachment is often an essential initial step in colonization of host tissues and subsequent establishment of functional relationships. Attachment can be a highly specific process that involves fimbrial or nonfimbrial proteins on the outer membrane of the bacteria (Costerton et al., 1978; Hacker, 1992; Hoepelman and Tuomamen, 1992) and structural adaptations of the gut wall (Crawford et al., 1983).

In this paper light and electron microscopy were used to describe, for the first time, the intestinal microbial flora in *Melipona quadrifasciata anthidioides*, (Cruz-Landim, 1990) a Brazilian native stingless bee. The intent was determine the morphological diversity of the bacteria that

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Fig. 1. TEM of bacteria in the crop of foragers of *M. q. anthidioides*: a, general view of the bacteria (b) in the crop lumen (l) (c= cuticle, ep= epithelium, n= nucleus); b, bacteria (b) presenting a tuff of pilli (p) directed toward the crop wall (w); c, cells showing division septa (s) and cross striated pilli (p); d, Aspects of the bacterial horns (h) formed by cross striated pilli (p) or fimbriae.
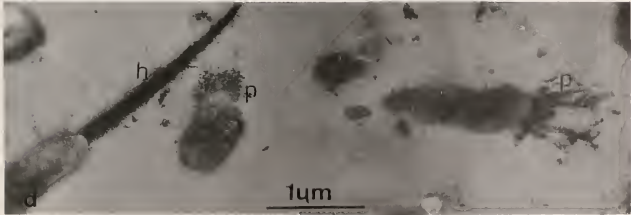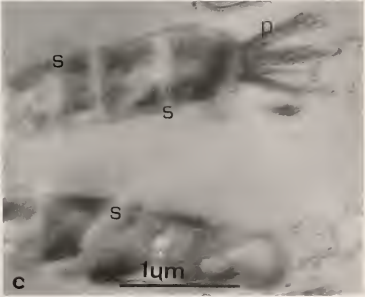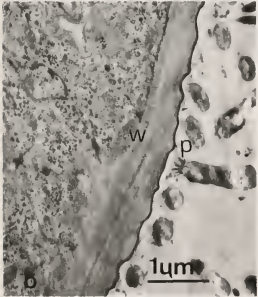
colonize the gut and whether the gut epithelium serves as a site for the attachment of these bacteria.

## MATERIAL AND METHODS

The descriptions in this study are based on guts of nurse workers of *Melipona quadrifasciata anthidiodies* collected directly from colonies mantained in cages at the Biology Department, apiary in Rio Claro, SP, Brazil. The workers were allowed to fly freely in nature, and no additional food was given to them. The capture was done in the summer time. The material examination was done with transmission (TEM) and scanning (SEM) electron microscopy.

Guts to be observed by SEM were excised from the workers under buffered saline for insects, cut into anatomic parts, and fixed in Karnowsky (1965) during 2h at room temperature. The pieces were then freeze-fractured in liquid nitrogen, dehydrated in a graded ethanol series, critical point dried and covered with sputtered gold.

Dissected gut tracts were also prepared for TEM by fixation of the pieces in 2.5% glutaraldehyde in 0,1M cacodylate buffer during 2h at 4°C. Tissues were then rinsed in the buffer, post-fixed in 1% osmium tetroxide in the same buffer and dehydrated in a graded series of ethanol. The specimens, embedded in Epon-Araldite were thin-sectioned with glass knives and stained with uranyl acetate and lead citrate. Some additional preparations were done by emptying the gut parts on to coated grids and staining with 1% PTA (phosphotungstic acid) for negatively contrasted examination of the microorganisms.

Micrographs were taken with an Zeiss EM9S2 (TEM) and a P15 JEOL (SEM).

## RESULTS

Microorganisms were found in all parts of the worker bees alimentary canal. In the foregut bacteria were observed in the crop (Fig. 1) where they were distributed freely and homogeneously in the lumen. In the sections, the cell profiles were mainly round shaped with, some rod-shaped ones among them (Fig. 1a). The cells are probably all bacillus, the round profiles being cross sections of the rods. The diameters of the rod and round cells are very similar, about 0,5 μm. The greater incidence of round-shaped bacteria could be due to a preferential orientation of most cells in relation to the plane of the section.

Some cells have tuffs of short pilli or fimbriae in one pole. In this case the pole provided with pilli is turned toward the crop wall (Fig. 1b). Other cells have "horns" apparently formed by the sticking together of long fimbriae (Fig. 1d). The "horns" show cross striations, and do not determine any special orientation of the cells. When the cells were observed in division (Fig. 1c), the cross traberculae separate short compartments and the walls between them are thick (about 160 nm). Some cells have an inconspicuous, fuzzy capsule.

In the midgut the bacteria are mainly long rods (Fig. 2a, b) with the same diameter as the foregut cells (0,5 μm). However their distribution seems to be chaotic, and no fimbriae or "horns" were ever seen. Some cells have irregular contours, indicative of the presence of an undulating membrane (Fig. 2b). The bacteria in the midgut seem to concentrate in the anterior portion, near to the esophagic valve and posteriorly, near the pylorus.

The hindgut has the richest microorganism flora of the bee digestive tract . Bacteria are found in the ileum and in the rectum. In the ileum the bacteria adhere to some regions of the cuticle (Figs. 3, 4b). The bacterial population, formed mainly by long rods (3–4 μm long × 0,4 μm diameter) occupies almost all the ileum lumen, leaving free only the spaces filled by food particles (Fig. 4a, b). The bacteria tend to group around electron-dense material near the ileum wall (Fig. 4b). This electron-dense material when located at some distance from the wall appear as
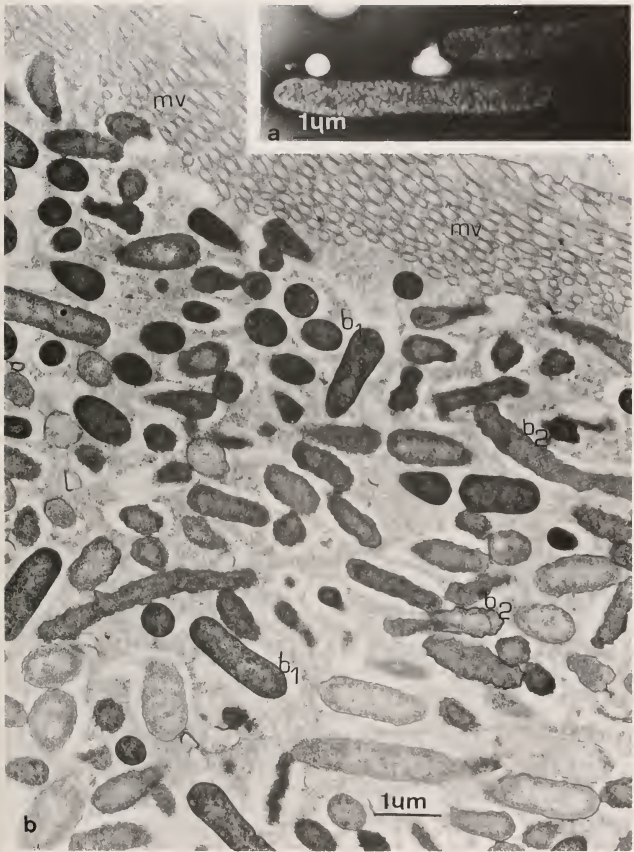
Fig. 2. Bacteria in midgut of *M. q. anthidoides*: a, negative staining of a bacillum from midgut. m = microvilli; b, bacteria in the anterior portion of the midgut, showing at least two morphotypes (b 1 and b2).

Fig. 3.   SEM of the hindgut cuticle of M. q. anthidioides (c) with adherent groups of bacteria b).

amorphous and irregular fragments, while close to the cuticle it appear formed by a fibrous material. Inside the cuticle it is possible to see some dots of electrondense content (Fig. 4b).

In the rectum, most bacteria are located over the rectal papilae (Fig. 5a, b), but are also attached to the rectum wall (Fig. 5a). They are rod shaped, mesuring 3–4 μm long by 0,5 μm wide. The bacteria linked to the rectum wall have a tuff of pilli by which they attach themselves to the rectal wall. The attachement is not direct but through a thin layer of fuzzy material (Fig.

5c). The rods are straight and have a thick wall.

DISCUSSION AND CONCLUSIONS

The "in situ" examination of the microbiota of Melipona quadrifasciata anthidioides bee workers shows that only bacteria are present. Only a few different morphotypes were apparent. For instance, three in the foregut (bacilli without pilli, bacilli with pilli and bacilli with horns); two in the midgut (long straight bacilli and bacilli with an ondulating membrane); three in the hindgut (long bacilli with pilli, bacilli

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Fig. 4.   TEM of bacteria in the hindgut of M. q. anthidioides: a, content of the hindgut showing the bacteria, an empty pollen grain (po) and digested food (dp); b, bacteria around amorphous material (am) near the hindgut lumen and fibrous (fm) material near the wall. The arrow points to electron-dense material inside the cuticle (c).
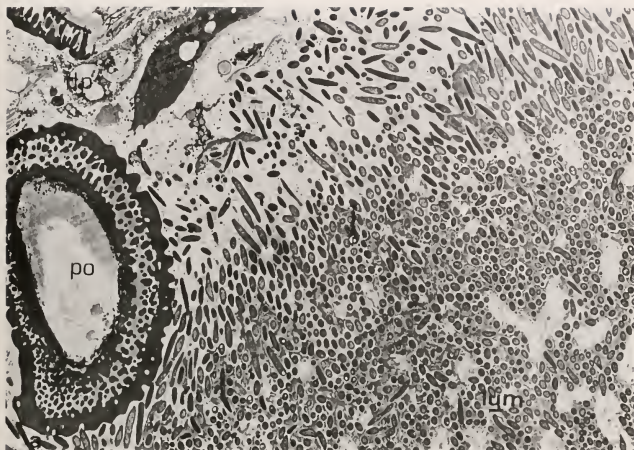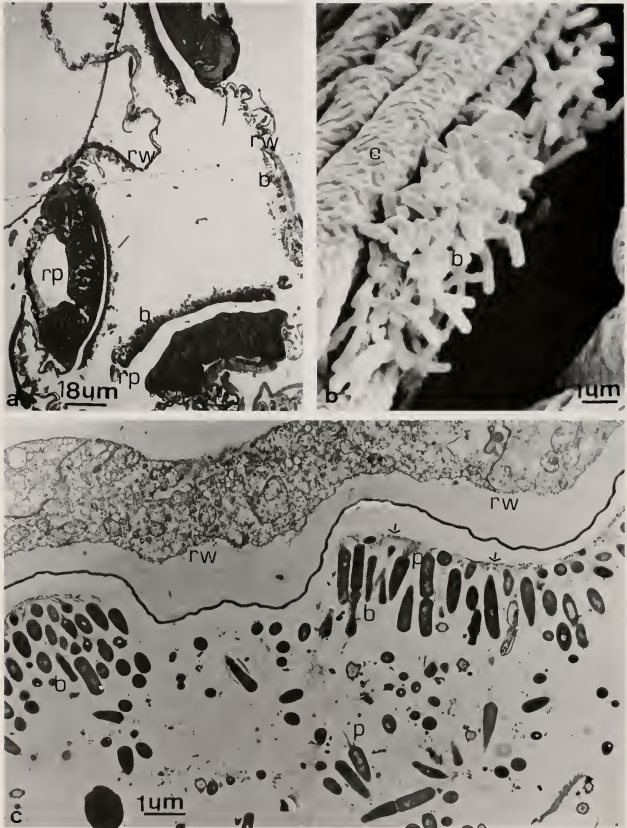
Fig. 5. Bacteria in the rectum of *M. q. anthidioides*: a, light microscopy of a thick section showing the rectum wall (rw) and the rectal papillae (rp) with masses of bacteria (b) over it; b, SEM of bacteria (b) attached to the rectum cuticle (c); c, TEM of the same region shown in b. The arrows point to a fuzzy material where bacteria (b) attach (p= pilli, rw= rectum wall).

without pilli and slim rods). Almost all animals have an autochthonous flora in the gut, formed by indigenous forms that colonize the individual early in its life, and remain throughout the life of the healthy animal (Savage, 1972).

*Melipona quadrifasciata* eats nectar and pollen. The pollen grain is difficult to digest because of its celulose envelope. Studies by Machado (1971) and Gilliam et al. (1990) show the presence of bacteria in the pollen reserves in the colonies of this bee, where they are supposed to play a part in pre-digestion of pollen. However, a role in cellulose digestion is also attributed to the microorganisms present in the gut (Gilliam et al., 1988; Breznak and Brune, 1987).

The arrangement of the bacteria in the different parts of the gut may give some clues of their function. The bacteria maintaining special relationships with the gut wall, or with a special localization, may be autochthonous while the others may have been ingested with food. Bacteria attached to the foregut or midgut wall were rare or absent, so the bacteria found there may be in transit. In agreement with this interpretation is the fact that no special spacial or morphological relationships were observed between the bacteria and the food present in the midgut lumen.

In the ileum the bacteria group around what seems to be fragments of the pollen shell (Fig.4b). Close to the gut wall, this material seems to have undergone some transformation. It changes from a compact amorphous appearance to a fibrilar one, perhaps due to bacteria action. Some of this electron-dense material may cross the cuticle covering the illeum epithelium, since electron-dense spots may be seen inside the cuticle.

A great concentration of bacteria may be observed, parallel to the wall, or randomly distributed, over the rectal pads as has already been reported for *Apis mellifera* (Cruz-Landim, 1972). The bacteria in the rest of the rectum are perpendicular to

the wall and linked to it by pilli tuffs. This special location seems to indicate particular functions of these bacteria, linked to bee physiology. The indications are that the microbial flora of the hindgut are authochthonous, or at least the parts close to the walls, or that maintain characteristic relationships with the wall or the food. However part of the bacterial flora in the bee gut is not authochthonous and may be digested or eliminated with the feces as seen in the honey bee by Gilliam and Prest (1987).

The physical intimacy of the autochthonous flora with the host probably reflects an underlying biochemical mechanism, such that the attachment of bacteria to the gut epithelium should afford a prime opportunity for nutrient exchange between the cells.

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# SCIENTIFIC NOTE

## Further Notes on the Family-Group Names of Ichneumoninae
### (Hymenoptera: Ichneumonidae)

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Since publication of Wahl and Mason (1995) on the family-group names of the Ichneumoninae, I have become aware of several errors and omissions.

1. The authorship of Heterischnini, Pristicerotini, Geodartiini, and Notosemini were attributed to Townes *et al.* (1961). Mason and I failed to note that the tribal and generic keys in Townes *et al.* (1961) were written solely by Henry Townes (Dicky Yu and Klaus Horstmann, pers. comm.). Since the keys validated the names in question, authorship should be "Townes, 1961".

2. The tribe Clypeodromini was overlooked. The entry should be:

16. **Clypeodromini** Tereshkin, 1992.
Clypeodromini Tereshkin, 1992: 194.
Type-genus: *Clypeodromas* Tereshkin.

3. The tribe Hemichneumonini was overlooked. It goes under the tribe Alo-

myini in the arrangement of Wahl and Mason (1995). The entry should be:

Hemichneumonini Wesmael, 1983:261.
Type-genus: *Hemichneumon* Valemberg.

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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.

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# Silk Glands in Adult Sphecid Wasps (Hymenoptera, Sphecidae, Pemphredoninae)

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*Abstract.*—Among the sphecid wasps, females of the genus *Psenulus* and some members of the subtribe Spilomenina are known to use silk for nest lining. In *Psenulus*, this behavior has been reported for a long time, but the source of the secretion has never been correctly recognized. Most authors have considered the lining material as derived from salivary glands. Dissection and KOH clearing of dried specimens and dissection of fixed specimens revealed that the glands in *Psenulus* are associated with the 4th and 5th sterna of the females and in the subtribe Spilomenina, they are associated with the 6th tergum. In both groups, the glands are composed of class 3 epidermal cells, in the classification of Noirot & Quennedey (1974). In *Psenulus*, the secretory cells associated with each sternum are numerous, exceeding one hundred. The duct cells are quite long and their opening on the integument is usually surrounded by cuticular seta-like projections, here called setiform spinnerets. In most cases, each spinneret includes more than one duct. External examination of 33 species of *Psenulus* revealed that the size, number and distribution of the setiform spinnerets are quite variable; moreover, the spinnerets are absent in the Neotropical group of species. In the subtribe Spilomenina, the secretory cells have the same morphology, but the setiform spinnerets are located at the apex of the 6th tergum. Several authors have misinterpreted this area in *Spilomena* as a pygidial plate. The shape, arrangement and location of the spinnerets vary greatly among species of *Spilomena*. Despite the similarity in morphology, the silk glands in *Psenulus* and Spilomenina probably evolved independently.

## INTRODUCTION

Production of silk or silk-like materials by adult insects is relatively rare and restricted to a few groups (Rudall and Kenchington 1971, Kenchington 1984, Sehnal and Akai 1990). Among Hymenoptera, it has been reported for *Eupelmus* (Chalcidoidea, Eupelmidae; Delanoue and Arambourg 1965), *Signophora coquilletti* Ashmead (Chalcidoidea, Signiphoridae; Woolley and Vet 1981), *Quartinia vagepunctata* Schulthess (Vespidae, Masarinae; Gess and Gess 1992), *Polistes* (Vespidae; Singer *et al.* 1992), *Hylaeus* (Apoidea, Colletidae; Espelie *et al.* 1992) and for two groups of sphecid wasps (Apoidea).

These two groups of sphecid wasps belong to the subfamily Pemphredoninae: the genus *Psenulus* (Psenini) and two genera of the subtribe Spilomenina, *Microstig-*

*mus* and *Arpactophilus* (Pemphredonini). In these wasps, silk is secreted only by females and is used in nest construction. Myers (1934) was the first to suggest that the nests of *Microstigmus theridii* Ducke were built with plant hairs held together by some kind of silk. Matthews (1968), based on observations of females of *M. comes* Krombein rubbing the tips of their abdomens over the nests and on dissections (KOH clearing of metasoma), suggested that the glands associated with the setal brush at the tip of tergum VI were involved in the production of silk. Matthews and Naumann (1988) found that *Arpactophilus mimi* Naumann builds its nest inside abandoned mud cells of *Sceliphron* wasps using only silk. The authors say that the silk is secreted from glands near the tip of the metasoma, and that these

glands appear to be homologous with those of *Microstigmus comes*. Carvalho and Zucchi (1989) mention briefly the use of silk for cell lining in *Spilomena*, but do not comment on the source of the silk.

Since the early studies of the nesting biology of *Psenulus*, it has been recognized that females use some sort of silk to line the nest walls and to make partitions between brood cells (Maneval 1932, Grandi 1934, 1935, Iwata 1938, Leclercq 1941). However, the source of the silk was never correctly recognized. Grandi (1935) was the first to suggest that the silk was secreted by the females, although he presented no evidence for the nature of the putative glands. Janvier (1975), based on evidence of use of salivary secretions in nest lining by colletid bees and on his own dissections of the mouthparts of *Psenulus concolor* (Dahlbom), concluded that the silk produced by *Psenulus* was secreted by labial glands. The labial structures illustrated by him seem to be some type of sensilla or may be openings of a true labial gland, but certainly these glands would not be responsible for the large amounts of silk found in the nests. Small epidermal glands are widespread in the mouthparts of social vespids (Landolt and Akre 1979). Florkin and Bricteux-Grégoire (1961) demonstrated that the substance secreted by females of *P. concolor* is silk. They found an amino acid composition similar to that of silk produced by other insects and spiders. In this paper, I describe for the first time the silk glands of *Psenulus*. Additional information on the morphology and taxonomic distribution of silk glands within Spilomenina is also presented.

MATERIAL AND METHODS

Most of the material used in this study were pinned museum specimens that were examined only under a dissecting microscope (up to 126 ×). A few dried, pinned specimens of *Psenulus frontalis* (Fox), *P. mayorum* Bohart & Grissell, *P.*

*puncticeps* (Cameron), and *Spilomena* sp. (from Australia) were dissected and had their sterna or terga cleared with KOH. Also, a few fresh and fixed (Kahle's fluid) specimens of *Psenulus mayorum*, *Microstigmus nigrophthalmus* Melo, *Spilomena alini* Antropov, *S. pusilla* (Say), *Spilomena* sp. (from Brazil) and *Xysma* sp. (from Brazil) were dissected. The dissected material was examined and photographed with an Olympus BH-2 microscope with differential interference contrast optics. The pinned specimens were photographed under an Olympus SZH dissecting microscope. In the descriptions, the term metasoma (Michener 1944) refers to the abdomen excluding the first segment (the propodeum). The metasomal sclerites are numbered with Roman numerals.

RESULTS AND DISCUSSION

*Psenulus*

Upon external examination, females of *P. frontalis* were found to have a row of long pale bristles on the apex of sterna IV and V (Fig. 1). These bristles have a blunt tip and are much thicker than the regular setae found on the sterna (Fig. 2). Their length varied from 120 to 155 µm, and an average of 47 bristles (range 41 to 56) was found on sternum IV and 51 (46 to 57) on sternum V. The bristles on sternum V are somewhat differentiated into two rows, the anterior row with shorter bristles. Examination of cleared specimens showed that these bristles were associated with long ducts of class 3 epidermal glands [in the classification of Noirot and Quennedey (1974, 1991)]; see Fig. 2. Numerous individual ducts enter each bristle and open at the bristle tip (Fig. 3).

Class 3 epidermal glands are widespread among insects (Noirot and Quennedey 1974), and a great number of glands in Hymenoptera are known to be composed with this kind of secretory unit (e.g. Youssef 1975, Hölldobler and Engel 1978, Landolt and Akre 1979, Jeanne *et al.* 1983,
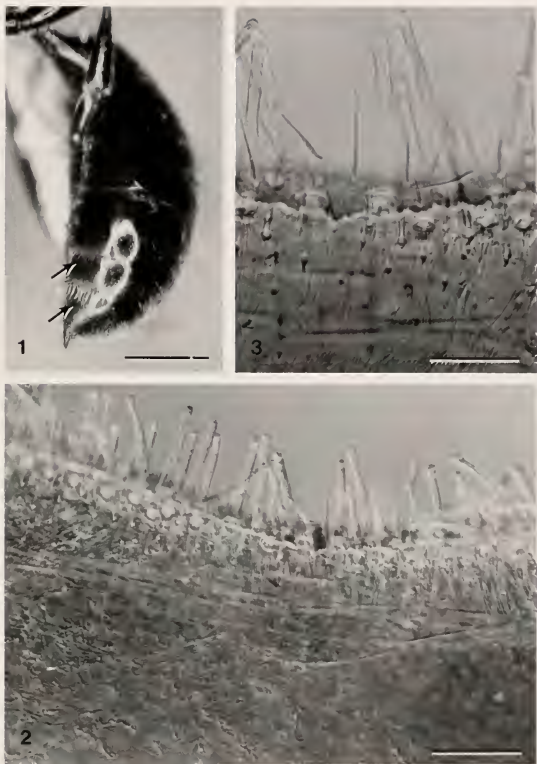
Figs. 1–3. Metasoma of *Psenulus frontalis*. 1. Lateral view, showing the setiform spinnerets (arrows); scale = 0.8 mm. 2. Posterior margin of a cleared sternum IV, showing the spinnerets and ducts of the silk glands; scale = 0.1 mm. 3. Enlargement of part of Fig. 2, showing spinnerets with several cell ducts entering it; scale = 50 μm.

Billen 1987, Cruz-Landim 1987). In most cases, the ducts open individually on the surface of the integument and are not associtated with any special cuticular pro-

tuberance. Ducts opening at tips of bristles, as in silk glands of *P. frontalis*, have been reported for abdominal glands in males of *Campodea* (Diplura) and silk

glands of machilids and lepismatids [see review in Bitsch and Bitsch (1991)], for an antennal gland in males of *Trissolcus* (Hymenoptera; Bin and Vinson 1986), for tarsal silk glands in males of empidids (Diptera; Eltringham 1928) and for tarsal silk glands of embiopterans (Nagashima *et al.* 1991).

With the possible exceptions of *Campodea* and *Trissolcus*, these glands are involved in the production of silk, and the bristles seem to be acting like spinnerets in the formation of silk threads. Bitsch (1990) named these special bristles as tubular bristles, while Bitsch and Bitsch (1991) called them glandular bristles. Considering the similarities in development among the different epidermal organules [sensillae, class 3 glandular cells, non-innervated setae, scales; reviewed in Gnatzy and Romer (1984)], it seems reasonable to consider these tubular bristles homologous only to the external part of setae and sensillae. In this case, the name glandular bristle seems preferable, since it makes reference to the whole organule, and not only to the external protuberance, as tubular bristle does. For the glands associated with the production of silk, I will refer to these cuticular protuberances as setiform spinnerets or just spinnerets (Fig. 4A).

In all the 33 additional species of *Psenulus* examined, the females have some sort of setiform spinnerets on the apices of sterna IV and V, with the exception of 3 species (*P. aztecus*, *P. mayorum*, and an undescribed species from Mexico), all belonging to the group occurring in the Neotropical region (5 species known to me). Among the species with spinnerets, 11 of them have long spinnerets distributed in a narrow band on the sternal apex, as in *P. frontalis* (*P. aurifasciatus*, *P. ealae*, *P. erusus*, *P. freetownensis*, *P. laevigatus*, *P. pallipes*, *P. patei*, *P. paulisae*, *P. tanakai*, *P. trisulcus*, *P. turneri*), while the remaining species have shorter and more numerous spinnerets distributed in broader bands on

the sternal apex (*P. alienus*, *P. bakeri*, *P. bidentatus*, *P. capensis*, *P. carinifrons*, *P. interstitialis*, *P. latiannulatus*, *P. leoninus*, *P. lubricus*, *P. luteopictus*, *P. luzonensis*, *P. nigeriae*, *P. onewi*, *P. philippinensis*, *P. puncticeps*, *P. scutatus*, *P. xanthognathus*, an unidentified species from Taiwan, and an undescribed species from Sierra Leone). In several species of the latter group, the width of the bands differed between sterna IV and V, with the band on sternum V always broader than the one on sternum IV.

In *P. puncticeps*, the bands do not differ in their width. The spinnerets are very numerous (over one hundred in each sternum) and approximately 40 μm long. Apparently, one to four ducts are associated with each spinneret (the spinnerets disappeared with the KOH clearing).

The condition in the Neotropical species is very peculiar. Sterna IV and V each have a broad semi-circular area covered with long erect setae (40 to 85 μm long in *P. mayorum*; longer setae toward sternum apex), located medially in the segment. Examination of the cleared sterna of *P. mayorum* showed that the ducts open directly on the integument surface (apparently individually, and not in groups) and do not have associated spinnerets. The silk is probably applied with the help of the erect setae. The absence of spinnerets and the more disperse distribution of the duct openings on the sterna suggest that this might be the primitive condition for the genus, while the opening of the ducts restricted to a band on the apex of the segment and associated with spinnerets evolved later. However, the phylogenetic relationships among the species in this genus have not been analyzed and the proposed transformation series can not be evaluated.

## Subtribe Spilomenina

The silk glands of this group are also composed of class 3 epidermal cells (Fig. 5). However, the setiform spinnerets and associated silk glands are located in the
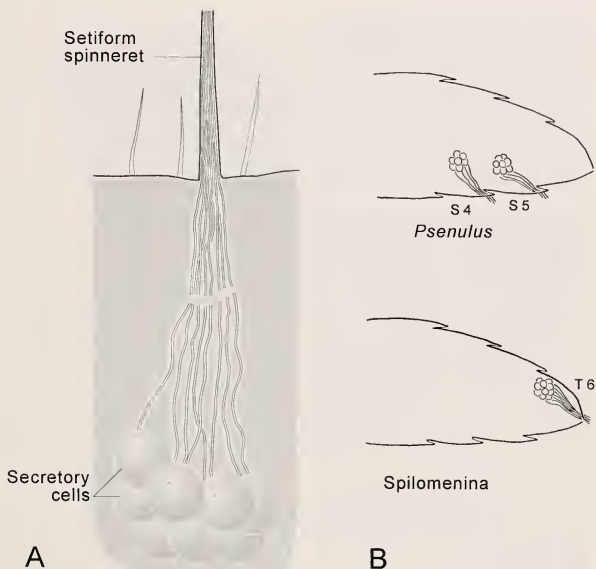
Fig. 4. A. Diagram of a group of glandular cells and ducts associated with a spinneret. B. Diagram showing the position of the silk glands in the metasoma of females in the genus *Psenulus* and in the subtribe Spilomenina.

tergum VI (Fig. 6). Three main lineages can be recognized in this subtribe (Melo, in prep.): *Arpactophilus*, *Spilomena* + *Microstigmus* + *Xysma*, and *Spilomena subterranea* McCorquodale & Naumann plus related undescribed species.

In *Arpactophilus*, the arrangement and shape of the spinnerets do not vary much among the species examined. They are branched, relatively short, and form a dense brush along the apex of tergum VI (Fig. 6). *Xysma* and some *Spilomena* have a condition similar to *Arpactophilus*, except that the spinnerets are less numerous, relatively longer, and without branches. In most *Spilomena* and *Microstigmus*, however, the spinnerets also occupy part of the tergum disc, along its midline (Fig. 7). *Microstigmus* has simple, non-branched spinnerets that form a small tuft at the tip of the metasoma. In several groups of *Spilomena*, the spinnerets are arranged in two parallel or diverging rows over the tergum. Most commonly, these rows extend over the apical third of tergum VI, but in some species they almost reach the anterior border of the tergum (Fig. 8). In some cases, each spinneret can have several
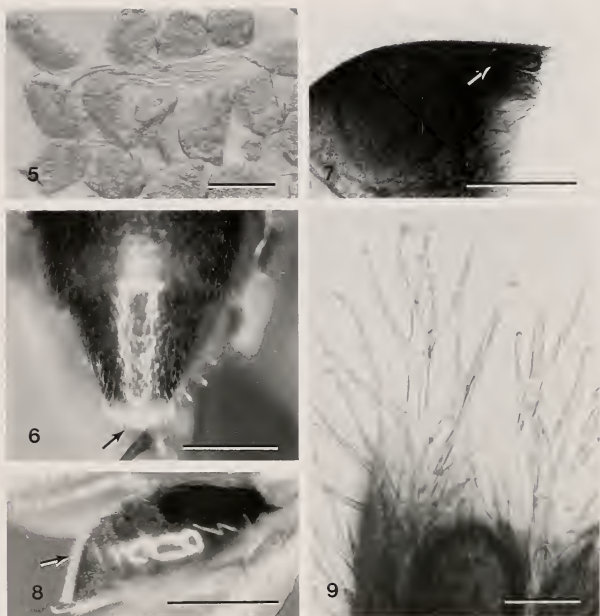
Figs. 5–9. Silk glands and associated structures in members of the subtribe Spilomenina. 5. Class 3 glandular cells from *Microstigmus nigrophthalmus* (fixed material); scale = 50 μm. 6. Posterior view of the metasoma of *Arpactophilus* sp., showing the brush of setiform spinnerets in the border of tergum VI (arrow); scale = 0.5 mm. 7. Dorsal view of tergum VI of *Spilomena* sp., showing the two rows of spinnerets along its midline (arrow); scale = 0.2 mm. 8. Lateral view of the metasoma of *Spilomena* sp., showing the spinnerets along the midline of tergum VI (arrow); scale = 0.5 mm. 9. Highly branched spinnerets in the border of the tergum VI of *Spilomena* sp. Scale = 20 μm.

branches (Fig. 9). Another interesting modification found in some of *Spilomena*, as *S. formosana* Tsuneki, is the fusion of the spinnerets to form a pair of erect laminar structures, which are very thin, transparent, and fringed along their edge.

Most authors have erroneously interpreted the two rows of spinnerets on tergum VI of females of *Spilomena* as carinae delimiting a pygidial plate. No species of *Spilomena* is known to have a pygidial plate, except *S. subterranea* and related undescribed species. When describing *S. subterranea*, McCorquodale and Naumann (1988) called attention to several features that this species does not share with other *Spilomena* or *Arpactophilus*. Dissection and clearing of tergum VI of a species closely
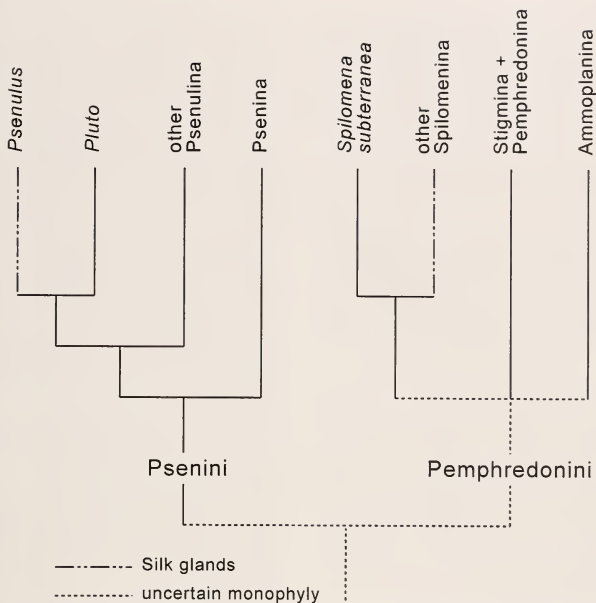
Fig. 10. Putative phylogeny for the major lineages of wasps of the subfamily Pemphredoninae [sensu Bohart and Menke (1976)]. Psenini based on Finnamore (1987); Pemphredonini based on Melo (in prep.).

related to *S. subterranea* revealed no evidence of silk glands. This could be considered a reversal (loss of the glands), but taking into consideration other features of *S. subterranea*, it seems more parsimonious to consider that this group of species diverged before the split that gave rise to the remaining *Spilomena* (including *Microstigmus* and *Xysma*) and *Arpactophilus* (Melo, in prep.).

## CONCLUSIONS

The silk glands in *Psenulus* and in the subtribe Spilomenina have many basic features in common, like the morphology of the secretory cells (class 3 epidermal cells), the long excretory ducts, and the presence of spinnerets associated with the ducts. The position of the glands, however, differs: in *Psenulus*, the glands are associated with sterna IV and V, while in Spilomenina, they are associated with tergum VI (Fig. 4B). Also, branched spinnerets were observed only in members of Spilomenina. Despite the similarity in morphology, the silk glands in *Psenulus* and Spilomenina probably evolved independently (Fig. 10).

Future research in this group of wasps should investigate the ontogeny of the multicellular glandular unit and its associated spinneret, especially in species with multibranched and laminar spinnerets. Several studies on the development of epidermal glands composed of class 3 cells have revealed that each glandular unit is an isogenic group of cells derived, by successive mitosis, from one epidermal stem cell (Noirot and Quennedey 1991). It would be interesting to know whether the multicellular units found in pemphredonine wasps are formed by additional successive mitoses of a single stem cell, forming a large isogenic group, or by association of several isogenic groups derived from different stem cells.

## ACKNOWLEDGEMENTS

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# Revision of North American *Aleiodes* Wesmael (Part 1): the *pulchripes* Wesmael Species-group in the New World (Hymenoptera: Braconidae, Rogadinae)

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*Abstract.*—The *Aleiodes pulchripes* Wesmael species-group is defined to include the following previously described New World species: *flavidus* (Cresson) 1865, *pedalis* Cresson 1869, *quebecensis* Provancher (1880), *geometrae* (Ashmead) 1889, *cameronii* (Dalla Torre) 1898, *insignipes* (Brues) 1912, and *vaughani* (Muesebeck) 1960. Six newly described species are also included: *arizonensis* Marsh and Shaw, *cazieri* Marsh and Shaw, *earinos* Shaw, *notozophus* Marsh and Shaw, and *rossi* Marsh and Shaw. The *pulchripes* species-group is defined by its exceptionally large ocelli and eyes, compact flagellomeres, pectinate tarsal claws, extensive granulate propodeal microsculpture, and first metasomal tergum with weakly rugulose to rugulocostate sculpture. Revised status is indicated for the species *cameronii, flavidus, insignipes, pedalis, quebecensis, geometrae,* and *vaughani,* which have been previously classified in the genus *Rogas* Nees. *Rhogas nigriceps* Enderlein is an older name for *vaughani,* but is a junior homonym of *nigriceps* Wesmael. *Rogas enderleini* Shenefelt is an unnecessary replacement name for *nigriceps* Enderlein, and a junior synonym of *vaughani.* A lectotype is designated for *Rhogas geometrae* Ashmead. A preliminary key is provided for the species-groups of Nearctic *Aleiodes,* a key to the New World species of the *pulchripes* species-group is provided, and species treatments are given including diagnostic characters, distribution, and biological information.

## INTRODUCTION

The rogadine braconid genus *Aleiodes* Wesmael is worldwide in distribution, but is particularly species-rich in the Holarctic region. *Aleiodes* is well diversified in North America, but anyone reviewing the recent synoptic literature (e.g. Marsh 1979; Shenefelt 1975) might overlook this fact. Marsh (1979) in the Catalog of Hymenoptera in North America north of Mexico treated only three species under *Aleiodes.* More recently authors have recognized that many of the species previously classified as *Rogas* Nees have been transferred to *Aleiodes* (van Achterberg 1982, 1985, 1991, 1995; Marsh 1989; M. Shaw 1994; M. Shaw and Huddleston 1991; S. Shaw 1993, 1995). Even so, the 1979 catalog greatly underestimates the diversity of the group in North America. Forty-one species are listed under *Rogas* and *Aleiodes* combined (all of which should be assigned to *Aleiodes*), but we now estimate that the total in the United States and Canada alone is at least 90 species, and new species are still being discovered.

The species of *Aleiodes* are koinobiont endoparasitoids of lepidopteran larvae, especially macrolepidoptera of the superfamilies Noctuoidea and Geometroidea, and to a lesser extent, Arctioidea, Sphingoidea, and Papilionoidea (M. Shaw 1983, 1994; M. Shaw and Huddleston 1991; S. Shaw 1995). The method of parasitism, unique to the tribe Rogadini, is noteworthy: the *Aleiodes* larva completes its feed-

ing and pupates within the shrunken and mummified remains of the host caterpillar. In all known cases, the form of the mummy caused by a particular *Aleiodes* species is characteristic for that host and parasitoid, so the mummified remains are of considerable diagnostic value and should be retained with the parasitoid, when reared. These host mummies are usually attached to the host plant substrate (leaf, grass blade, stem) at the prothoracic region of the host larva, by a glue-like substance that exudes through a prosternal hole chewed by the parasitoid larva. Exit from the host mummy is always postero-dorsally, through a circular hole. The inside of the mummy is lined with silk by the parasitoid larva, but the main support for the mummy seems to be the formation of a premature host pupal cuticle below the remaining larval cuticle. The physiological basis for host mummification has not been investigated experimentally in *Aleiodes*, but we speculate that it may involve the physical elimination of the host's corpora allatum by the developing parasitoid larva, which would reduce juvenile hormone levels and induce the premature formation of pupal cuticle. This hypothesis is consistent with the observation that larval feeding by *Aleiodes* is usually (all groups except *albitibia*) located initially in the prothoracic region of the host (e.g. the chewing of the glue-hole).

Currently, two of us (JCF and SRS) are conducting a phylogenetic analysis of the species of *Aleiodes* worldwide, and this is now complete enough to provide us with a logical framework for dividing the North American species into monophyletic species groups. Therefore, our present plan is to publish a series of shorter papers on species-groups, of which this paper is the first.

Our original intent was to provide revisionary coverage of North America north of Mexico, and for this area our study is most complete. Nevertheless, it is clear that this boundary is quite artificial and that some coverage of Neotropical species may be necessary. For example, two species of the *pulchripes* group (*cameronii* and *notozophus*) have ranges that extend from the southern United States southwards to Costa Rica. Three Neotropical species (*flavidus*, *pedalis*, and *vaughani*) have ranges that extend to areas just south of the U.S. borders (northern Mexico and Cuba), and it seems likely to us that they may eventually be found in southern parts of the U.S. With this paper we have decided to treat a complete monophyletic assemblage of species rather than some subset as circumscribed by geographical boundaries.

## METHODS

Species covered in this paper can be identified as members of the subfamily Rogadinae using the keys of S. Shaw (1995) or M. Shaw and Huddleston (1991). Our definition of *Aleiodes* follows that of S. Shaw (1993) and van Achterberg (1991). Specimens can be determined as *Aleiodes* using the keys of van Achterberg (1991), or Marsh et al. (1987). Specimens keyed through Marsh et al. (1987) will key to couplet 185, at which point they can be separated from *Rogas* by the presence of a discrete median carina on the propodeum, the lack of a foveate sternaulus on the mesopleuron, and the lack of a blunt basal tooth on the tarsal claw. In practice, more than 99% of U.S. and Canadian specimens encountered will be *Aleiodes*, as true *Rogas* is mainly a tropical group that is infrequently encountered north of Mexico.

Terminology mostly follows that used for *Aleiodes* by S. Shaw (1993) and Marsh (1989). Microsculpture terminology follows that of Harris (1979). Wing venation terminology agrees with the system being adopted for the Identification Manual for New World Genera of the Family Braconidae, and agrees closely to that of Goulet and Huber (1993). To avoid confusion, wing illustrations with veins and cells

used in this paper are provided (Figs. 41–43).

Abbreviations for museums are as follows: ANSP, Academy of Natural Sciences, Philadelphia, PA; AEI, American Entomological Institute, Gainesville, FL; AMNH, American Museum of Natural History, New York, NY; ABS, Archbold Biological Station, Lake Placid, FL; CAS, California Academy of Sciences, San Francisco, CA; CNC, Canadian National Collection, Ottawa; CUI, Cornell University, Ithaca, NY; FSCA Florida State Collection of Arthropods, Gainesville, FL; INHS, Illinois Natural History Survey, Urbana, IL; INBio Instituto Nacional de Biodiversidad, Heredia, Costa Rica; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MISU, Michigan State University, East Lansing, MI; MSSU, Mississippi State University, Mississippi

State, MS; NNML, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; OKSU Oklahoma State University, Stillwater, OK; TAMU, Texas A&M University, College Station, TX; NHM, The Natural History Museum, London; UCD, University of California, Davis, CA; ULQ, Universite Laval, Quebec; UKL, University of Kansas, Lawrence, KS; UMCP, University of Maryland, College Park, MD; UMSP, University of Minnesota, St. Paul, MN; RMSEL, Rocky Mountain Systematic Entomology Laboratory, University of Wyoming, Laramie, WY; USNM, U.S. National Museum of Natural History, Washington, D.C.

Authorship of the new species is attributed to the senior authors in the order indicated for each species, Marsh and Shaw, except for *earinos* which is attributed to Shaw.

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PRELIMINARY KEY TO THE SPECIES-GROUPS OF NEARCTIC *ALEIODES*

1.  Apex of hind tibia with a row of flattened setae along inner margin . . . . . . . . . . . .
    . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *seriatus* species-group
  — Apex of hind tibia without a row of flattened setae along inner margin, setae normal
    and hair-like . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2(1).  First metasomal tergum parallel sided; apex of metasoma laterally compressed in
    female . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
  — First metasomal tergum not parallel sided, wider apically than at base; apex of me-
    tasoma not laterally compressed in female . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
3(2).  Marginal cell of hind wind narrowest at middle, vein RS sinuate; body color mostly
    pale yellowish brown . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *compressor* species-group
  — Marginal cell of hind wind narrowest at base and widening towards wing apex; body
    color boldly contrasting black and red . . . . . . . . . . . . . . . . . . . . . . . . . . *ufei* species-group
4(2).  Vein RS of hind wing strongly sinuate, nearly reaching anterior wing margin near
    middle of marginal cell; parasitoids of Sphingidae . . . . . . . . . . . . . *praetor* species-group
  — Vein RS of hind wing straight, bent, or slightly sinuate, not close to wing margin near
    middle of marginal cell; parasitoids of various groups but never Sphingidae . . . . . . . 5
5(4).  Central disc of mesopleuron smooth and highly polished; parasitoids of Notodonti-
    dae, host mummy with an unusual expanded balloon-like anteroventral area . . . . . .
    . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *albitibia* species-group
  — Central disc of mesopleuron with various types of surface microsculpture, but not
    smooth and highly polished; parasitoids of various groups but host mummy never
    with an expanded balloon-like anteroventral area . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6(5).  Clypeus at least 3× wider than tall, with a carina across anterior surface; oral space
    large and broad, clypeo-antennal space/width of oral space less than or equal to 0.69;
    malar space narrow, less than mandibular base width . . . . . *melanopterus* species-group
  — Clypeus taller or not so wide, and usually without a transverse carina; oral space

smaller and less broad, clypeo-antennal space/width of oral space greater than 0.69; malar space variable, sometimes wider than mandibular base width ................. 7

7(6). Median length of pronotum greater than distance between occipital carina and lateral ocellus; pronotum shelf-like, dorsal surface parallel to dorsal surface of mesonotum ................................................................ *dispar* species-group

— Median length of pronotum shorter than distance between occipital carina and lateral ocellus; pronotum not shelf-like, or dorsal surface not parallel to dorsal surface of mesonotum ................................................................................ 8

8(7). Metasomal tergite 3 entirely smooth and shining ............. *gressitti* species-group

— Metasomal tergite 3 with various types of surface sculpture, especially on basal ½, often with a median carina ............................................................... 9

9(8). Ocelli very large, ocell-ocular distance ⅔ width of lateral ocellus or smaller ....... 10

— Ocelli smaller, ocell-ocular distance broader than ⅔ width of lateral ocellus, often wider than ocellus ...................................................................... 11

10(9). Flagellomeres compact, middle flagellomeres less than 2× longer than wide, usually about 1× as long as wide or just slightly longer; males sometimes with setose, circular pits medially on terga 5–7; parasitoids of geometrids, notodontids, and noctuids ... .................................................................. *pulchripes* species-group

— Flagellomeres elongate, middle flagellomeres 2× longer than wide or longer; males with terga 5–7 normal, unmodified; parasitoids of lymantriids .................... .................................................................. *pallidator* species-group

11(9). Marginal cell of hind wing narrowest at base and widening toward wing apex, vein RS straight entire length, or parallel with anterior wing margin along basal half only, thus marginal cell suddenly widening ........................................... 12

— Marginal cell of hind wing narrowest at middle, vein RS slightly sinuate ......... 15

12(11). Tarsal claws strongly pectinate over entire length; males with terga 4–6 densely setose (subdivided medially) .................................................. *ductor* species-group

— Tarsal claws not pectinate, or with pectin concentrated at base of claw; males with terga 4–6 normal, not densely setose ....................................................... 13

13(12). Metasomal terga 1 and 2 extremely coarsely sculptured, strongly porcate with rugae between ridges; body color black ......................... *rugulosus* species-group

— Metasomal terga 1 and 2 more finely sculptured, finely rugose, to costate rugose or coriaceous rugose; body usually not all black, varying from brown, to orangish brown, black and brown, or black and orange ..................................................... 14

14(13). Malar space narrow, less broad than basal width of mandible; body color black with bicolored black and orange metasoma ...................... *unipunctator* species-group

— Malar space wide, broader than basal width of mandible; body color variable but commonly brown or orangish brown, and never with a bicolored black and orange metasoma .......................................................... *gasterator* species-group

15(11). Vertex sculpturing rugose, with strong laterally-running ridges; metasomal tergum 4 mostly covered with coarse granular punctate or rugose sculpture; several species with metasomal terga 1–4 forming a partial to complete carapace ................ ..................... *coxalis* species-group (including *Tetrasphaeropyx* Ashmead)

— Vertex sculpturing either smoother or more irregular, not dominated by strong laterally-running ridges; metasomal tergum 4 mostly covered with fine granular sculpture, or mostly smooth and shining; metasomal terga 1–4 never carapace-like, terga 5–7 exposed ...................................................................... 16

16(17). Ocelli small, ocell-ocular distance larger than width of lateral ocellus; metasoma always bicolored with black anteriorly and laterally, yellow to yellowish white medially, black sometimes continuing posteriorly to enclose lighter median spot ........... ................................................................ *circumscriptus* species-group

— Ocelli larger, ocell-ocular distance smaller than width of lateral ocellus; metasoma

color variable, but often mostly yellow or with black restricted to anterior parts of
tergum 1, less commonly with dark markings as above . . . . . . . . *gastritor* species-group

## ALEIODES PULCHRIPES
SPECIES-GROUP

Included species: *pulchripes* (Wesmael)
1838, *fortipes* (Reinhard) 1863, *flavidus*
(Cresson) 1865, *pedalis* Cresson 1869, *que-
becensis* Provancher (1880), *geometrae* (Ash-
mead) 1889, *cameronii* (Dalla Torre) 1898
(=*mexicanus* Cameron [preoccupied]), *in-
signipes* (Brues) 1912, *vaughani* (Muese-
beck) 1960 (=*nigriceps* Enderlein [preoc-
cupied], =*enderleini* Shenefelt [unneces-
sary replacement name]), *caucasicus* (To-
bias) 1975, *antennatus* (Belokobylskij) 1988,
*arsenjevi* (Belokobylskij) 1988; *arizonensis*
new species, *cazieri* new species, *earinos*
new species, *notozophus* new species and
*rossi* new species.

Remarks.–A small, but distinctive, pre-
sumably monophyletic group restricted to
the New World. As far as known, they are
associated with exposed-feeding geome-
trids, notodontids, and noctuids, mostly
on arboreal vegetation. Members of the
*pulchripes* species-group have strongly

pectinate tarsal claws (Figs. 14, 16, 18), of-
ten with more than 10 teeth comprising
the pectin. Sculpturing of the first meta-
somal tergum is weakly rugulose to faint-
ly rugulocostate; while the third metaso-
mal tergum sculpturing is shallowly ru-
gulose or rugulocostate anteriorly, and
finely punctate and nitid posteriorly, or
completely punctate-nitid. They have
large to enormous ocelli, ranging from
1.5–9.0 times wider than the ocell-ocular
distance. The malar space is shorter than
the mandibular base, thus the compound
eyes appear very large as well. The anten-
na is long, with 43–70 antennomeres, but
individual flagellomeres are short and
compact. All members of the group have
the antero-lateral margin of the propo-
deum granulate, with just a trace of cos-
tation. In some the propodeum is almost
entirely granulate. This group includes all
known species with males having setose
pits on terga 4–7 (a striking synapomor-
phy), but some included species never
evolved this character.

KEY TO THE NEW WORLD SPECIES OF THE *PULCHRIPES* SPECIES GROUP

1.   Fore wing longer than 9mm, deeply tinted with yellow, usually with dark blackish
     patches apically, and sometimes medially (Figs. 36–37) . . . . . . . . . . . . . . . . . . . . . . . . 2
—    Fore wing shorter than 9mm, clear or only lightly tinted with blackish pigmentation,
     and lacking dark patches (Figs. 38–40) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2(1). Head yellowish orange; apical ¼ of female hind tibia black (Fig. 26); female forewing
     lacking a dark medial cloud below pterostigma (Fig. 36) . . . . . . . . . . . *flavidus* (Cresson)
—    Head and apical ½ or more of female hind tibia black (Fig. 28); wing sometimes with
     a faint to very distinct darkened medial cloud below pterostigma (Fig. 37) . . . . . . . .
     . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *pedalis* Cresson
3(1). Marginal cell of hind wing narrowest at apical ²⁄₃, vein RS slightly arched at its apical
     ²⁄₃; hind tarsus pale yellowish or white (Fig. 24) . . . . . . . . . . . *quebecensis* (Provancher)
—    Marginal cell of hind wing narrowest at base and usually widening toward wing
     apex, vein RS straight entire length or parallel with wing margin on basal half only,
     thus suddenly widening (Figs. 41–43); hind tarsus variable, but not white . . . . . . . . . 4
4(3). Body multicolored, head black or dark brown, mesosoma variously marked with
     black, brown, yellow or orange . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
—    Body unicolored orange or honey-yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
5(4). Tarsal claw strongly pectinate, without a distinct gap between apical claw and basal

pectination; hind tarsus dark reddish brown; male with small setose pits medially on terga 4–7. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *notozophus* new species

— Tarsal claw more weakly pectinate or with pectination reduced to mostly seta-like spines, always with a distinct gap between apical claw and basal pectination; hind tarsus dark, usually black or rarely brown; male without setose pits medially on terga 4–7. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6(4). Ocelli enormous, lateral ocellus about 15 times wider than ocell-ocular distance, nearly touching compound eye; malar space very small, only about half as wide as basal width of mandible; tarsal claw pectination greatly reduced, pectination mostly comprised of seta-like spines concentrated at extreme base; Brazil . . . . . . *insignipes* (Brues)

— Ocelli smaller, lateral ocellus about 3 times wider than ocell-ocular distance, clearly separated from compound eye; malar space larger, only slightly shorter than basal width of mandible; tarsal claw pectination visible over at least basal half of claw, pectination mostly spine-like or tooth-like; Central America south to Ecuador . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *vaughani* (Muesebeck)

7(4). Tarsal claws with a wide gap between the apical claw and basal pectination (Fig. 19); occipital carina broadly effaced medially (Figs. 6, 35) . . . . . . . . . . . . . . . . . . . . . . . . . . 8

— Tarsal claws with basal pectination extending fully to base of apical claw (Figs. 16, 18, 20, 21); occipital carina complete or only slightly interrupted medially . . . . . . . . . . 9

8(7). First metasomal tergum shorter than wide; propodeal sculpture mostly granulate dorsally; vein 1cu-a of fore wing beyond vein 1M by distance greater than length of 1cu-a . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *geometrae* (Ashmead)

— First metasomal tergum distinctly longer than wide; propodeal sculpture mostly rugose dorsally, greatly obscuring granulate base sculpture; vein 1cu-a of fore wing beyond vein 1M by distance equal to or less than length of 1cu-a    *earinos* new species

9(7). Vein 1cu-a of fore wing beyond vein 1M by distance less than length of vein 1cu-a (Fig. 41); tarsal claw with very large pectination, with 3–6 stout spines of the basal pectin about as large as the apical claw (Fig. 16); males with exceptionally large, circular setose pits on metasomal terga 4–7 (as in Fig. 13) . . . . . *cameronii* (Dalla Torre)

— Vein 1cu-a beyond vein 1M by distance greater than length of vein 1cu-a (Figs. 49, 40); tarsal claw with smaller pectination, stout spines of the basal pectin obviously smaller than apical claw (Figs. 18, 20); males with smaller setose pits on terga 4–7 (as in Fig. 15) or none . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

10(9). Antennal flagellum entirely brown . . . . . . . . . . . . . . . . . . . . . . . . . . . . *rossi* new species

— Antennal flagellum black on basal half, orange on most or all apical half . . . . . . . . . 11

11(10). Apical 3–5 flagellomeres black or brown; stigma of fore wing entirely yellow (Fig. 39); vein 1M of hind wing 1.5 times longer than vein r-m; male with median dorsal pits on metasomal terga 4–7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *arizonensis* new species

— Apical half of flagellum entirely orange; stigma dark brown to black medially, yellow only basally and at extreme apex (Fig. 40); vein 1M of hind wing only slightly longer than r-m, at most 1.2 times longer; male without median dorsal pits on metasomal terga 4–7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *cazieri* new species

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**Aleiodes arizonensis** Marsh and Shaw, new species
(Figs. 2, 39)

*Female.*—Body color: unicolored honey yellow, antenna black on basal half, orange on apical half except apical 3–5 flagellomeres darkening to brown, ocellar triangle black, wings lightly yellowish, veins brown except C+Sc+R, stigma and 1R1 yellow (Fig. 39). **Body length**, 8.0 mm; fore wing length, 8.0 mm. **Head:** 64 antennomeres, all flagellomeres, except apical $\frac{1}{2}$, as wide as long, those in apical $\frac{1}{3}$ slightly longer than wide; malar space short, less than basal width of mandible and $\frac{1}{5}$ eye height; temple very narrow, about $\frac{1}{3}$ eye
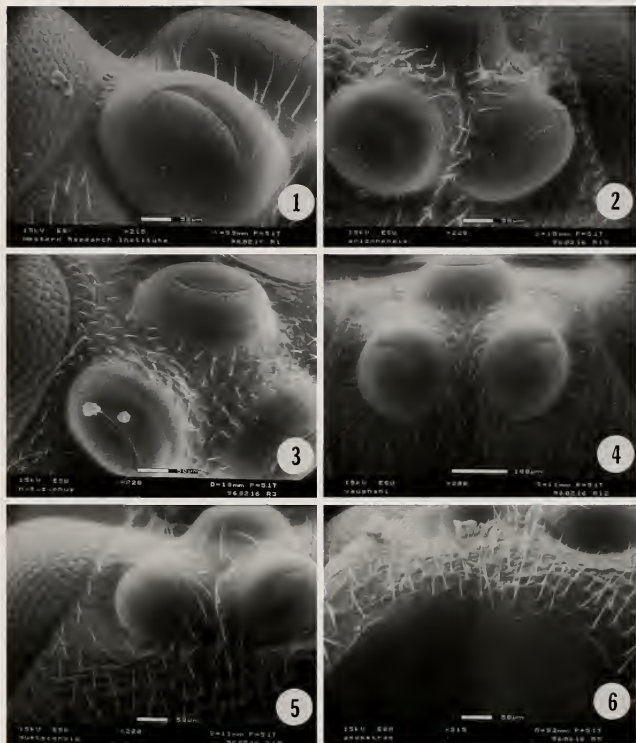
Figs. 1–6. Head vertices of *Aleiodes* spp.: 1, ocelli of *flavidus* (215×); 2, ocelli of *arizonensis*, (220×); 3, ocelli of *notozophus*, (220×); 4, ocelli of *vaughani*, (200×); 5, ocelli of *quebecensis*, (220×); 6, head of *geometrae*, postero-dorsal view showing effaced occipital carina (215×).

width; occipital carina not reaching hypostomal carina, weakly interrupted on vertex behind ocelli; oral space small and circular, diameter about equal to basal width of mandible; clypeus weakly swollen; ocelli large, ocellocular distance ¼ diameter of lateral ocellus (Fig. 2); face rugulose-costate, frons smooth, vertex and temple granulate; maxillary palpus not swollen. **Mesosoma**: pronotum with me-

dian scrobiculate line, rugulose above, granulate below; mesonotum and scutellum granulate, notauli weakly scrobiculate, meeting in triangular rugose area before scutellum; mesopleuron smooth and shining, subalar sulcus carinate, sternaulus absent; propodeum rugose-granulate dorsally, smooth laterally, median carina complete. **Legs:** tarsal claws strongly pectinate; inner spur of hind tarsus $\frac{1}{2}$ length of hind basitarsus; hind coxa granulate dorsally. **Wings** (Fig. 39): fore wing with vein r $\frac{2}{3}$ length of 3RSa and $\frac{2}{3}$ length of m-cu, vein 1cu-a beyond 1M by distance greater than length of 1cu-a, vein 1CUa $\frac{2}{5}$ length of 1CUb; hind wing with marginal cell gradually widening, vein RS straight, vein 1M about 1.5 times longer than 1r-m, vein M+CU slightly longer than 1M, vein m-cu absent. **Metasoma:** first tergum rugulose, longer than apical width, median carina complete; second tergum costate-rugulose, median carina complete; third tergum weakly costate-rugulose basally, granulate apically, median carina present on basal half; remainder of terga granulate; ovipositor about $\frac{1}{2}$ length of hind basitarsus.

*Male.*—Essentially as in female; metasomal terga 4–6 with small circular median dorsal pits.

*Holotype female.*—ARIZONA: Ramsey Canyon, 5000 ft., 15 mi. S. Sierra Vista, Huachuca Mountains, September 17, 1967, Sternizky. Deposited in CNC.

*Paratypes.*—ARIZONA: 1 male, 1 female, same data as holotype except female with date of May 1968. Paratypes deposited in USNM, RMSEL.

*Distribution.*—Known only from the type locality in Arizona.

*Biology.*—Unknown.

*Comments.*—This species is similar in morphology and distribution to *cazieri* but is distinguished by the males with median pits on metasomal terga 4–6, by the entirely yellow pterostigma (Fig. 39), by the longer vein 1M in the hind wing, and by the dark tip of the antenna.

*Etymology.*—Named after the type locality of Arizona.

## Aleiodes cameronii (Dalla Torre),
new combination
(Figs. 10–13, 16, 21, 33, 41)

*Rhogas mexicanus* Cameron, 1887, Biol. Cent.-Amer., Hym. 1:389. Preoccupied in *Aleiodes* by *mexicanus* Cresson, 1869.

*Rhogas cameronii* Dalla Torre, 1898, Cat. Hym. 4: 216. Replacement name for *mexicanus* Cameron.

*Diagnosis.*—Body color honey yellow, antennae and ocellar triangle brown, wings hyaline, veins brown except stigma and occasionally C+Sc+R yellow; 60–65 antennomeres, first flagellomere only slightly longer than second, flagellomeres 2–30 as long as wide, remainder slightly longer than wide; malar space (Fig. 33) short, $\frac{1}{10}$ eye height and $\frac{1}{2}$ basal width of mandible; temple narrow, $\frac{1}{3}$ eye width; occipital carina not quite meeting hypostomal carina; oral space (Fig. 33) small and circular, width twice malar space and about equal to length of face; ocelli large, lateral ocellus nearly touching eye, ocellar distance $\frac{1}{12}$ greatest diameter of lateral ocellus; face finely costate-rugulose, clypeus rugulose; frons, vertex, and temple finely granulate; maxillary palpus not swollen; mandibles small; mesonotum and scutellum granulate; notauli weakly scrobiculate, meeting posteriorly in triangular rugulose area; mesopleuron smooth except for hair pits, subalar sulcus costate, sternaulus absent; propodeum (Fig. 10) granulate, rugulose at apex and along complete median carina; tarsal claws strongly pectinate on entire inner edge (Fig. 16, 21); inner spur of hind tibia about $\frac{1}{2}$ length of hind basitarsus; hind coxa smooth dorsally; fore wing (Fig. 41) with vein r about $\frac{2}{3}$ length of 3RSa and about $\frac{3}{4}$ length of m-cu, vein 1cu-a beyond 1M by distance equal to half length of 1cu-a, vein 1CUa about $\frac{1}{5}$ length of 1CUb; hind wing (Fig. 41) with marginal cell suddenly wid-
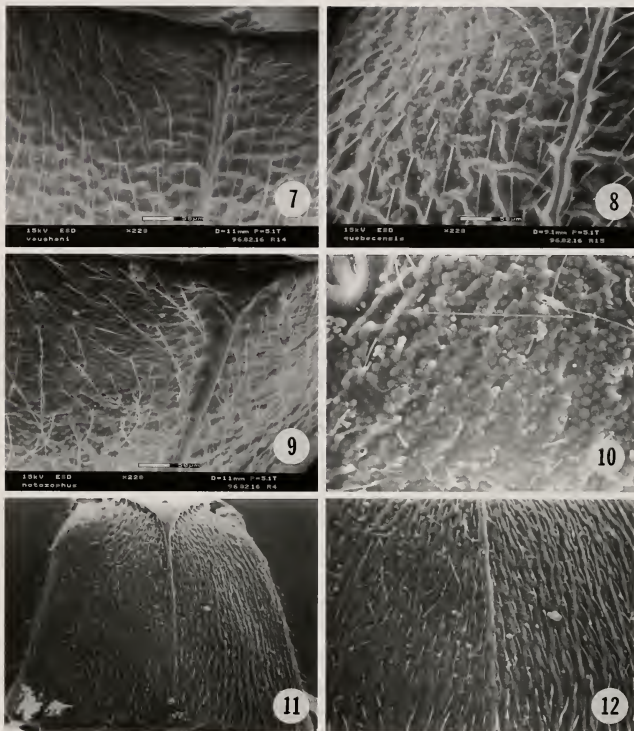
Figs. 7–12.  Figs 7–10. Propodea of *Aleiodes* spp.: 7, *vaughani*, dorsal view of left antero-lateral area (220×); 8, *quebecensis*, dorsal view of left antero-lateral area (220×); 9, *notozophus*, dorsal view of left antero-lateral area (220×); 10, *cameronii*, dorsal view of left antero-lateral area (300×). Figs 11–12. First metasomal terga of *Aleiodes* spp. 11, *cameronii* (78×); 12, *cameronii* (110×).

ening from basal ¼ of cell, vein RS sharply curved downward, vein 1r-m ½ length of 1M, veins M+CU and 1M about equal in length, vein m-cu short and distinct, often arising from 2M; first metasomal tergum (Figs. 11, 12) costate-rugulose, slightly longer than apical width, median carina complete; second tergum costate-rugulose, median carina complete; third tergum costate at base, granulate on apical half, me-
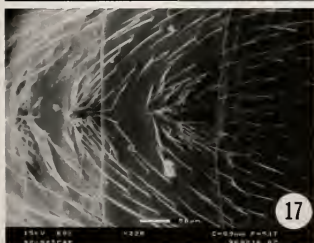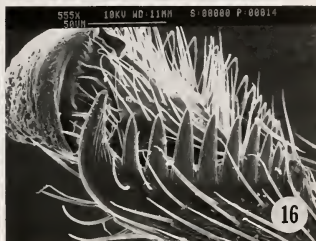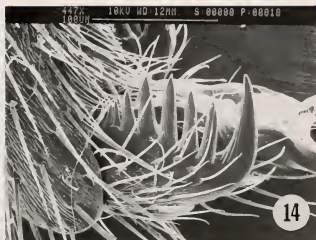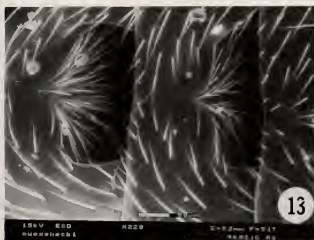
Figs. 13–18. Figs 13, 15, 17. Setose dorso-medial tergal pits of male *Aleiodes* spp.: 13, *cameronii* (220×); 15, *rossi* (335×); 17, *geometrae* (220×). Figs. 14, 16, 18. Tarsal claws of *Aleiodes* spp.: 14, *quebecensis* (447×); 16, *cameronii* (555×); 18, *cazieri* (505×).

dian carina on basal half; remainder of terga granulate; ovipositor barely exerted, about ¼ length of hind basitarsus; male metasomal terga 5–7 with large dorsal median circular pits (Fig. 13).

*Type material examined.*—*Rhogas mexicanus* Cameron, holotype male, ''Mexico, Presidio'' [NHM].

*Distribution.*—This species occurs throughout the entire southern United States, and southwards through Mexico to Costa Rica. In the United States it ranges
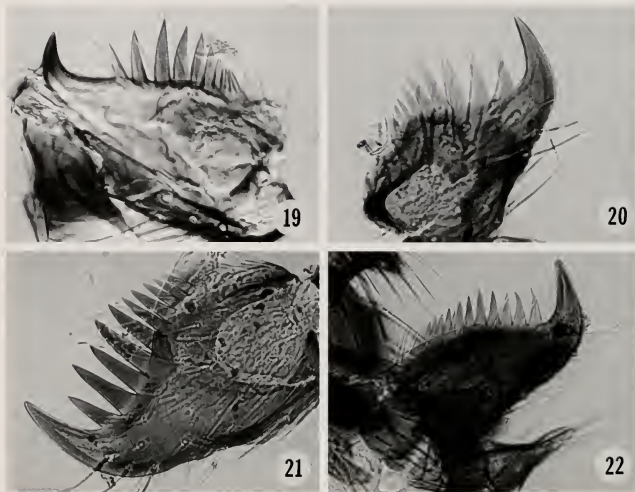
Figs. 19–22.   Compound microscope photographs of slide-mounted claws of *Aleiodes* spp.: 19, *geometrae*; 20, *rossi*; 21, *cameronii*; 22, *vaughani*.

from Massachusetts, Maryland, and Virginia in the east, southwards to Florida, and westwards to California. The northern-most record is from Michigan. Cameron indicates the type locality as Presidio, Mexico but we could not find this locality in any atlas. Perhaps the correct location was Presidio, Texas from which we have seen many specimens.

*Biology.*—*Aleiodes cameronii* has been reared in Maryland by Paul Gross, Alex Segarra and Pedro Barbosa from three hosts on willow (*Salix nigra*): a geometrid, *Eutrapela clemataria* (J.E. Smith), and two catocaline noctuids, *Zale lunata* (Drury) and *Catocala cara* Gn. The mummy formed in the later case is about 1.5 cm long, dark brown, densely wrinkled over the apical ½, and terminating with long caudal prolegs that form a conspicuous forked "tail" at

the tip of the mummy. Another specimen has a host mummy attached with it, which is presumed to be an unidentified species of Notodontidae. Also, several specimens were collected at lights indicating this species is nocturnally active.

*Comments.*—This species belongs to the group in which the males have distinctive setose median pits on the apical metasomal terga, but the pits in *cameronii* are larger than in any other known species. *Aleiodes cameronii* is distinguished from most others in the species-group by vein 1cu-a of the forewing being close to 1M (Fig. 41). Only *earinos* has similar venation, but in *earinos* the occipital carina is not complete and the tarsal claw is not so fully and extremely pectinate as in *cameronii* (Fig. 16). The pits on the male metasomal terga are curious and their detailed mor-

Figs. 23–24. Color patterns of *Aleiodes* spp.: 23, apical flagellomeres of *quebecensis*; 24, hind tibia and tarsus of *quebecensis*.

phology, both external and internal, need to be studied further. We hypothesize that these probably may serve to disperse sex pheromones, and behavioral studies of the courtship in this and related species might be interesting.

## *Aleiodes cazieri* Marsh and Shaw, new species
### (Figs. 18, 40)

*Female.*—**Body color**: unicolored, entire body including legs honey yellow, antenna with scape, pedicel and basal ½ of flagellum black, apical ½ of flagellum orange, wings slightly yellowish, veins brown, fore wing with vein C+Sc+R, basal and apical spots on stigma, and vein 1R1 yellow. **Body length**, 9 mm; fore wing length, 8 mm. **Head**: 65 antennomeres, first flagellomere slightly longer than second, remainder slightly longer than wide; malar space short, slightly shorter than basal width of mandible and about ⅕ eye height; temple narrow, about ⅓ eye width; occipital carina meeting hypostomal carina; oral space small and circular, width equal to malar space and about ½ face height; clypeus not swollen; ocelli large, ocellocular distance about ⅓ diameter of lateral ocellus; face rugulose, with median ridge below antennae; frons smooth; vertex and temple granulate; maxillary palpus not swollen; mandibles small, tips not overlapping when closed. **Mesosoma**: pronotum rugose laterally, granulate dorsally; mesonotum and scutellum granulate; notauli scrobiculate, meeting in triangular rugose area before scutellum; mesopleuron smooth, subalar sulcus rugose; sternaulus absent; propodeum rugose, median carina obscured apically. **Legs**: tarsal claws completely pectinate, with 10–15 stout spines on inner edge (Fig. 18); inner spur of hind tibia about ⅓ length
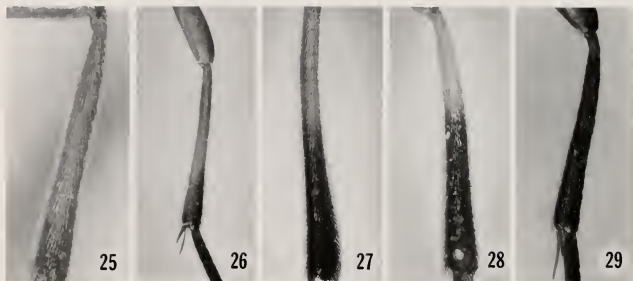
Figs. 25–29.  Variation in hind tibia color patterns of *Aleiodes* spp.: 25, *geometrae* female; 2, *flavidus* female; 27, *flavidus* male; 28, *pedalis* female; 29, *notozophus* female.

of hind basitarsus; hind coxa rugose dorsally. **Wings**: (Fig. 40) fore wing with vein r about ⅓ length of 3RSa and about ½ length of m-cu, vein 1cu-a beyond 1M by twice length of 1cu-a, vein 1CUa slightly more than ½ length of 1CUb; hind wing with vein RS straight, marginal cell gradually widening to wing apex, vein 1r-m equal in length to 1M, vein M+CU longer than 1M, vein m-cu short and distinct,

leaving 1M before junction with 1r-m and 2M. **Metasoma**: first tergum longer than wide, costate-rugulose, median carina complete; second tergum costate-rugulose, median carina complete; third tergum costate on basal ¾, granulate on apical ½; remainder of terga weakly granulate; ovipositor short, about ⅓ length of hind basitarsus.

*Male.*—Essentially as in female; meta-



Figs. 30–32.  Mummified noctuid host larvae parasitized by *Aleiodes* spp.: 30, *geometrae*; 31, *vaughani*; 32, *quebecensis*.
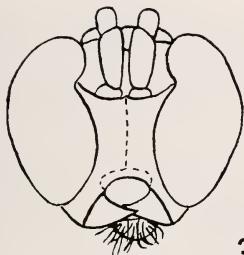
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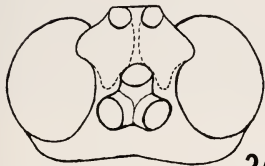


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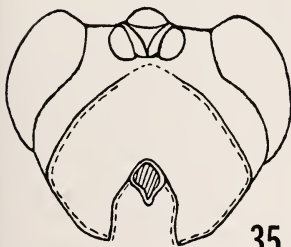


**35**

Figs. 33–35. Head morphology of *Aleiodes* spp.: 33, *cameronii*, anterior view; 34, *notozophus*, dorsal view; 35, *geometrae*, postero-dorsal view showing effaced occipital carina.

somal terga 4–6 without dorsal median pits.

*Holotype.*—Female: ARIZONA, South West Research Station, 5 mi W. Portal, 5400 ft., Cochise Co., August 4, 1956, C. and M. Cazier collectors. Deposited in AMNH.

*Paratypes.*—ARIZONA: 1 female, 1 male, same data as holotype except dates of July 27 and August 8, 1956; 2 males, S.W. Res. Sta., 5 mi. W. Portal, August 5, 1959, H. E. Evans, 5400'; 1 male, Ramsey Canyon, 5000 ft., 15 mi S. Sierra Vista, Huachuca Mts., Sternitzky, July 1968. Paratypes deposited in CNC, USNM, AMNH, CUI.

*Distribution.*—Known only from Arizona.

*Biology.*—Unknown.

*Comments.*—This species is somewhat similar to *arizonensis*, but is distinguished by the much smaller ocelli, shorter vein 1M in the hind wing, and the absence of median pits on metasomal terga 4–6 of the male.

*Etymology.*—Named for its collector, Mont Cazier, who was in charge of the Southwest Research Station in Portal, Arizona for many years.

**Aleiodes earinos Shaw, new species**
(Fig. 44)

*Female.*—**Body color**: Body unicolored yellowish to reddish brown, antenna black, wings hyaline, veins light brown, tegula orange. **Body length**, 6.0–7.0 mm; forewing length 5.8–7.3 mm. **Head**: 57–65 antennomeres; malar space short, equal to or less than basal width of mandible; oral opening small, circular; occipital carina weak or absent on vertex; ocelli large, lateral ocellus 4.3 times wider than ocell-ocular distance; face weakly costate, frons, vertex and temple granulate. **Mesosoma**: mesonotum and scutellum granulate; mesopleuron smooth, subalar sulcus weakly rugose, sternaulus absent; propodeum granulate anteriorly, grading to rugose posteriorly (Fig. 44), median carina
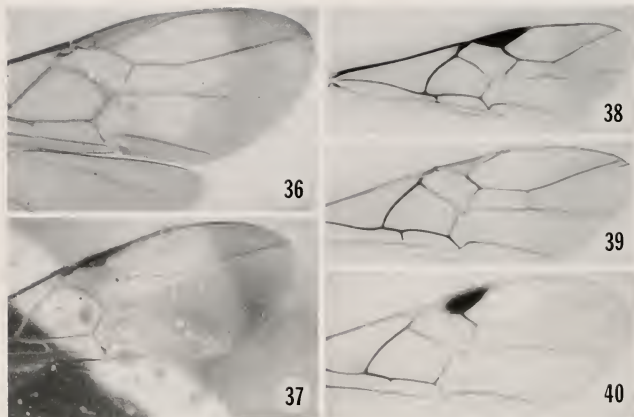
Figs. 36–40. Forewings of *Aleiodes* spp.: 36, *flavidus*; 37, *pedalis*, holotype; 38, *notozophus*; 39, *arizonensis*; 40, *cazieri*.

complete. **Legs**: tarsal claws with a wide gap between the apical claw and basal pectination. **Wings**: fore wing with vein 1cu-a beyond 1M by distance equal to or less than length of 1cu-a; hind wing with marginal cell gradually widening apically, vein RS straight, vein r-m nearly as long as 1M. **Metasoma**: first metasomal tergum slightly longer than wide; first and second metasomal terga costate, median carina complete, third tergum costate on basal $\frac{1}{3}$, median carina absent.

*Male.*—Essentially as in female, except metasomal terga 4–6 with small circular seta-lined median dorsal pits.

*Holotype female.*—FLORIDA: Alachua Co., Gainesville, Beville Heights, April 14, 1979, L. Stange, blacklight trap. Deposited in FSCA.

*Paratypes.*—ARKANSAS: 1 female, Logan Co., Magazine Mt., 2500', T6N, R25W, sec. 23NW, May 15–16, 1989, J. MacGown, Q. Fang, blacklight trap, William H. Cross Expedition. FLORIDA: 2 females, 1 male,

same data as holotype except females collected 12–13 April, 1980, male collected April 4, 1979; 5 females, Lk. Placid, Archbold Biological Station, R.A. Morse, March 23–25, 1964, coll. at light. TEXAS: 1 female, Del Rio, (date illegible), Timberlake coll.; 1 female, Bastrop, Lost Pines Pk., April 6, 1959, W.R.M. Mason. Paratypes deposited in FSCA, MISS, USNM, CNC, RMSEL, CUI.

*Distribution.*—Known only from Arkansas, Florida, and Texas.

*Biology.*—The host is unknown, but the flight period is early in the season and *carinos* is attracted to lights.

*Comments.*—This species is similar to *geometrae*, with which it has been previously confused. Similarities with *geometrae* include a claw with a gap between the apical claw and the basal pectin, weak to incomplete occipital carina, and pits in the male terga 5–7. Differences of *carinos* from *geometrae* include the larger body size, often darker reddish brown color, longer fla-
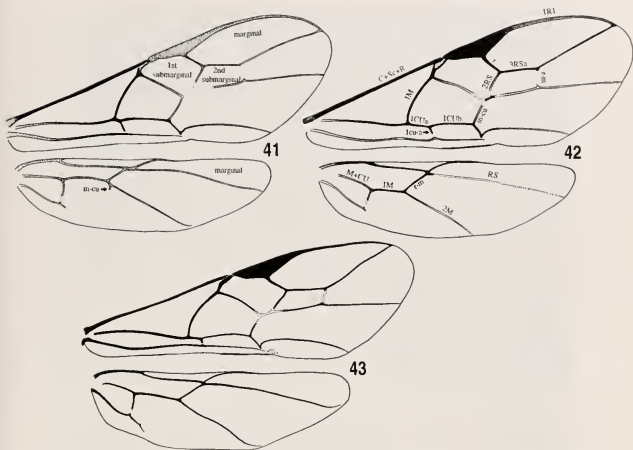
Figs. 41–43. Wings of *Aleiodes* spp. with principal veins and cells mentioned in descriptions labeled: 41, *cameronii*; 42, *geometrae*; 43, *notozophus*.

gellum, less broad gap in the occipital carina, vein 1cu-a positioned more basally (more like *cameronii* than *geometrae* with respect to this character), coarser propodeal sculpture (Fig. 44), and much longer first metasomal tergum.

*Etymology.*—From the Greek *earinos* meaning "of spring," in reference to the early seasonal occurrence of this species.

**Aleiodes flavidus** (Cresson),
new combination
(Figs. 1, 26–27, 36)

*Rogas flavidus* Cresson, 1865, Proc. Ent. Soc. Philadelphia 4:83.

*Re-description of type series.*—**Body color:** yellow to yellowish orange, except ocellar triangle, antenna, apical ¼ to ½ hind tibia (Fig. 26–27), and hind tarsi black; maxillary palpi yellow; wings yellow, except tips blackish. **Body length:** 9.8 mm; fore-

wing length 9.7 mm. **Head:** ocelli enormous (Fig. 1), lateral ocellus 7.6 times wider than ocell-ocular distance; vertex granulate to very finely rugulose; 70 antennomeres, 15th flagellomere from base width/length less than 0.84, basal flagellomeres not longer than wide; medial facial ridge extending down frons less than 0.55 of distance from line between bases of scapes to clypeus; malar space very short, shorter than basal width of mandible, malar space/eye height ratio = 0.11; temple/eye height ratio = 0.11; occipital carina effaced medially, complete or nearly so at hypostomal carina; clypeal shape rounded, not abruptly edged, not flat ventrad, clypeus rugulose, without transverse carina, clypeal height/width 0.42–0.65; oral opening circular, width shorter than the clypeo-antennal distance. **Mesosoma:** pronotum granulate medio-

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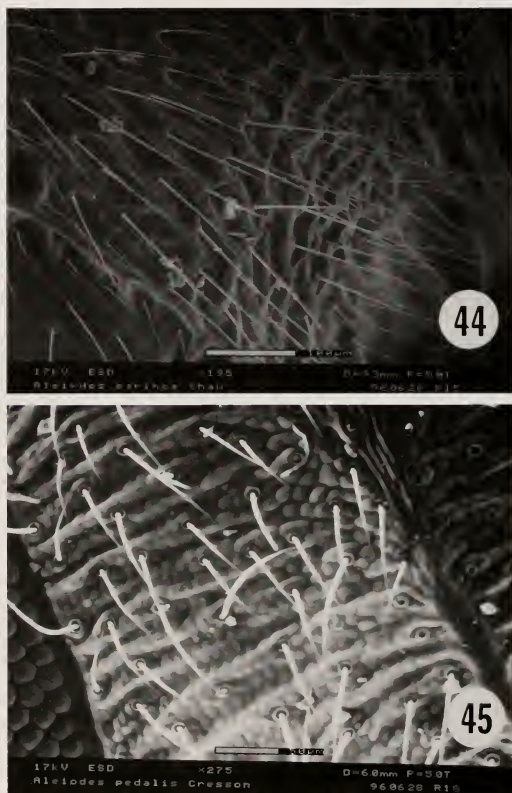




Figs. 44–45. Sculpturing on *Aleiodes* spp.: 44, postero-lateral section of propodeum of *earinos* showing rugose sculpture (195×), 45, face of showing lateral striations (275×).

anteriad, pronotum laterally costate; pronotum declining at angle greater than 45 degrees from mesonotum, pronotal anterior flange less than 0.28 pronotal length, pronotal medial length longer than length between occipital carina and lateral ocellus; mesopleuron sculpturing on and posteriad to central disc smooth, punctate;

sternaulus absent; mesopleural pit posteriad to central disk absent; posterio-dorsal surface of mesonotum with some strong, smooth carinae, notauli at mid-dorsal surface of mesonotum not coarsely foveate but with a long longitudinal carinae, mesonotal sculpturing excluding postero-dorsal surface of mesonotum granulate; scutellum granulate, with pronounced setal pits; median carina of propodeum usually complete to apex; sculpturing of propodeum antero-laterally granulate, faintly rugulose. **Legs:** inner apex of hind tibia with setae normal and unmodified; tarsal claw not fully pectinate, gap between apical tarsal tooth and claw greater than apical tooth length; 6–7 teeth in basal pectin; apical tarsal tooth with a small seta-like tip. **Wings:** forewing with second submarginal cell irregular in shape, vein 2RS not parallel with r-m; forewing width/length at widest point greater than .29, less than .35; length ratio of veins 3RSa/r about 1.43, vein 1cu-a positioned $\frac{1}{3}$ distance between veins 1M and m-cu (closer to 1M); hindwing marginal cell narrowest at base, RS gradually curved to wing margin; vein r-m length 0.6 times 1M. **Metasoma:** tergum I elongate, apical width/tergum length ratio less than 0.87; tergum I sculpturing faintly rugulocostate; median carina pronounced; median carina of tergum II pronounced; median triangle at base of tergum II large and associated with anterior carinae which run laterally to margins of tergum; tergum III sculpturing shallowly rugulose or rugulocostate anteriad, finely punctate posteriad; medial pits on terga 4–7 of males absent; ovipositor short, less than $\frac{1}{2}$ length of metafemur.

*Type material examined.*—Holotype male, pinned, 4 labels (excluding ANSP tag), Cuba, Prof. Poey, type #1663.1 (Philadelphia). Condition of holotype fair; distal ends of both antennae lost, left antenna 25% shorter than right; left middle leg lost; tarsi of right middle leg and both hind legs lost. One male paratype, Cuba, type #1663.2 (Philadelphia).

*Other Specimens Examined.*—Only two non-type specimens were seen (females from the USNM collection).

*Distribution.*—Cuba.

*Comments.*—*Aleiodes flavidus* is a distinctive species that can be recognized by its exceptionally large body size, enormous eyes and ocelli (Fig. 1), deeply yellow-colored and black-tipped wings (Fig. 36), and extensive granulate sculpture. It is, however, rare in North American collections (we have only seen the holotype, paratype, and two other specimens). Its nearest relative is *pedalis*, which differs by having the head and apical $\frac{1}{2}$ (or more) of the middle tibia black in females (see Figs. 26, 28), and sometimes by having a black median wing band or cloud.

**Aleiodes geometrae** (Ashmead),
new combination
(Figs. 6, 17, 19, 25, 30, 35, 42)

*Rhogas geometrae* Ashmead, 1889 (1888), Proc. U.S. Nat. Mus. 11: 633.

*Diagnosis.*—Body unicolored honey-yellow to orange, antenna black, wings hyaline, veins light brown, tegula yellow; body length, 5.0–6.0 mm; 43–56 antennomeres; malar space short, equal to or less than basal width of mandible; oral opening small, circular; occipital carina weak or absent on vertex (Figs. 6, 35); ocelli large, lateral ocellus 1.5 times wider than ocell-ocular distance (Figs. 6, 42); face weakly costate, frons, vertex and temple granulate; mesonotum and scutellum granulate; mesopleuron smooth, subalar sulcus weakly rugose, sternaulus absent; propodeum rugose-granulate, median carina complete; forewing (Fig. 42) with vein 1cu-a beyond 1M by distance greater than length of 1cu-a; hind wing with marginal cell gradually widening apically, vein RS straight, vein 1r-m nearly as long as 1M; tarsal claws with a wide gap between the apical claw and basal pectination (Fig. 19); first and second metasomal terga costate, median carina complete, third tergum cos-

tate on basal $\frac{1}{2}$, median carina absent, metasomal terga 4–6 in male with small pits medially (Fig. 17).

*Type material examined.*—*Rhogas geometrae* Ashmead, lectotype male (here designated), USA, Missouri, reared from an unknown geometrid larva, May 5, 1877, C.V. Riley [USNM]; 2 paralectotype males, same data, [USNM].

*Distribution.*—Ontario south to Florida, west to North Dakota, Colorado, and Texas. The period of flight activity for adults ranges from mid-March to mid-August.

*Biology.*—Reared from the geometrids *Paleacrita vernata* (Peck) and *Semiothisa ocellinata* (Gn.). One specimen from Texas was reared from an unidentified host on honey locust.

*Comments.*—This species is not very common in collections, considering the usual abundance of the hosts. Collecting efforts should focus on trying to rear it from host larvae. It can be recognized most easily by its broadly effaced occipital carina, tarsal claws with a wide gap between the apical claw and basal pectination, and median pits on the male metasomal terga 4–6. We have seen one unusual male specimen from Rio Grande Valley State Park, Hidalgo County, Texas [TAMU] that has some dark markings on the metasoma, a white annulus on the flagellum, and the first metasomal segment longer than wide. This may represent an additional new species near *geometrae*, but we hesitate to describe it until more material is available.

## Aleiodes insignipes (Brues), new combination

*Rhogas insignipes* Brues, 1912, Ann. Ent. Soc. Amer. 5: 221.

*Diagnosis.*—Body uniformly pale yellow, except head, antenna, pterostigma, last segment of fore tarsus, middle leg beyond basal $\frac{1}{3}$ of tibia, and hind leg beyond extreme base of tibia black; wings hyaline to pale yellow-fuscous, veins light brown;

body length, 8.0 mm; 65 antennomeres; malar space extremely short, $\frac{1}{2}$ as wide as basal width of mandible; oral opening small, circular; occipital carina weak or absent on vertex; ocelli extremely large, lateral ocellus 15 times wider than ocellocular distance, nearly touching compound eye; face weakly transversely rugose aciculate; frons, vertex and temple granulate; mesonotum and scutellum granulate; mesopleuron smooth, subalar sulcus weakly rugulose, sternaulus absent; propodeum granulate, median carina complete; forewing with vein 1cu-a beyond 1M by distance greater than length of 1cu-a; hind wing with marginal cell strongly widening apically, vein RS slightly curved medially, vein 1r-m about $\frac{2}{3}$ as long as 1M; tarsal claws with a wide gap between the apical claw and basal pectination, pectination reduced to 4–5 seta-like spines; first metasomal tergum long and narrow, 1.3 times longer than wide; first and second metasomal terga weakly costate to granulate, median carina complete, third tergum weakly granulate, median carina absent, metasomal terga 4–6 in male without small pits medially.

*Type material examined.*—*Rhogas insignipes* Brues, holotype male, BRAZIL, "Parahyba" [Paraiba], Independencia, Stanford University Expedition, 1911, Mann and Heath, type #29922 [MCZ].

*Distribution.*—Known only from the type-locality in north-east Brazil.

*Biology.*—Unknown.

*Comments.*—This species is quite similar to *vaughani*, with respect to most aspects of body form and color. However, *insignipes* has much larger eyes and ocelli, smaller malar space, darker middle tibia, reduced tarsal claw pectination, and longer first metasomal tergum. The female of *insignipes* is unknown. Brues (1912) noted that this species has "about 65" antennomeres. The apices of the antennae are now missing from the holotype, so we were unable to check this observation. If

correct, this is substantially more than the usual number (43–56) in *vaughani*.

## Aleiodes notozophus Marsh and Shaw, new species
(Figs. 3, 9, 29, 34, 38, 43)

*Female.*—**Body color**: head including antennae dark brown to black; apical palpomeres varying from light brown to nearly white; mesosoma except propodeum brown to dark brown, propodeum always light brown; metasoma light brown; legs light brown, occasionally fore leg and hind tibia darker; wings hyaline, veins brown, tegula brown. **Body length**, 6.5–7.0 mm; fore wing length, 7.0–7.5 mm. **Head** (Figs. 3, 34): 51–54 antennomeres, basal flagellomeres about as wide as long; malar space very short, $\frac{1}{5}$–$\frac{1}{8}$ eye height and $\frac{2}{3}$ basal width of mandible; temple very narrow, at its narrowest $\frac{1}{5}$ eye width; occipital carina meeting hypostomal carina; oral opening small, circular, width equal to basal width of mandible and about $\frac{2}{3}$ face height; clypeus swollen, striate; ocelli large, ocellocular distance at most $\frac{1}{4}$ diameter of lateral ocellus, often lateral ocellus nearly touching eye; face costate, frons smooth, vertex and temple granulate, malar space sometimes weakly costate; maxillary palpus not swollen. **Mesosoma**: propleuron weakly costate, porcate medially; mesonotum and scutellum granulate, notauli weakly scrobiculate, meeting before scutellum in shallow costate area; mesopleuron smooth, subalar area weakly costate, sternaulus absent; propodeum granulate to granulate dorsally, smooth laterally, median carina complete. **Legs**: tarsal claws strongly pectinate with 7–8 large spines on inner edge; hind coxa weakly granulate dorsally; inner spur of hind tibia equal to $\frac{1}{2}$ length of basitarsus. **Wings** (Figs. 38, 43): fore wing with vein r nearly $\frac{1}{2}$ length of 3RSa and about $\frac{3}{4}$ length of m-cu, vein 1cu-a beyond 1M by distance slightly greater than length of 1cu-a, vein 1CUa about $\frac{1}{3}$ length of 1CUb; hind wing with vein RS straight,

marginal cell gradually widening to wing apex, veins M+CU and 1M about equal in length, vein 1r-m $\frac{3}{5}$ length of 1M, vein m-cu absent. **Metasoma**: first tergum strigate, length longer than apical width, median carina complete; second tergum strigate, median carina complete; third tergum weakly strigate at base, remainder smooth, median carina absent; remainder of terga smooth; ovipositor short, about $\frac{1}{4}$ length of hind basitarsus.

*Male.*—Similar to female; fore legs light brown to yellow; median pits present on metasomal terga 4–7.

*Holotype.*—Female: CALIFORNIA, Tin Mine Canyon, Riverside County, December 14, 1963, ex. oak gall, M. E. Irwin collector. Deposited in USNM.

*Paratypes.*—COSTA RICA: 2 females, Guanacaste Prov., Derrumbe, Est. Cacao, lado oeste del V. Cacao, III curso Parataxon., May 1992, L-N 323700, 376700, INBio barcodes CR1000–423504 and CR1000–423594. UNITED STATES: ARIZONA: 1 female, Ramsey Canyon 6000', 15 mi. S. Sierra Vista, Huachuca Mts., October 23, 1967, Sternitzky; 1 female, Parker Creek, Sierra Ancha, May 2, 1947, H. and M. Townes. CALIFORNIA: 5 females, Santa Margarita, 20 mi. ESE, 2200', October 9, 1966, D. F. Hardwick; 1 male, Cypress Ridge, Marin Co., May 7, 1922, E. C. van Dyke collector; 1 male, Calaveras Co., 4.8 km S. West Point, July 26, 1980, Stanley C. Williams; 1 male, Mill Valley, Marin Co., March 16, 1959, H. B. Leech collector; 1 female, Meadow Vista, Placer Co., October 19, 1972, T. A. Sears; 1 female, S. D. Co., Potrero, April 8, 1974, H. and M. Townes; 1 male, Lake Wohlford, April 20, 1974, H. and M. Townes; 1 female, same data except April 24; 1 female, same data except April 27; 2 females, same data except April 30. FLORIDA: 1 male, Putnam Co., 2 mi. NW Orange Springs, May 22, 1975, D. Bowman, blacklight trap. Paratypes deposited in USNM, CNC, RMSEL, CAS, UCD, AEI, INBio, FSCA.

*Distribution.*—Known only from Flori-

da, the southwestern U.S., and Costa Rica, suggesting that *notozophus* may occur in the gulf states, Mexico, and other parts of Central America as well. Possibly occurring in Brazil (see comments below).

*Biology.*—Unknown. The holotype is labeled as having emerged from an oak gall, but this seems unlikely. Possibly a mummified host caterpillar was confused with a gall or a parasitized caterpillar sought shelter in the gall. It is attracted to lights.

*Comments.*—This species is similar in habitus to *arizonensis*, including the males with the medial pits on metasomal terga 4–7, but is distinguished by the darker colored head, mesosoma, and legs (Fig. 29). It is also similar to *vaughani* from Central America but is distinguished by the maxillary palpi being slender (not swollen), and by the longer first metasomal tergum. One male specimen from Paraná, Brazil [CNC] fits this description but has lighter colored orbits around the eyes, light medial bands on the antennae, and reduced pectination on the tarsal claws. Based on this specimen alone, we are not able to judge if this is normal variation at the southern part of the range of this species, or whether this lone male represents another species near *notozophus*.

*Etymology.*—The specific name is from the Greek *noto* meaning "south" and *zophos* meaning "western" in reference to the more frequent occurrence of this species in the southwestern U.S.

## Aleiodes pedalis Cresson
### (Figs. 28, 37, 45)

*Aleiodes pedalis* Cresson, 1869, Trans. Am. Ent. Soc. 2:379–380.

*Re-description of holotype female.*—**Body color**: yellowish orange, except head, antenna, fore basitarsus, apical ½ middle and hind tibiae and tarsi, stigma medially, and ovipositor sheath black; palpi and basal ½ middle and hind tibiae pale yellowish white; wings hyaline except faint infumation medially on forewing, darker infumation apically. **Body length**, 8.3 mm; forewing length 9.0 mm. **Head**: ocelli enormous, lateral ocellus 8 times wider than ocell-ocular distance; 66 antennomeres, basal flagellomeres shorter than wide, 15th flagellomere width/length ratio less than 0.84, apical flagellomere terminating in a sharp point; malar space very short, shorter than basal width of mandible; malar space/eye height ratio 0.06; temple/eye width ratio 0.10; occipital carina meeting hypostomal carina ventrally, absent at vertex; oral space/malar space ratio 3.0, oral space small, circular, and polished, oral opening width shorter than clypeo-antennal distance; clypeal height/width ratio 0.67; clypeal sculpturing finely rugulose; medial ridge extending down frons less than 0.55 distance from scape to clypeus; face granulate medially, striate laterally (Fig. 45); frons smooth; vertex striate; temple granulate; maxillary palpus not swollen. **Mesosoma**: pronotum granulate medio-anteriad, rugose laterally, declining at angle of greater than 45° from mesonotum, medial pronotal length short, about equal to length between occipital carina and lateral ocellus; mesonotum granulate, postero-dorsally with one smooth carina (otherwise mesonotum damaged by pinning); notauli smooth, not coarsely foveate; scutellum granulate, without pronounced setal pits; mesopleuron smooth, sternaulus absent; mesopleural pit posteriad to central disk absent; propodeum granulate, antero-laterally with faint rugation; propodeal median carina present, complete to apex. **Legs**: inner apex of hind tibia with setae normal and unmodified; tarsal claw with basal lobe strongly pectinate, gap between apical pectin tooth and claw greater than apical tooth length, 7–8 teeth in pectin; hind tibial spur/hind basitarsus length ratio 0.30; hind coxa dorsally granulate. **Wings**: yellowish hyaline, except apex and median band infumate; forewing width/length at widest point 0.29–0.35, forewing with vein 2RS not parallel with r-m;

3RSa/r ratio 2.0; 1cu-a beyond basal vein by 3 times 1cu-a length; vein 1cu-a about $\frac{1}{3}$ of way between veins 1M and m-cu (closer to 1M); hind wing with marginal cell gradually widening, RS gradually curved to wing margin; M+CU/1M ratio 0.53; vein r-m 0.6 times length of 1M; m-cu absent. **Metasoma:** carapace absent, terga 1–8 visible; first and second terga with distinct median carina; first tergum elongate, faintly rugulose to granulate, length/width ratio 1.13; second tergum rugulose to granulate, length/width ratio 0.71, median triangle of second tergum large, with anterior carinae running laterally to margins; third tergum length/width ratio 0.44; third and forth terga granulate; ovipositor length/hind basitarsus length ratio 0.60.

*Type material examined.*—Holotype female, minuten-mounted into cork, 3 labels (excluding ANSP tag), Mexico, Prof. Sumichrast, (Philadelphia). Condition fair; left flagellum broken near middle, about $\frac{1}{2}$ as long as right flagellum.

*Distribution.*—Mexico, Costa Rica, Panama, Venezuela, and Bolivia.

*Biology.*—Unknown.

*Comments.*—A very distinctive species that can easily be recognized by its exceptionally large body size, very large eyes and ocelli, black head, extensive granulate sculpture, and face laterally with well-developed parallel striations (Fig. 45). It is, however, quite rare in North American collections (we have only seen the holotype, three specimens from Costa Rica, and single specimens from Panama, Venezuela, and Bolivia). The female from Costa Rica is somewhat larger than the holotype from Mexico, and differs by having darker black wing bands, and the hind femur mostly black. Two males from Costa Rica, and one from Panama, lack the medial wing band, have the hind femur orange, and do not have setose pits on the apical terga. The specimens from Venezuela and Bolivia are unusual in lacking dark wing patches, but otherwise are within the observed range of variation for Central American specimens. Its nearest relative is *flavidus* (Cresson) from Cuba, which differs by having a yellowish orange head and middle tibia The face is faintly striate in *flavidus*, but not so strongly as in *pedalis*. Although originally described as an *Aleiodes* species, *pedalis* has been classified as *Rogas* by recent authors (e.g. Shenefelt, 1975), and it is here reassigned to its original generic combination.

## Aleiodes quebecensis (Provancher), new combination
### (Figs. 5, 8, 14, 23–24, 32)

*Rogas quebecensis* Provancher, 1880, Nat. Can. 12:145.

*Diagnosis.*—Body unicolored honey yellow or light brown, antenna usually black on basal $\frac{1}{2}$, yellowish-white to orange on apical $\frac{1}{2}$, occasionally entirely black, or with apical 10–18 flagellomeres black, fore leg yellow, apical tarsomere brown, middle leg with coxa brown, trochanters and basal $\frac{1}{4}$ of femur yellow, apical $\frac{3}{4}$ of femur brown, basal $\frac{1}{2}$ of tibia yellow, apical $\frac{1}{2}$ brown, tarsomeres 1–4 yellowish white or white, apical tarsomere brown, hind leg with coxa brown, trochanters yellow, femur brown, basal $\frac{1}{3}$ of tibia yellow or white, apical $\frac{2}{3}$ brown, tarsomeres 1–4 white or light yellow, apical tarsomere brown, wings hyaline, veins including stigma brown, tegula yellow; body length, 6.0–8.0 mm; 45–55 antennomeres; malar space short, less than basal width of mandible and about $\frac{1}{6}$ eye height; face rugulose, frons smooth, vertex and temple granulate; oral opening small and circular, diameter greater than malar space; ocelli large, lateral ocellus 3 times wider than ocell-ocular distance (Fig. 5); pronotum rugose; mesonotum and scutellum granulate; mesopleuron smooth or weakly granulate, subalar sulcus rugose, sternaulus absent; propodeum rugose granulate, median carina complete; first and second metasomal terga rugulose to granulate,

median carinae complete, third tergum smooth or weakly granulate, median carina absent, terga 4–6 of males with dense patches of long hair on each side of mid line; tarsal claws strongly pectinate (Fig. 14); fore wing with vein 1cu-a beyond 1M by distance greater than length of 1cu-a; hind wing with vein RS slightly arched at apical $\frac{2}{3}$, marginal cell narrowest at apical $\frac{2}{3}$ and suddenly widened to apex, vein m-cu very short and indistinct.

*Type material examined.*—*Rogas quebecensis* Provancher, holotype female, Quebec [ULQ].

*Distribution.*—Quebec south to Florida, west to Wisconsin, South Dakota, British Columbia, and Oregon. The period of flight activity for adults ranges from early June through mid-August.

*Biology.*—Reared from *Acronicta furcifera* Guen. and *Acronicta grisea* Wlk. One reared specimen from Indiana has been associated with *Prunus sordinia* and another from New Brunswick has been associated with choke cherry, indicating the possibility that several other *Acronicta* are potential hosts. Another from Wisconsin has been associated with *Tilia americana*. It has been collected at blacklights.

*Comments.*—This species is very distinctive and can be distinguished from all other members of the *pulchripes* group by the arched vein RS in the hind wing, and the hind legs with their pale white or yellowish tarsomeres (Fig. 24). A single specimen examined from Oregon is much darker than eastern specimens in the color of the head, mesosoma, and apical $\frac{1}{2}$ of the hind tibia.

## Aleiodes rossi Marsh and Shaw, new species
### (Figs. 15, 20)

*Female.*—**Body color**: entire body light yellow, antennal flagellum brown, scape and pedicel honey yellow, ocellar triangle black, all apical tarsal segments brown, apex of hind tibia black, wing veins yellow except costa, stigma and metacarpus which are brown. **Body length**, 6.5 mm; fore wing length, 5.5 mm. **Head**: 44 antennomeres, first flagellomere longer than second, remainder as wide as long; malar space short, slightly less than basal width of mandible and about $\frac{1}{4}$ eye height; occipital carina not reaching hypostomal carina; oral space small and circular, width equal to basal width of mandible and $\frac{1}{2}$ length of face; clypeus not swollen; ocelli large, ocellocular distance less the $\frac{1}{2}$ diameter of lateral ocellus; face granulate, costulate below antennae; frons, temples and vertex granulate; maxillary palpus not swollen; mandibles small, tips not crossing when closed. **Mesosoma**: propleuron porcate; mesonotum and scutellum granulate, notauli weakly scrobiculate, meeting in rugose triangular area before scutellum; mesopleuron smooth, subalar sulcus rugose, sternaulus absent; propodeum granulate laterally, rugose granulate dorsally, median carina complete. **Legs**: tarsal claws pectinate but with only 8–9 stout spines, with the basal 5 being much larger than the rest (Fig. 20); inner spur of hind tibia less than $\frac{1}{2}$ length of hind basitarsus; hind coxa granulate dorsally. **Wings**: fore wing with vein r $\frac{1}{2}$ length of 3RSa and $\frac{2}{3}$ length of m-cu, vein 1cu-a beyond 1M by distance greater than length of 1cu-a, vein 1CUa $\frac{2}{3}$ length of 1CUb; hind wing with vein RS nearly parallel for short distance at base and then widening to apex, marginal cell wide at apex, vein 1r-m slightly longer than 1M, vein M+CU longer than 1M, vein m-cu absent. **Metasoma**: first tergum costate, apical width longer than length, median carina complete; second tergum costate, median carina complete; third tergum costate on basal $\frac{1}{2}$, granulate on apical $\frac{1}{2}$, median carina distinct on basal $\frac{1}{2}$; remainder of terga smooth; ovipositor short, less than $\frac{1}{2}$ length of hind basitarsus.

*Male.*—As in female; metasomal terga 4–7 with dorsal median pits (Fig. 15).

*Holotype.*—Female: TEXAS, Brownsville,

October, 1942, E. S. Ross, at light. Deposited in CAS.

*Paratypes.*—MEXICO: 2 males, San Luiz, Potosi, El Salto, 1800', June 8, 1961, U. Kans. Mex. Exped. UNITED STATES: TEXAS: 1 male, Brownsville, September 16, 1942, T. M. Burns collector; 1 male, Brownsville, June 29, 1938, L. W. Hepner; 1 female, S. Patricio Co., Welder Wildlife Ref., 8 mi. NE Sinton, May 13–15, 1985, R. Brown, black light trap, William H. Cross Expedition. Paratypes deposited in USNM, MSSU, UKL.

*Distribution.*—Known only from southern Texas and Mexico.

*Biology.*—Hosts unknown. Adults are attracted to lights.

*Comments.*—This species belongs to the group in which the males have the medial pits on the apical metasomal terga; it can be distinguished from *cameronii* by the position of vein 1cu-a in the fore wing and from *cazieri* by its brown antenna and stigma. It can be distinguished from *geometrae* by the presence of dark black markings on the apices of the tibiae, especially the hind tibia.

*Etymology.*—This species is named for the collector of the holotype, E. S. Ross.

### Aleiodes vaughani (Muesebeck),
### new combination
### (Figs. 4, 7, 22, 31)

*Rhogas nigriceps* Enderlein, (1918) 1920, Arch. Naturgesch. 84A(11):155. New junior homonym, preoccupied by *nigriceps* Wesmael 1838 and *nigriceps* Brethes 1909. All three nominal taxa are different species.

*Rogas vaughani* Muesebeck, 1960, Ent. News 71: 257.

*Rogas enderleini* Shenefelt, 1975, Hym. Cat. 12(8):1227–1228. New synonymy. Unnecessary replacement name for *nigriceps* Enderlein.

*Description of female.*—**Body color**: reddish yellow to yellow; head and antennae black; palpi piceous; wings hyaline, the stigma and veins very dark; middle tarsus dusky; apex of hind tibia and the hind tar-

sus blackish; ovipositor sheath black. **Body length** about 6 mm. **Head**: ocelli large, lateral ocellus 3 times wider than ocell-ocular distance; 43–48 antennomeres, basal flagellomeres longer than wide, 15th flagellomere from base width/length less than .84; malar space slightly shorter than basal width of mandible; oral opening circular, width shorter than the clypeo-antennal distance; clypeus without a carina, clypeal height/width between .65 and .42, clypeal sculpturing finely rugulose, clypeal shape rounded, not abruptly edged, not flat ventrad; vertex granulate; occipital carina strong and complete medially, but effaced well before juncture with hypostomal carina; medial ridge extending down frons less than .55 of distance from line between bases of scapes to clypeus. **Mesosoma**: pronotum granulate medioanteriad, laterally costate, pronotum declining at an angle of greater than 45 degrees from mesonotum, pronotal anterior flange less than .28 of pronotal length, pronotal medial length longer than length between occipital carina and lateral ocellus; mesopleuron sculpturing on and posteriad to central disk smooth, punctate; sternaulus smooth, sometimes slightly indented; mesopleural pit posteriad to central disk absent; posterio-dorsal surface of mesonotum with some strong, smooth carinae; notauli at mid-dorsal surface of mesonotum not coarsely foveate, but with a long longitudinal carina; mesonotal sculpturing excluding postero-dorsal surface granulate; scutellum granulate, without pronounced hair pits; median carina of propodeum frequently interrupted before reaching propodeal apex; sculpturing of propodeum antero-laterally finely rugulose. **Legs**: inner apex of hind tibia with setae normal and unmodified; metatarsal segment IV length less than 1.5 times width; tarsal claw strongly pectinate with 10–12 tarsal teeth in pectin; gap between apical and subapical tarsal teeth; apical tarsal tooth with a small seta-like tip. **Wings**: forewing with second submargin-

al cell irregular in shape, 2RS not parallel with r-m; forewing width/length greater than or equal to .35; length ratio of vein 3-RS/r about 2.5; vein 1cu-a about halfway between veins 1M and m-cu; hindwing marginal cell narrowest at base, RS straight; veins M+CU and 1M about equal in length; vein 1r-m about $\frac{3}{5}$ length of 1M. **Metasoma**: first tergum not elongate, sculpturing weakly rugulose to faintly rugulocostate, median carina pronounced; median carina of second tergum pronounced, basal median triangle large and associated with carinae which run laterally to margins of tergum; third metasomal tergum sculpturing shallowly rugulose or rugulocostate anteriad, finely punctate posteriad, or completely finely punctate; medial pits on terga 4–7 of males absent; ovipositor short, less than $\frac{1}{2}$ length of metafemur.

*Males.*—Essentially as in female; greater tendency in males for third metasomal tergum to have more rugation and to be less nitid.

*Type material examined.*—*Rogas vaughani* Muesebeck, holotype female, type #65047, Managua, Nicaragua, ex. *Laphygma* (= *Spodoptera*) *frugiperda*, deposited in USNM. The holotype female of *Rhogas nigriceps* Enderlein was also examined.

*Distribution.*—Found in the Neotropical region from Mexico southwards to Honduras, Nicaragua, Costa Rica, and Ecuador. A series of specimens from Costa Rica (INBio) indicates that *vaughani* occurs from sea level to 1050m elevation, but seems to be most common at lower elevations (0–200m).

*Biology.*—The type-series from Nicaragua was associated with host material identified as *Laphygma* (= *Spodoptera*) *frugiperda* (Noctuidae). One specimen of *vaughani* from Honduras was associated with host material identified as *Spodoptera sunia* (Noctuidae). Several specimens from Ecuador were reared from *Spodoptera latifascia*. This species is attracted to lights.

*Comments.*—*Aleiodes vaughani* is one of only four species in the group that have a dark-colored head (the other three being *pedalis*, *insignipes* and *notozophus*). It differs from *pedalis* in that the wings are not banded; it differs from *notozophus* by having the maxillary palpus somewhat swollen and by having a gap between the apical tarsal claw and its basal pectination; it differs from *insignipes* by having smaller ocelli, larger malar space and more distinct tarsal claw pectination. Of the four species, *vaughani* is by far the most common and appears to readily attack several species of noctuids that infest agroecosystems. We have also examined a dark-colored form from Ecuador which has the anterior half of the mesosoma black in addition to the head. However, these do not differ morphologically from typical *vaughani*.

## ACKNOWLEDGMENTS

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# Contributions to the knowledge of *Ceramius* Latreille, *Celonites* Latreille, *Jugurtia* Saussure and *Masarina* Richards (Hymenoptera: Vespidae: Masarinae) in South Africa

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*Abstract.*—Descriptions are given of the following new species of Masarinae from South Africa: *Ceramius brevitarsis* (female and male), *Celonites gariepensis* (female and male); *Celonites tumidiscutellatus* (female and male); *Celonites lobeliae* (female and male); *Jugurtia tigrina* (female and male); *Jugurtia codoni* (female and male); *Jugurtia koeroegabensis* (female and male); *Masarina ceres* (male); *Masarina mixtoides* (female and male); *Masarina namaqua* (female and male); *Masarina parvula* (female and male); *Masarina peliostomi* (female and male); and *Masarina tylecodoni* (female and male). Also described are the previously unknown male of *Ceramius peringueyi* Brauns, female of *Jugurtia duplicata* Richards and male of *Masarina strucki* Gess. *Jugurtia polita* Richards, 1962 is synonymized with *Jugurtia eburnea* (Turner, 1935) new status.

## INTRODUCTION

The present contribution names and describes species of *Ceramius* Latreille, *Celonites* Latreille, *Jugurtia* Saussure and *Masarina* Richards, in order that observations on flower visiting and, for two of the species, nesting may be presented in a companion paper (Gess, S. K. et al. 1997). Names and descriptions are furthermore given for three species previously (Gess, S. K. 1996) identified only by letters of the alphabet.

Comparison of the newly described *Jugurtia tigrina* with two similarly coloured species has revealed that these two have been persistently confused with each other. This confusion is discussed in full and resolved. A key to separate the three species is given, as are available collecting data to elucidate their distributions.

The six new species of *Masarina, M. ceres, M. mixtoides, M. namaqua, M. parvula, M. peliostomi,* and *M. tylecodoni,* raise the number of species assignable to the genus from four to ten. The listing by van der Vecht and Carpenter (1990) of *Masarina* as a junior subjective synonym of *Jugurtia* is reassessed and it is concluded that *Masarina* should retain generic status. A key to the presently known species of *Masarina* is given.

The opportunity is taken to complete the descriptions of *Jugurtia duplicata* Richards, hitherto known from the male, of *Masarina strucki* Gess, hitherto known from the female, and of *Ceramius peringueyi* Brauns, hitherto known from the female. Collecting data for the above three poorly known species are given.

A supplement to the previously published key to the southern African (in effect Afrotropical) species of *Ceramius* (Gess 1973) is provided to include the presently described species, *C. brevitarsis,* the only additional species discovered to date, and male of *C. peringueyi.*

Acronyms for institutions in which material is housed are: AMG = Albany Museum, Grahamstown, South Africa; NCP = National Collection of Insects, Pretoria, South Africa; NHML = National History Museum, London, United Kingdom; SAM = South African Museum, Cape Town, South Africa; TMP = Transvaal Museum, Pretoria, South Africa.

## SPECIES DESCRIPTIONS

**Ceramius** Latreille, 1810
**Ceramius brevitarsis** Gess, sp. nov.

*Female.*—Black. The following are lem-on-yellow: spot on proximal two-fifths of mandible; hexagonal marking covering almost entire clypeal disc; large transverse rectangular supraclypeal marking on lower half of frons between antennal sockets; narrow band margining inner orbits from clypeo-frontal suture to level of bottom of anterior ocellus; elongate spot on top of tempora; diffuse streak on scape; almost entire pronotum (excepting black band margining ventral margin and black pronotal lobe); longitudinal streaks laterally and medially on posterior third of mesoscutum; upper part of axilla; large spot on prepectus; posterior two thirds of scutellar disc (extending onto sides and posterior declivous face of scutellum); transverse marking on middle of metanotum; irregularly shaped marking on propodeal angle; tergum I (except for black anterior declivous face); wide, laterally expanded, transverse posterior bands on terga II–IV; entire tergum V; tergum VI (except for narrow black margin); markings laterally on sternum II; most of sterna III–V; variously developed spot on underside of coxa of all legs; distal two thirds of outer aspect of front femur, entire outer aspect of middle femur and isolated spot on outer aspect of hind femur; most of outer aspect of tibia of all legs and most of front basitarsus. The following are reddish: mandible (other than yellow part indicated above and black apical teeth); narrow ventral margin of clypeus; apex of labrum; entire antenna (excluding yellow streak on scape); most of tegula; extreme sides of terga II and III; a basi-medial spot on sternum II; diffuse posterior bands on sterna II–IV; legs other than yellow parts listed above. Wings fuscous; costa and stigma of front wing and all veins of hind wing reddish brown, other veins of front wing dark

brown; thickening at junction of Rs and M black.

Melanistic specimens differ most strongly in the following respects: markings on mandible and scape absent (or, if present, reddish); marking on clypeal disc somewhat narrower and barrel-shaped; supraclypeal marking absent; band margining inner orbits reduced in width and height; spot on tempora reduced; yellow on pronotum reduced postero-laterally to a narrow dorsal band and a wider but shorter lower one; markings on mesonotum and metanotum absent and those on axilla, scutellum, prepectus and propodeum reduced; yellow bands on terga I–IV reduced in width and that of tergum I not attaining hind margin.

Length 12.5–13.3 mm (average of 7: 12.7 mm); length of front wing 8.3–9.0 mm (average of 7: 8.6 mm); hamuli 17–19.

Head, thorax, propodeum and tergum I with long erect pilosity; hairs on clypeus in region below antennal sockets, on frons (in particular), vertex, pronotum and anterior portion of mesoscutum coarse and golden, those on other parts much finer and silvery-white.

Head noticeably wider (1.15×) than long. Eyes seen in frontal view strongly convex; lateral margin of eye and lateral margin of closed mandible (apex touching that of opposing mandible) forming two distinct convex curves. Clypeus 1.5 × longer than wide at ventral margin, truncate with definite but narrowly rounded angles separating ventral and lateral margins; disc finely longitudinally striate and shallowly depressed medially. Frons and vertex closely and coarsely punctured, POL (distance between posterior ocelli):OOL (distance between eye and a posterior ocellus) = 1:1.5 (average value for 7 specimens).

Thorax with pronotum and mesoscutum similarly punctured to frons and vertex but with mesopleura and scutellum more finely punctured. Mesoscutum with prescutal furrows well marked posteriorly

and parapsidal furrows distinct. Scutellum anteriorly steeply raised above level of mesoscutum; disc weakly carinate medially and laterally and with its surface between these carinae slightly depressed.

Propodeum with sparse shallow punctures and microsculptured interspaces, laterally with pronounced sharply pointed processes.

Gaster shiny, uniformly microsculptured; tergum I transverse, subapically 3 × wider than long, barely noticeably constricted just anterior to posterior margin; tergum II anteriorly narrowing and posteriorly 1.3 × wider than I; terga II–VI together progressively and smoothly narrowing posteriorly and with tergum VI pointed but narrowly rounded.

Front tarsus noticeably short and wide; middle tibia with 2 apical spurs.

*Male.*—The following are lemon-yellow: mandible (other than extreme base and apical teeth); hexagonal marking covering almost entire clypeal disc; lateral angles of clypeal wings adjacent to mandibular articulation; irregularly shaped and variously developed supraclypeal markings on lower half of frons; narrow band margining inner orbits from clypeo-frontal suture to level of about one ocellar diameter below anterior ocellus; elongate spot on top of tempora; scape (except for black, dorsal longitudinal streak); sometimes upper surface of last flagellomere; pronotum (except black band margining ventral and postero-lateral margins); upper part of axilla; spot on prepectus; posterior half or less of scutellar disc; propodeal angles (sometimes only spine-like processes); subapical transverse band widened laterally and frequently interrupted medially on tergum I; wide, laterally expanded, transverse posterior bands on terga II–VI; basi-lateral spots on tergum VII; irregularly shaped and variously developed markings on discs of sterna II–VII; most of underside of front coxa and the entire underside of middle and hind coxae; mesosternal projections adjacent to coxae; process of front

trochanter; small spot on middle and hind trochanters; entire outer aspect and underside of front and middle femora; basal and apical spots on outer aspect of hind femur; longitudinal streak on basal tarsomere of all legs. The following are reddish: flagellomeres (other than occasionally last flagellomere as noted above and dorsal infuscation of other flagellomeres); most of tegula; extreme sides of terga and parts of sterna; legs other than yellow parts listed above and strongly contrasting black last tarsomeres, claws and pulvilli of middle and hind legs. Wings similar to those of female but less heavily infuscated.

Length 12.0–12.7 mm (average of 7: 12.4 mm); length of front wing 8.2–8.5 mm (average of 7: 8.3 mm); hamuli 14–18.

In general facies similar to female, the chief differences being as follow. Head width relative to head length even greater (1.3×); disc of clypeus 1.8 × longer than wide at ventral margin; POL : OOL = 1:1.4 (average value for 7 specimens). All flagellomeres longer; VI–IX each with a low, shiny, longitudinal swelling beneath; ultimate flagellomere a little longer than penultimate, a little flattened and weakly concave beneath. Tergum I noticeably constricted dorsally and dorso-laterally just anterior to posterior margin. Tergum VII subtruncate with hind margin widely rounded laterally. Sterna III, VII and VIII with processes; process of III small, steeply raised above middle of disc, with its transverse distal edge about one sixth of the width of the sternum at its midlength; process of VII postero-ventrally directed and spatulate in ventral view; basal process of VIII poorly developed. Sternum VIII with disc posterior to basal process medially deeply depressed, shiny, and on each side produced into a prominent postero-ventrally directed, bluntly pointed, pilose projection. Trochanter of front leg produced into an anteriorly directed, apically rounded process. Front femur with surface depressed in proximal half.

*Material examined.*—Holotype: female,

Cape Province: Namaqualand, Richtersveld N[ational] Park, bet[ween] hills (28.10S, 17.02E), NW Koeroegabvlakte, 14.ix.1996 (F.W., S.K. and R.W. Gess) (at water) [AMG]. Paratypes (51 females, 7 males): same locality, date and collectors (50 females, 6 males at water; 1 female, 1 male on cream fl[ower]s [of] *Zygophyllum prismatocarpum* E. Mey. ex Sond., Zygophyllaceae) [AMG].

All specimens are free of mites.

*Discussion.*—*Ceramius brevitarsis* is most closely allied to *cerceriformis* Saussure and *peringueyi* Brauns. In both sexes it differs from these species in its smaller body size (marked with respect to *cerceriformis*), in the greater width relative to length of the head resulting from its more strongly convex eyes, and in the form of the clypeus—truncate with definite angles separating the ventral and lateral margins rather than (particularly in the female) rounded and without definite angles. It differs markedly from *peringueyi* in coloration. The female is further distinguished by the shortness of the tarsus of the front legs. The male is in addition distinguishable in having the last flagellomere only minimally modified, in the different form of the sternal prominences and of the disc of sternum VIII.

*Etymology.*—The name *brevitarsis* serves to draw attention to the short tarsus of the front leg of the female.

## Ceramius peringueyi Brauns

*Ceramius peringueyi* Brauns, 1913: 194, female. Holotype: female, South Africa: Stellenbosch (TMP).—Richards, 1962: 100 (female only, male = *richardsi* Gess, 1965); Gess, 1965: 220.

*Male.*—Black. The following are creamy-white: broad streak on mandible, clypeus except lateral wings, inner orbit from near mandibular articulation to bottom of ocular sinus, small spot on top of tempora, streak on underside of scape, pronotal band wide anteriorly where extended onto sides but narrow laterally as far as posterior angles of pronotum whence a well marked streak extends ventrally onto spiracular lobes, small postero-lateral streak on each side of mesonotum, large spot on dorsal part of axilla, transverse streaks on posterior declivous portion of scutellum and median portion of metanotum, anterior margin of tegula, minute to small spots at top of mesopleura, propodeal spines dorsally, sometimes small diffuse median and lateral spots posteriorly on tergum I, transverse median streaks and variously sized lateral spots posteriorly on terga II–V (markings sometimes reduced or conversely narrowly connected along hind margin of terga IV and V), sometimes single median spot posteriorly on tergum VI, projection on sternum III, streak on front tibia dorsally, spots on underside of middle and hind coxae, small spots on underside of trochanters and sometimes base and apex of femora of front and middle legs and spots on knees of all legs. The following are reddish: underside of flagellomeres I–IX and whole of X, transverse band on declivous anterior face of pronotum and large area on sides of same, terga I and III predominently (tergum III sometimes with black area), sterna II and III and isolated diffuse spots on sternum IV, legs (excluding yellow markings and black fifth tarsomeres of middle and hind legs). Wings fuscous, venation dark brown.

Length 13.0–15.2 mm (average of 5: 14.2 mm); length of front wing 8.8–9.7 mm (average of 5: 9.2 mm); hamuli 15–19.

In general facies and coloration very similar to the female, the chief differences being as follow. Disc of clypeus narrower at base and proportionately longer. Ultimate flagellomere enlarged, hook-like, folding back against flattened ventral surfaces of flagellomeres VII–IX, similar in general plan to that of *C. cerceriformis*. Sterna III, VII and VIII with pronounced processes and IV with basal quarter markedly transversely raised and posteriorly falling abruptly to disc. Processes similar

to those of *C. cerceriformis* but that on sternum III more gracile, its anterior edge transversely much narrower, sublamellate and sharply bipointed, seen in side view raised higher above the convex posterior part and with anterior face almost straight, subvertical, and with apical tubercles ventrally directed. Trochanter of front leg produced into a process similar to that of *C. cerceriformis* but not as wide and thick.

The front femur, as in the female, is unmodified and is therefore different from that of the male of *C. cerceriformis* which, to a variable degree, has its outwardly facing surface depressed in the proximal half.

*Material examined.*—Cape Province: 10–20 km E Lambert's Bay (32.08S, 18.28E), 3.x.1990 (C. Eardley), 1 male [NCP]; 5 km E of Vredendal on road to Vanrhynsdorp, 30.ix.1985, 14 females (all on flowers of *Psilocaulon acutisepalum* (Berger) N.E.Br., Aizoaceae: Mesembryanthema); Graafwater (32.09S, 18.33E), 14.x.1994, 4 females (all on flowers of *P. acutisepalum*); Klipfontein (32.00S, 18.31E), 14.x.1994, 4 females, 1 male (all on pink flowers of *Psilocaulon* sp.) (all F. W. and S. K. Gess) [all AMG]; Graafwater dist., Heerenlogement (31.58S, 18.33E), 6.x.1995, 5 males (all on pink flowers of *P.* cf. *subnodosum* (Berger)

N.E.Br.); same locality, 8.x.1995, 5 females, 10 males (all on pink flowers of *Psilocaulon* spp.); Graafwater/Ratelfontein (32.09/02S, 18.36/35E), 7.x.1995, 1 male (on pink flowers of *P. acutisepalum*); Ratelfontein/Oloff Berghfontein (32.02S, 18.35/31E), 7.x.1995, 1 female (ex nest); same locality, 8.x.1995, 2 males (both on pink flowers of *P. acutisepalum*) (all F. W., S. K. and R. W. Gess) [all AMG].

*Discussion.*—*Ceramius peringueyi* was described from a single female, collected by L. Péringuey, of which the provenance was given as the vicinity of Cape Town, with the suggestion that it was probably from the Peninsula (Brauns 1913). The label on the specimen, however, gives the collection locality as Stellenbosch (Richards 1962 and Gess 1965). The species was subsequently recorded from Het Kruis and Paleisheuwel (Gess 1965). Apart from the cited type locality, attended by uncertainty, all collecting localities suggest a limited distribution centred upon the sandveld west of the Olifants River.

The male collected in 1990 carries 14 mites, situated mostly on the metapleura, and two of the females collected in 1995 bear a single mite each. The remainder of the total of 19 males and 33 females examined at different times by the author are without mites.

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SUPPLEMENT TO THE PREVIOUSLY PUBLISHED KEY TO SOUTHERN AFRICAN SPECIES OF *CERAMIUS* LATREILLE (GESS 1973)

16  Males . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16a
–   Females . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17
16a Head noticeably wider (1.3×) than long. Last flagellomere minimally modified, hardly longer than that immediately preceding it, not hook-like, gradually narrowed towards rounded apex. Body black and yellow, length less than 13 mm . . . *brevitarsis* Gess sp. nov.
–   Head at most only minimally wider (less than 1.1×) than long. Last flagellomere much modified, as long or longer than preceding two together, broadened on inner side beyond base and then narrowed again . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16b
16b Body predominantly black and reddish with pale yellow markings, length 13.0–15.2 mm. Prominence on sternum III when seen in profile with anterior face almost straight, subvertical, and with apical tubercles ventrally directed. Front femur unmodified . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *peringueyi* Richards
–   Body predominantly black and yellow, length 14.5–17.2 mm. Prominence on sternum III when seen in profile with anterior face posteriorly curved and with apical tubercles

postero-ventrally directed. Front femur to variable degree with outwardly facing surface depressed proximally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *cerceriformis* Saussure

17  Head noticeably wider (1.15×) than long. Eyes seen in frontal view strongly convex; lateral margin of eye and lateral margin of closed mandible [apex touching that of opposing mandible] forming two distinct convex curves. Clypeus truncate with definite angles separating ventral and lateral margins. Body black and yellow, length 12.5–13.3 mm. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *brevitarsis* Gess sp. nov.

–   Head as wide as long or at most only minimally wider than long. Eyes seen in frontal view only moderately convex; lateral margin of eye and lateral margin of closed mandible [apex touching that of opposing mandible] forming a smooth or almost smooth line. Clypeus rounded and without definite angles separating ventral and lateral margins . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .  17a

17a  Body predominantly black and reddish with pale yellow markings, length 13.6–14.5 mm. Pronotum predominantly reddish. Prepectus always immaculate. Metasoma with terga I, II and frequently III reddish; tergum I either immaculate or with pale yellow medial and lateral spots posteriorly, terga II–V (or fewer) with narrow pale yellow transverse posterior bands not anteriorly expanded laterally. . . . . . . . . . . . . . . . . *peringueyi* Richards

–   Body predominantly black and yellow, length 16.7–17.8 mm. Pronotum predominantly yellow. Prepectus always with a large yellow spot. If melanistic and with pronotum and tergum I (and sometimes II) reddish then terga II–V with yellow transverse posterior bands much anteriorly expanded laterally. . . . . . . . . . . . . . . . . . . . . . . *cerceriformis* Saussure

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## Celonites Latreille, 1802
## Celonites gariepensis Gess, sp. nov.

*Female.*—(Figs. 1–3). Black. The following are yellowish-white: occasionally a small irregularly-shaped spot medially in top third of clypeus, small (occasionally minute) spot on either side of frons close to margin of upper eye (that is, above ocular sinus), continuous medially widened band on posterior margin of pronotum (sometimes interrupted laterally, or interrupted and reddish brown rather than yellowish-white, or occasionally almost totally extinguished), spot of variable size (occasionally totally extinguished) on humeral angle, a spot of variable size (sometimes totally extinguished) on mesopleuron immediately below tegula, outer two-thirds or less of propodeal lamellae (if coloured area much reduced then reddish-brown rather than yellowish-white), postero-lateral markings on terga I–IV and posteromedial markings on terga V and VI (all may be reduced or totally extinguished). The following are reddish-brown: apical half of mandible, posterior margin of pronotum (if coloured band reduced, interrupted and not yellowish-white), tegula, costal margin of front wing at its base, outer margin of propodeal lamellae (if coloured area much reduced and not yellowish-white), occasionally the visible median part of the metanotum, transverse bands (incorporating within them the yellowish-white markings) on posterior half of terga I–V (colour progressively darker towards end of metasoma, tergum VI dark brown; all transverse bands but that on tergum I extinguished in some specimens), distal ends of femora and to a variable extent tibiae and tarsi of all legs. Wings infuscated.

Length 6.9–7.3 mm (average of 4: 7.0 mm); length of front wing 4.9–5.3 mm (average of 4: 5.1 mm); hamuli 8. Length of extended tongue 5.6–5.8 mm (average of 2: 5.7 mm); tongue length: body length = 0.81.

Head (Fig. 1). Clypeus and frons shiny, coarsely rugoso-punctate; vertex dull, less coarsely sculptured. Clypeus with wide, shallow M-shaped carina, on each side (where strong) originating from near mandibular articulation and rising in outwardly directed arc to angle a little below and
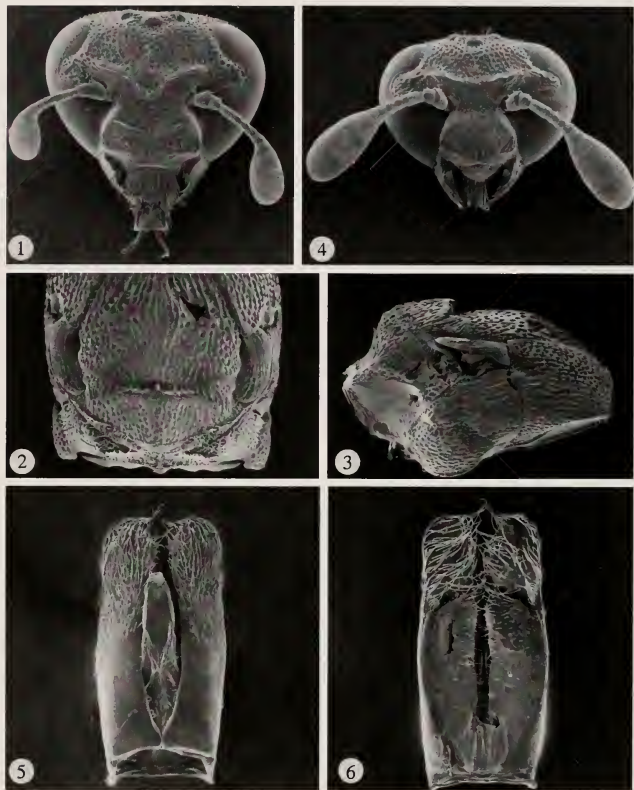
Figs. 1–6. *Celonites gariepensis*. 1, Frontal view of head of female (× 20). 2, Dorsal view of posterior two-thirds of mesosoma of female (× 20). 3, Lateral view of right side of mesosoma of female (× 20). 4, Frontal view of head of male (× 20). 5, Dorsal view of genitalia of male (× 50). 6, Ventral view of genitalia of male (× 50).

medial to antennal socket (where most pronounced), thence on each side directed medially and ventrally (where almost extinguished) to meet in obtuse angle or gentle curve. Frons above antennae with shallow, V-shaped carina, pronounced other than at ends and at medial angle, arising laterally opposite but outside middle of ocular sinuses and meeting at widely obtuse angle at level of upper margin of antennals sockets.

Thorax (Figs. 2 and 3). Upper surface of pronotum, mesoscutum, scutellum, tegula and mesopleuron more or less longitudinally rugoso-punctate; mesoscutum in posterior half markedly depressed on either side of midline; scutellum anteriorly very steeply raised above level of adjacent depressed mesoscutum and triangularly forwardly produced to almost overhang the latter. Propodeal lamella of each side wide, obliquely truncate distally, with outer edge gently convex, separated from median part of propodeum by narrow parallel-sided subtransverse slit the inner end of which is not enlarged; lateral projection of ventral margin of each side of the median part of the propodeum with its hind edge directed anteriorly and its apex acute.

Gastral tergum I shiny, with dense punctures of moderate size; remaining terga with sides and extreme base similarly punctured but less shiny and rest of each tergum matt with much finer punctures separated by microsculptured interspaces.

*Male.*—(Figs. 4–6). Black. Coloration similar to that of female. On the head the following are yellowish-white: usually a diffuse spot on disc of labrum, variably sized (but larger than in female) irregularly-shaped spot on clypeus, usually a transverse streak in each ocular sinus, sometimes small spot on frontal carina above each antennal socket. Flagellomeres II–V sometimes reddish-brown and contrasting with black of rest of antenna.

Length 6.5–7.0 mm (average of 3: 6.7 mm); length of front wing 4.4–5.1 mm (av-

erage of 4: 4.6 mm); hamuli 7–8. Length of extended tongue 5.0 mm (only one measured); tongue length: body length = 0.77.

Structure much like that of female differing most noticeably with respect to the following: antennal club both longer and wider and with three sensory depressions beneath; clypeal carina almost obliterated medially; frontal carina entire but less developed, especially medially; scutellum though steeply raised not antero-medially forwardly produced; gastral terga more uniformly punctured, with postero-lateral angles more strongly projecting; tergum VII compared to tergum VI of female with posterior margin of median part a much flatter curve.

Genitalia (Figs. 5 and 6).

*Material examined.*—Holotype: female, Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess) (in deep violet flowers of *Peliostomum* sp., Scrophulariaceae) [AMG]. Paratypes (38 females, 12 males): Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess), 32 females, 3 males (all in deep violet flowers of *Peliostomum* sp.), 1 female, 5 females, 1 male (both in purple-violet flowers of *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae); same locality, 6.ix.1996 (F. W., S. K. and R. W. Gess), 1 female, 7 males (female and all but 1 male on ground near flowering *Peliostomum* sp.); Namaqualand, Richtersveld National Park, Paradise Kloof (28.19S, 17.01E), 22.ix.1995 (F. W., S. K. and R. W. Gess), 1 female (associated with nest); Namaqualand, Richtersveld National Park, 1.5 km from Helskloof gate (28.18S, 16.57E), 8 and 9.ix.1996 (F. W., S. K. and R. W. Gess) 3 females, 1 male (all on ground near *Aptosimum spinescens*) [all AMG].

*Discussion.*—*Celonites gariepensis* falls into the group of southern African species in which the propodeal lamella is separat-

ed from the median part by a more or less spiral slit that usually ends in a circular emargination, with the projection of the median part, bordering the slit, very markedly projecting into it. Within this group it is closest to *clypeatus* Brauns and *andrei* Brauns, sharing with them a carina not only on the frons but also on the clypeus. It is distinguishable from both, however, by a very different colour pattern, the possession of whitish-yellow markings being particularly diagnostic. The raised anterior part of the scutellum differentiates *gariepensis* markedly from *clypeatus* but less so from *andrei* from which, however, it differs in both sexes in having narrower and straighter tegula. The male genitalia though similar in plan to those of *andrei* are noticeably narrower.

*Etymology.*—The name *gariepensis*, an adjective, is derived from Gariep, the Nama name for the Orange River which within its great northward curve embraces that part of the Richtersveld in which the present specimens were collected.

## Celonites tumidiscutellatus Gess, sp. nov.

*Female.*—(Figs. 7–9). Black. The following are reddish-brown: apical half of mandible, underside of antennal club, entire dorsal surface of pronotum, tegula, scutellum to varying degree (ranging from narrow band on posterior margin, through postero-medial marking, to entire posterior two-thirds), middle of metanotum, transverse bands on posterior half of terga I–IV (in the specimen from Willowmore only terga I–III) and entire sides of same, knees, extreme apices of tibiae and all tarsi. The following are dark brown: upperside of antennal club, propodeal lamellae postero-laterally, terga V and VI, sterna, legs (other than parts listed above). Wings infuscated.

Length 7.7–7.9 mm (average of 3: 7.8 mm); length of front wing 5.0–5.2 mm (average of 3: 5.1 mm); hamuli 7–8. Length of extended tongue 4.8–5.0 mm (average of

3: 4.9 mm); tongue length: body length = 0.63.

Head (Fig. 7). Clypeus and frons shiny, coarsely rugoso-punctate; vertex dull, less coarsely sculptured. Clypeal carina of the same basic pattern as in *clypeatus*, *andrei* and *gariepensis* (that is shallowly M-shaped) but medially very indistinct (where indicated forming an extremely shallow angle). Frons with shallow V-shaped carina, conspicuous except laterally and at medial angle, arising laterally opposite but outside middle of ocular sinuses and meeting at widely obtuse angle just above antennal sockets. Frons, midway between V-shaped carina and anterior ocellus, weakly raised into shallow transverse arc indicated by change in direction of rugosity (transverse as opposed to longitudinal in area below).

Thorax (Figs. 8 and 9). Upper surface of pronotum, mesoscutum, scutellum, tegula and mesopleuron more or less longitudinally rugoso-punctate; mesoscutum in posterior half moderately and evenly depressed; scutellum markedly swollen medially, rising above level of the mesoscutum. Propodeal lamella of each side wide, subtruncate distally, with outer edge convex, separated from median part of propodeum by a spiral slit ending in a circular emargination, with projection of median part somewhat forwardly directed and projecting into it.

Gastral terga uniformly and evenly covered with moderately sized shallow punctures; interspaces of about width of punctures and finely microsculptured.

*Male.*—(Figs. 10–12). Coloration very similar to that of female but: antenna dark brown overall; scutellum only exceptionally with more than posterior margin reddish-brown; middle of metanotum black; number of gastral terga with transverse reddish-brown posterior bands variable, ranging from I–III to I–IV.

Length 6.7–7.5 mm (average of 3: 7.0 mm); length of front wing 4.4–4.9 mm (average of 3: 4.6 mm); hamuli 6–7. Length of
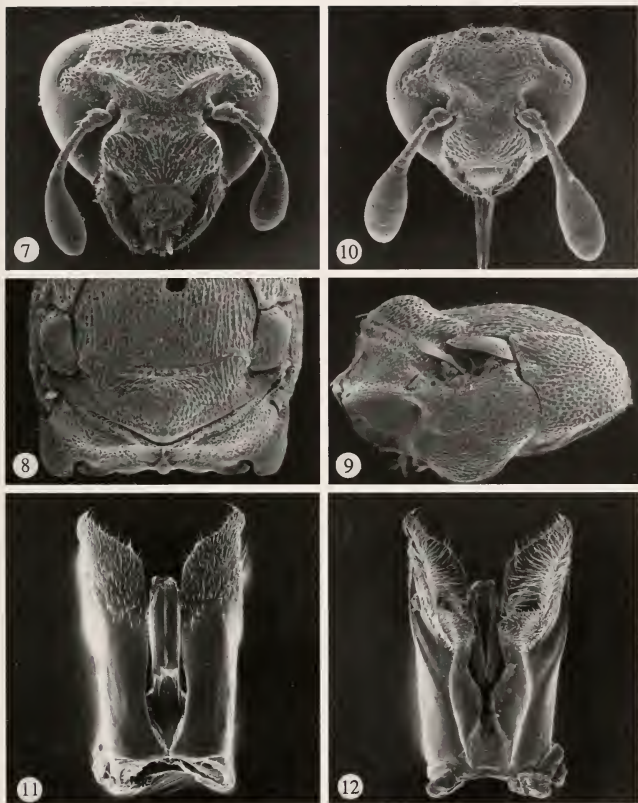
Figs. 7–12.  *Celonites tumidiscutellatus.* 7, Frontal view of head of female (× 20). 8, Dorsal view of posterior two-thirds of mesosoma of female (× 20). 9, Lateral view of right side of mesosoma of female (× 20). 10, Frontal view of head of male (× 20). 11, Dorsal view of genitalia of male (× 50). 12, Ventral view of genitalia of male (× 50).

extended tongue 4.2–4.4 mm (average of 3: 4.3 mm); tongue length: body length = 0.61.

Structure much like that of female differing most noticeably in the following: antennal club both wider and longer, with three sensory depressions beneath; clypeal carina effaced, frontal carina much reduced; gastral terga with postero-lateral angles more strongly projecting; tergum VII compared to tergum VI of female with posterior margin of median part a much flatter curve.

Genitalia (Figs. 11 and 12).

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Reserve, 10–11.x.1989 (F. W. and S. K. Gess) (in flowers of *Aptosimum spinescens* (Thunb.) Weber, Scrophulariaceae) [AMG]. Paratypes (34 females, 23 males): Cape Province: Namaqualand, Richtersveld National Park, 1.5 km from Helskloof gate (28.18S, 16.57E), 8.ix.1996 (F. W., S. K. and R. W. Gess) 3 males (all on ground near *Aptosimum spinescens*); Namaqualand, Springbok, Hester Malan [now Goegap] Nature Reserve, 15–22.x.1987 (F. W. and S. K. Gess), 2 females (1 in flower of *Aptosimum spinescens*; 1 in Malaise trap); same locality, 10–12.x.1988 (F. W. and S. K. Gess), 1 female, 4 males; same locality and date (D. W. Gess), 5 females, 4 males; same locality, 10–11.x.1989 (F. W. and S. K. Gess), 17 females, 5 males (1 female in flower of *Aptosimum indivisum* Burch. ex Benth., Scrophulariaceae; 1 female, 1 male in flowers of *Aptosimum spinescens*; 2 females, 1 male in flowers of *Peliostomum virgatum* E. Mey., Scrophulariaceae; same locality and date (D. W. Gess), 3 females, 6 males; Springbok, Goegap Nature Res[erve] (plains), 7.ix.1992 (F. W. and S. K. Gess), 1 male; [Springbok], Goegap [Nature Reserve] (windmill, 29.37S, 17.59E), 4–8.x.1994 (F. W. and S. K. Gess), 3 females (all in flowers of *Aptosimum indivisum*; Namaqualand, [Springbok], Voëlklip (29.45S, 17.22E), 2.x.1994 (F. W.

and S. K. Gess), 1 female (on dry sandy ground); Namaqualand, Klipfontein (29.51S, 17.47E), 14.x.1989 (D. W. Gess), 1 female; Willowmore, 7.x.1971 (C. Jacot-Guillarmod), 1 female [all AMG].

*Discussion.*—*Celonites tumidiscutellatus* falls into the group of species made up of *clypeatus* Brauns, *andrei* Brauns and *gariepensis* Gess. It differs from *gariepensis* in lacking yellowish-white markings and from the more similarly coloured *clypeatus* and *andrei* in lacking orange markings on the prepectus. The scutellum is more strongly swollen and raised than that of *clypeatus* and totally different from those of the other two species. The female differs from those of the other species in that the clypeal carina is differently formed and very weak medially and is unique in the development of the raised transverse arc on the upper frons. The male genitalia differ from those of *clypeatus* in that the parameres are distally asymmetrically narrowed and end in a narrowly rounded point rather than being apically broadly rounded. The volsella is of totally different shape.

*Etymology.*—The name *tumidiscutellatus*, a male adjective, is compounded from the Latin words *tumidus*, swollen, and *scutellatus*, distinguished by the scutellum. It serves to draw attention to a diagnostic character of the species.

## Celonites lobeliae Gess, sp. nov.

*Celonites* sp. E. (Gess, S. K. 1996: Appendices 1 and 2)

*Female.*—Black. The following are yellowish-white: small spot on either side of frons close to margin of upper orbit (that is, above ocular sinus), small spot on humeral angles, postero-lateral angles of pronotum next to tegulae, lateral margins of propodeal lamellae, small transverse streaks postero-laterally on terga I–IV and minute postero-medial spot on tergum V. The following are reddish-brown: apical half of mandible, underside of antennal

club, continuous very narrow band along posterior margin of pronotum, pronotal lobe, tegula, metanotum, transverse posterior bands (anteriorly expanded laterally) on terga I–III, lateral margins of terga IV and V, diffuse area on tergum VI, sterna I–III and parts of sterna IV–VI, most of front femora and apices of middle and hind femora, and all tibiae and tarsi. The following are dark brown: upper side of antenna, postero-medial parts of terga IV–V, legs other than for parts already noted. Wings lightly infuscated.

Length 8.2 mm; length of front wing 5.4 mm; hamuli 10.

Head and clypeus coarsely rugoso-punctate, clypeus steeply raised laterally, its disc flat, not carinate. Frons obliquely raised and subtuberculate immediately above each antennal socket, raised areas separated medially by a little less than interantennal distance, therefore not forming a V-shaped carina.

Upper surface of pronotum, mesoscutum, scutellum, propodeum and gastral terga moderately coarsely and closely punctured with narrow microsculptured interspaces; scutellum almost flat, only slightly raised above adjacent part of mesoscutum. Propodeal lamella of each side subtruncate distally, with outer edge gently convex and postero-lateral corner smoothly rounded, separated from median part of propodeum by a wide spiral slit; projection of median part of the propodeum transverse, apically rounded.

Male.—(Figs. 13 and 14). Black. The following are yellowish-white: labrum, transverse marking flanking anterior margin of clypeus, one or two small spots proximally on clypeal disc, variously shaped spot within each ocular sinus and pair of spots on supra-antennal tubercles, small spot on humeral angles, very narrow interrupted band on posterior margin of pronotum (present in one specimen only), variously sized spot on prepectus, pair of small spots laterally on scutellum (present in one specimen only), lateral margin of propodeal lamellae, small transverse streaks postero-laterally on terga I–IV and small postero-medial spots on terga I–VI (both series of markings in one specimen only), spot on distal end of front femora, base of front tibia and to a lesser extent bases of middle and hind tibiae. Distribution of reddish-brown and dark brown markings similar to those of female.

Length 6.7–7.7 mm; length of front wing 4.3–4.8 mm; hamuli 6–7. Length of extended tongue of larger specimen 4.3 mm; tongue length: body length = 0.55.

Apart from the usual secondary sexual differences of the antennal club and gastral terga, the structure is very similar to that of the female.

Genitalia (Figs. 13 and 14).

Material examined.—Holotype: female. Cape Province: Betw[een] Nieuwoudtville and top of Vanrhyns Pass, 29–30.ix.1990 (F. W. and S. K. Gess) (on purple flowers of Lobelia sp., Lobeliaceae) [AMG]. Paratypes (2 males): Cape Province: Betw[een] Nieuwoudtville and top of Vanrhyns Pass, 29–30.ix.1990 (F. W. and S. K. Gess) (1 on purple flowers of Lobelia sp., 1 on ground in the vicinity of the plant) [both AMG].

Discussion.—Celonites lobeliae can easily be confused with C. promontorii Brauns for not only do the two species look superficially similar but, judging from the type locality, they may at least partially overlap in distribution. Celonites lobeliae can be distinguished in having the antennal club more gracile, the sides of the clypeus more strongly raised, the swelling on the frons above the antennal sockets stronger and subtuberculate, the puncturation of the head (and to a less extent of the thorax) coarser, the clypeus and frons not shiny, the mesonotum hardly depressed posteriorly and the scutellum flatter and hardly raised above the level of the mesonotum, the postero-lateral angles of terga II–V of the female and II–VI of the male almost right-angled (not acutely produced) and the last tergum with lateral angles obtuse-
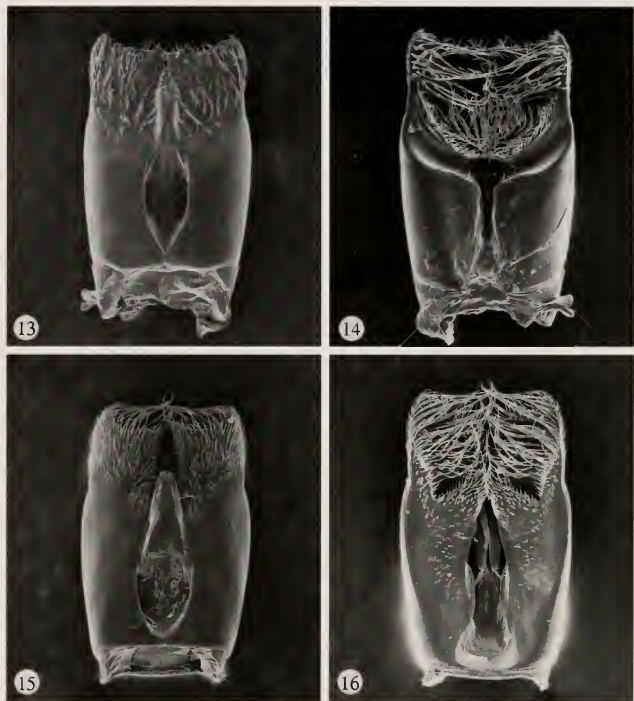
Figs. 13–16. *Celonites lobeliae.* 13, Dorsal view of genitalia of male (× 50). 14, Ventral view of genitalia of male (× 50). 15–16. *Celonites promontorii.* 15, Dorsal view of genitalia of male (× 45). 16, Ventral view of genitalia of male (× 45).

ly rounded (not acutely produced). In *lobeliae* the ratio of the distance between an eye and a posterior ocellus: distance between the posterior ocelli is 5.2: 10 in the female and 4.1: 10 in the male, whereas in *promontorii* the ratio is 6.7: 10 and 6.2: 10, respectively. The male genitalia are markedly different (compare Figs. 13 and 14 with 15 and 16).

*Etymology.*—The name *lobeliae,* genitive singular, is formed from the generic name of the plant, *Lobelia* (Lobeliaceae), in the flowers of which the wasp was found foraging for nectar or nectar and pollen.

**Jugurtia** Saussure, 1854
**Jugurtia duplicata** Richards

*Jugurtia duplicata* Richards, 1962: 263, male. Holotype: male, South Africa: Van Rhynsdorp [sic] (SAM).

This species was described from 6 males collected at Vanrhynsdorp during the months of July and August, 1927. The female of this very distinct species has hitherto been undescribed.

*Female.*—Black. Lamellate margin of scutellum creamy-white. The following are reddish-brown: mandible to variable extent (all but extreme base, only distally, or not at all), underside of swollen distal flagellomeres (to variable extent), narrow streak at top of tempora behind eyes, tegula and dorso-lateral angle of pronotum adjacent to it, terga I and II (except base of I, diffuse antero-medial patch and sometimes extreme sides of II), posterior transverse band not reaching sides on tergum III and usually IV, knees of all legs (sometimes), dorsal proximal streak on front tibia (usually), all tarsomeres (to variable extent). Wings subhyaline, darker than those of male, venation brown.

Length 8.6 mm; length of front wing 5.8 mm; length of extended tongue 3.7 mm; hamuli 8.

Antenna short, rather abruptly clavate; scape (with radicle) 3.2 × as long as greatest width and 2 × as long as combined length of pedicel and flagellomere 1; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [the length of flagellomere I being taken as 1.0]—1.0 (0.63), 0.63 (0.65), 0.50 (0.85), 0.63 (1.0), 0.85 (1.44), 0.88 (1.75), 1.0 (1.95), 0.90 (1.88), 0.81 (1.80), 0.94 (end rounded). Vertex behind ocelli depressed in front of preoccipital carina (as in male). Propodeum laterally obtusely angulate in profile. Puncturation of head and body similar to that of male.

*Material examined.*—Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E),

19.ix.1995 (F. W., S. K. and R. W. Gess), 1 female (at water) [AMG]; Namaqualand, Richtersveld National Park, Paradise Kloof (28.19S, 17.01E), 22.ix.1995 (F. W., S. K. and R. W. Gess), 5 females (4 at water and 1 on pink flowers of *Drosanthemum* sp., Aizoaceae: Mesembyanthema) [AMG]; Namaqualand, Springbok, Goegap Nature Res[erve] (hills), 8–10.ix.1992 (F. W. and S. K. Gess), 1 female, 3 males (1 male on wet sand) [AMG]; Namaqualand, [Springbok], Goegap [Nature Reserve] nr Kraaiwater (29.37S, 18.00E), 3–4.x.1994 (F. W. and S. K. Gess), 2 females (1 on white-centred pink flowers of *Drosanthemum* cf. *hispidum*, Aizoaceae: Mesembyanthema and 1 on sand in dry water course) [AMG]; Namaqualand, W end of Wildeperdehoek Pass (29.56S, 17.37E), 14.x.1989 (F. W. and S. K. Gess), 5 females (at water) [AMG]; same locality and date (D. W. Gess), 1 female (at water) [AMG]; Namaqualand, ca. 5 km NNW of Kamieskroon, 21.viii.1991 (T. F. Houston), 1 male [AMG]; Namaqualand, Grootvlei Pass, 16 km W of Kamieskroon, 11.ix.1992 (F. W. and S. K. Gess), 1 female (on pink flowers of *Leipoldtia constricta* (L. Bol.) L. Bol., Aizoaceae: Mesembyanthema) [AMG]; Namaqualand, Knersvlakte (31.26S, 18.42E), 4.ix.1996 (F. W., S. K. and R. W. Gess), 1 female (visiting deep pink flowers of "mesem," Aizoaceae: Mesembyanthema) [AMG]; 15 km N of Nieuwoudtville on road to Loeriesfontein, 3–8.x.1989 (F. W. and S. K. Gess), 27 females (25 at water and 2 visiting flowers of *Pteronia* cf. *divaricata* (Berg) Less., Asteraceae) [AMG]; same locality and date (D. W. Gess), 11 females (3 at water) [AMG]; Nieuwoudtville, Skuinshoogte Pass (31.16S, 19.08E), 23–30.ix.1994 (F. W. and S. K. Gess), 17 females (10 at water, 2 on dry river bed, 1 on ground above river bed, 3 on white cone flowers of Aizoaceae: Mesembyanthema, 1 on purplish-pink flowers of Aizoaceae: Mesembyanthema) [AMG]; Clanwilliam distr., Biedouw Valley (32.08S, 19.14E), 7.ix.1988 (C. D. Eardley), 1 female [NCP].

## Jugurtia tigrina Gess, sp. nov.

*Jugurtia* sp. C. (Gess, S. K. 1996: Appendices 1 and 2)

*Female.*—Black. The following are whitish-yellow to yellow: roughly triangular, basomedian spot on clypeus and broad oblique band on each side of raised disc of same (leaving V-shaped black area, of which arms arise near antennal sockets and point ends in middle of clypeal emargination); large, strongly upwardly bilobed marking on frons between and above antennal sockets (narrowly separated from median clypeal marking); minute elongate spot on inner orbits below level of antennal sockets; broad marking that fills ocular sinus and extends obliquely upwards to level of lower margin of hind ocelli; broad streak on outer orbits from below level of ocular sinus to top of eye; anterior and posterior margins of dorsal surface of pronotum; median streak on posterior half of mesoscutum; small spot on axilla, posterior half of raised scutellar disc, lamellate margin of scutellum, anterior and posterior parts of tegula (leaving between them a clear testaceous area); large dorsal spot anteriorly on mesopleuron (on prepectus) and contiguous smaller dorsal spot posterior to it; most of dorsolateral surface of propodeum; broad transverse posterior bands on terga I–V (sometimes somewhat widened laterally), sometimes a pair of spots on tergum VI; diffuse posterior markings on sterna II–V; apex of femora and most of tibiae. The following are various shades of light brownish-orange: mandible, palps, antenna (except for black upper surface of scape and pedicel), tarsomeres, ill-defined areas within pale bands on terga and flanking pale markings on sterna, sometimes middle of tergum VI. Wings nearly hyaline.

Length 7.7–8.3 mm, length of front wing 5.0–5.3 mm; hamuli 10.

Antenna sort, abruptly clavate; scape (with radicle) 2.8 × as long as greatest width and 2 × as long as combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [the length of flagellomere I being taken as 1.0]—1.0 (0.82), 0.64 (0.91), 0.64 (0.91), 0.64 (1.18), 0.64 (1.55), 1.09 (2.09), 1.18 (2.36), 1.18 (2.45), 1.18 (2.36), 1.27 (end rounded). Clypeus, frons and vertex shiny, with coarse, shallow punctures; clypeus with ventral emargination curved but shallow and with margin slightly upwardly produced; vertex behind ocelli not depressed in front of preoccipital carina.

Pronotum and mesoscutum shiny, coarsely and closely punctured; median longitudinally keeled depression on posterior half of mesoscutum less coarsely punctured; scutellum similarly punctured to mesoscutum, weakly depressed centrally, moderately bituberculate posteriorly; mesopleuron shiny, coarsely and closely punctured dorsally, more finely and more sparsely punctured with unsculptured interspaces ventrally; propodeum laterally smoothly curved in profile, moderately coarsely and closely punctured and sides in addition longitudinally rugose.

Gastral terga shiny, microscopically punctured, with in addition coarse close punctures on tergum I and baso-lateral parts of tergum II and smaller well separated punctures (becoming progressively weaker on posterior terga) on rest of terga.

*Male.*—Black. The following are whitish-yellow to yellow: scape, pedicel and first two or three flagellomeres; mandible (except apical tooth); palps; entire labrum and clypeus; large and sometimes bilobed marking on frons between and above antennal sockets; band margining entire lower inner orbits and merging above with marking that fills ocular sinus and is sometimes carried obliquely upwards to level of lower edge of fore-ocellus (in some specimens median and lateral frontal markings largely fused, leaving only narrow oblique black streak above antennal sockets); outer orbits from below level of ocular sinus to top of eye; entire dorsal

surface of pronotum (that is, entire surface between anterior and posterior margins other than for occasional small irregular black marks); median streak on posterior half of mesoscutum; small spot on axilla; posterior half of raised scutellar disc; lamellate margin of scutellum; anterior and posterior parts of tegula (leaving between them a clear testaceous area); large dorsal spot anteriorly on mesopleuron (on prepectus) and two smaller spots contiguous with and situated posteriorly and ventrally to it; two small spots on mesosternum anterior to coxae; broad transverse posterior bands on terga I–VI (hardly widened laterally); most of normally exposed part of tergum VII; sterna to a large extent; coxae, trochanters, femora (except for limited dark stripes), tibiae and at least first tarsomeres of all legs. The following are various shades of light brownish-orange: flagellomeres III or IV–X (except for dorsal infuscation); ill defined and diffuse areas within pale bands on terga and on sterna; sometimes distal tarsomeres. Wings nearly hyaline.

Length 7.3–7.5 mm, length of front wing 5 mm; hamuli 8.

Antenna of normal length, flagellomeres IV–X forming elongate, curved and simple club (not hollowed out beneath); scape (with radicle) 2.4 × as long as greatest width and 1.4 × as long as combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [the length of flagellomere I being taken as 1.0]—1.0 (0.59), 0.73 (0.59), 0.73 (0.64), 0.82 (0.86), 0.82 (1.14), 0.91 (1.36), 1.0 (1.45), 0.91 (1.55), 0.91 (1.45), 1.18 (end rounded). [The foregoing description and measurements are taken from one paratype; the other from the same locality has both flagella appearing 9-segmented, flagellomeres III and IV being almost completely fused and together being only slightly longer (1.2–1.3) than the normal length of either of the constituent flagellomeres alone.]

Gastral terga II–VI moderately constricted anteriorly, narrower than corresponding terga of female; tergum VII produced and narrowly emarginate apically. Puncturation similar to that of female.

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess) (at water) [AMG]. Paratypes (39 females, 5 males): Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess) 34 females (29 at water, 1 on ground, 3 Malaise trap) [AMG]; same locality, 10–12.x.1988 (F. W. and S. K. Gess), 1 female [AMG]; Namaqualand, [Springbok], 5 km from Kokerboom Hotel on road to Droëdap (29.44S, 17.55E), 8.x.1994 (D. W. Gess), 1 female [AMG]; Namaqualand, Klipfontein (29.51S, 17.47E), 14.x.1989 (D. W. Gess), 1 female [AMG]; Namaqualand, 6–13 mi[les] S Mesklip, 21.x.1968 (J. G. Rozen and E. Martinez), 1 female [AMG]; Namaqualand, Farm Arkoep, 6 km N Kamieskroon (30.19S, 17.56E), 1–2.x.1990 (C. D. Eardley), 1 female, 3 males [NCP]; Nieuwoudtville Falls, 5 km N of Nieuwoudtville, 28.ix.1990 (F. W. and S. K. Gess), 2 males (on yellow flowers of *Leysera gnaphaloides* (L.) L., Asteraceae) [AMG].

*Etymology.*—The name *tigrina*, a Latin female adjective meaning tiger-like, refers to the yellow and black markings and in particular to the tiger-like banding of the abdomen.

## *Jugurtia eburnea* (Turner), new status

*Masariella turneri eburnea* Turner, 1935: 299, fig. 3, male holotype, female allotype (SAM).

*Masariella turneri* (non Schulthess 1929) Schulthess, 1935: 384, male allotype [= male holotype of *Jugurtia polita* Richards, 1962] (NHML).

*Jugurtia polita* Richards, 1962: 256, male holotype, female allotype (NHML). New synonymy.

*Material examined.*—Cape Province: 15 km N of Nieuwoudtville on road to Loeriesfontein, 3–8.x.1989 (F. W. and S. K. Gess), 3 females (visiting flowers of *Osteospermum* cf. *oppositifolia* (Ait.) T.Norl., Asteraceae), 1 male (visiting flowers of *Senecio* sp. prob. *nivea* Less., Asteraceae) [AMG]; same locality and date (D. W. Gess), 1 male [AMG]; Nieuwoudtville Falls, 5 km N of Nieuwoudtville, 28.ix.1990 (F. W. and S. K. Gess), 1 female (without flower visiting record), 6 males (on yellow flowers of *Leysera gnaphaloides* (L.) L., Asteraceae) [AMG]; Nieuwoudtville, Skuinshoogte Pass (31.16S, 19.08E), 23–30.ix.1994 (F. W. and S. K. Gess), 7 females, 1 male (6 females at water, 1 female on ground above river bed, male on dry river bed) [AMG]; Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess), 2 males (Malaise trap) [AMG]; same locality, 10–12.x.1988 (F. W. and S. K. Gess), 1 female, 7 males [AMG]; Namaqualand, [Springbok], Goegap [Nature Reserve] (windmill, 29.37S, 17.59E), 4–8.x.1994 (F. W. and S. K. Gess), 3 females (all on wet sand) [AMG]; Namaqualand, Farm Arkoep, 6 km N Kamieskroon (30.19S, 17.56E), 1–2.x.1990 (C. D. Eardley), 1 male [NCP]; Namaqualand, Kamieskroon, Sept. 1930 (Museum Staff), holotype male and allotype female [SAM].

*Discussion.*—Schulthess (1929) described the species *turneri* from 4 females from 38 m[iles] E of Ceres (17–25.xi.24). Subsequently Schulthess (Sept. 1935) described as the male of *turneri* a specimen collected together with 14 females from a locality given by him as Calvinia, Niewoudtville [sic] (11–22.xi.31). This provenance is inexact as the two towns are separated by 69 km! Amongst other characters of this male Schulthess mentioned the very long antennae. He made no comment with regard to the females.

Richards (1962) examined Schulthess' material and recognized that the male and associated females of Schulthess (1935)

were not conspecific with the females of Schulthess (1929). At the same time he correctly recognized a male from Matjesfontein as the true male of *turneri* and described it as such. The specimens of Schulthess (1935) were believed by Richards to represent a new species which he named *polita*. The male described by Schulthess (1935) and erroneously designated by him as the allotype of *turneri* was designated by Richards as the holotype of *polita*. Collection data of this specimen were given more precisely than before as Calvinia (11–16.xi.31). Of the associated conspecific females mentioned by Schulthess, Richards' allotype and eight paratypes have the same data as the holotype and two further paratypes have the data Blaukrans, near Calvinia (17.xi.31).

Preceding by a few months the second Schulthess publication, Turner (Febr. 1935) under the name *eburnea* described both sexes of what was believed to be a subspecies ("race") of *turneri* of Schulthess (1929) from Kamieskroon, Namaqualand. He briefly compared the females and stated how they differed. The more comprehensive description of the male not only described the antennae in detail but also figured them.

Richards (1962) under his account of *turneri* mentioned that Turner had described a subspecies *eburnea* but stated that he had not seen Turner's specimens. These specimens, a holotype male and an allotype female, housed in the South African Museum, have been examined by the present author. They are not *turneri* nor a subspecies thereof but are conspecific with *polita* Richards. The name *eburnea* Turner, 1935 has priority over *polita* Richards, 1962, and the latter name therefore becomes a synonym.

## Jugurtia turneri (Schulthess)

*Masariella*(?) *turneri* Schulthess, 1929: 499, 500–501, fig. 1, female. Holotype: female, South Africa: Little Karoo, 38 m[iles] E of Ceres (NHML)
not *Masariella turneri* Schulthess subsp. *eburnea*

Turner, 1935: 384, male, female [= *Jugurtia eburnea* (Turner)]
not *Masariella turneri* Schulthess, Schulthess, 1935: 384, male [= *Jugurtia eburnea* (Turner)]
*Jugurtia turneri* (Schulthess): J. Bequaert, 1937: 343; Richards, 1962: 257.

*Material examined.*—Cape Province, Doringbos, 3.xi.1966 (J. G. Rozen), 3 males [AMG]; 43 km ENE of Ceres on road to Sutherland, 2–3.xii.1989 (S. K. Gess), 3 females, 1 male (on flowers of *Athanasia trifurcata* (L.) L., Asteraceae); same locality and date (F. W. Gess), 4 females, 2 males (3 females, 1 male on flowers of *Athanasia* sp.; 1 female, 1 male on flowers of *Senecio rosmarinifolia* L.f., Asteraceae; same locality and date (R. W. Gess), 1 male (on flowers of *Athanasia* sp.) and (H. W. Gess), 1 female, 1 male (without flower visiting records) [all AMG].

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KEY TO SOUTHERN AFRICAN *JUGURTIA* WITH EXTENSIVE PALE (WHITE, CREAM OR YELLOW) MARKINGS (THAT IS *EBURNEA, TIGRINA* AND *TURNERI*)

1. Males. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
– Females. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
2. Antennae very long, reaching back beyond tergum I; flagellomeres I–VII greatly elongated (ratio of length to breadth being 2.3:1 for I, 5:1 for II–VI, 3.8:1 for VII), VIII–X forming an oval sharply defined club . . . . . . . . . . . . . . . . . . . . . . *eburnea* (Turner) (syn. *polita* Richards)
– Antennae of normal length, reaching back at most to middle of mesoscutum; flagellomeres I–VII not greatly elongated (ratio of length to breadth never exceeding 2.4:1 and generally much smaller), VI–X forming an elongate curved club . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3. Flagellomeres I–III gracile, long relative to breadth, ratio of length to breadth being 2.4:1, 2:1, and 1.6:1, respectively. Mesoscutum entirely black. Gastral terga II–V with punctures close, with transverse posterior pale bands narrow, considerably and abruptly widened medially and laterally; tergum VI black except on extreme sides and at apex . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *turneri* (Schulthess)
– Flagellomeres I–III robust, short relative to breadth, ratio of length to breadth being 1.7:1, 1.2:1, and 1:1, respectively. Mesoscutum with median yellow streak in posterior half. Gastral terga II–V with punctures well separated, with transverse posterior pale bands wide, slightly and gradually widened laterally; tergum VI yellow except at extreme base . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tigrina* Gess sp. nov.
4. Propodeum laterally with conspicuous tubercle. . . . . . . *eburnea* (Turner) (syn. *polita* Richards)
– Propodeum laterally without tubercle. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
5. Propodeum laterally obtusely angulate in profile. Mesoscutum entirely black. Gastral terga II–V with punctures close, with transverse posterior pale bands narrow, considerably and abruptly widened medially and laterally; tergum VI black. . . . . . . . . . . . . *turneri* (Schulthess)
– Propodeum laterally smoothly curved in profile. Mesoscutum with a median yellow streak in posterior half. Gastral terga II–V with punctures well separated, with transverse posterior pale bands wide, slightly and gradually widened laterally; tergum VI brownish-orange and sometimes with a pair of yellow spots . . . . . . . . . . . . . . . . *tigrina* Gess sp. nov.

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## Jugurtia codoni Gess sp. nov.

*Female.*—Black. The following are yellowish-white: small crescent-shaped mark at bottom of ocular sinus; streak at top of tempora behind eyes; narrow transverse streak medially on pronotal dorsum (streak sometimes broken up into separate dots or totally effaced); narrow streak on humeral angles; posterior angles of pronotum adjacent to tegulae; lateral margins of scutellum; narrow transverse posterior bands (generally of even width but occasionally slightly widened medially and laterally) on terga I–IV. Underside of flagellomeres VI–X orange. The following

are various shades of reddish-brown: usually distal half of mandible; tegula; knees of all legs; short streak dorsally on basal half of front tibia; and front tarsomeres. Remaining parts of legs brown. Wings lightly infuscate.

Length 7.7–8.3 mm (average of 5: 8.0 mm); length of front wing 4.9–5.3 mm (average of 5: 5.2 mm); hamuli 7–9 (usually 7). Length of extended tongue 3.2–3.6 mm (average of 5: 3.5 mm); tongue length: body length = 0.43.

Antenna short, abruptly clavate; scape closely and finely punctured; scape (with radicle) 2.6 × as long as greatest width and 2.2 × as long as combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [the length of flagellomere I being taken as 1.0]—1.0 (0.9), 0.6 (1.7), 0.7 (1.7), 0.8 (1.8), 0.8 (2.1), 1.0 (2.2), 1.3 (2.0), 1.3 (2.2), 1.5 (1.7), 1.4 (end rounded). Clypeus, frons and vertex shiny, coarsely but shallowly reticulate punctate; vertex behind ocelli weakly depressed in front of preoccipital carina.

Pronotum and mesoscutum shiny, coarsely and closely punctured; mesoscutum in posterior half almost flat (that is lacking a carinate depression), with interspaces (especially in a median longitudinal band and posteriorly) closely and finely punctured; scutellum similarly punctured to posterior portion of mesoscutum, only slightly raised above mesoscutum, anteriorly sloping down onto it (that is, not falling to mesoscutum abruptly and step-like), only inconspicuously depressed centrally, hardly tuberculate posteriorly; mesopleura shiny, punctured like pronotum in upper half, with sparser and smaller punctures in lower half; angles of propodeum with bluntly rounded projections. Tegula shiny, virtually impunctate, in basal half with sides subparallel, in apical half with outer margin slightly expanded before curving smoothly and obliquely to rounded inner posterior corner. Spurs of middle tibia of average length; outer spur

markedly curved apically; inner spur straight.

Gastral terga shiny, with microscopical punctures interspersed with larger but shallow, well separated punctures that become progressively smaller on apical terga. Sterna shiny, sparsely punctured.

*Male.*—Coloration and markings similar to those of female, with additional yellowish-white markings as follows: small spot at base of mandible; small streak on inner orbits above level of antennal sockets; sometimes a small supraclypeal marking variously broken up into spots; narrow transverse posterior band on tergum V; postero-medial spot on tergum VI. Antenna black throughout.

Length 7.5–7.6 mm; length of front wing 4.7–5.1 mm; hamuli 7–8. Length of extended tongue 3.0 mm; tongue length: body length = 0.40.

Structure similar to that of female, differing most noticeably in the following: antenna longer; flagellomeres VI–X forming an elongate markedly curved club; last three flagellomeres flattened beneath and together forming a wide hook; scape (with radicle) 2.2 × as long as greatest width and 1.2 × as long as combined length of pedicel and flagellomere I; flagellomeres I–X respectively with the following relative lengths (and breadths) [the length of flagellomere I being taken as 1.0]—1.0 (0.55), 0.80 (0.60), 0.80 (0.70), 0.90 (0.80), 0.90 (0.90), 1.0 (1.55), 1.20 (1.70), 1.10 (1.70), 1.20 (1.50), 2.1 (end rounded); metasoma narrower relative to its length; tergum VII with posterior margin rounded except for small semi-circular emargination medially; sternum II posteriorly with a pair of pronounced, widely separated and smoothly rounded transverse tubercles; sternum III posteriorly with a pair of low transverse swellings.

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess) (on white flow-

ers of *Codon royenii* L., Hydrophyllaceae) [AMG]. Paratypes (72 females, 4 males): Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995 (F. W., S. K. and R. W. Gess) 63 females (54 on white flowers of *Codon royenii* L., Hydrophyllaceae; 5 in deep violet flowers of *Peliostomum* sp., Scrophulariaceae; 3 on deep pink flowers of *Hermbstaedtia glauca* (Wendl.) Reichb. ex Steud., Amaranthaceae); same locality, 6.ix.1996 (F. W., S. K. and R. W. Gess) 2 females (1 in deep purple flowers *Peliostomum* sp.; 1 on ground nr flowering *Peliostomum* sp.); Namaqualand, Richtersveld National Park, betw[een] hills (28.08S, 17.01E), NW of Koeroegabvlakte, 14.ix.1996 (F. W., S. K. and R. W. Gess) 4 females, 3 males (1 female on yellow flowers of *Zygophyllum meyeri* Sond., Zygophyllaceae; 3 females on pink flowers of *Senecio arenarius* Thunb., Asteraceae; 2 males sunning themselves on rocks nr last named plant; 1 male on dry sandy river bed); Namaqualand, Richtersveld National Park, Paradise Kloof (28.19S, 17.01E), 22.ix.1995 (F. W., S. K. and R. W. Gess), 2 females (at water); Namaqualand, Richtersveld National Park, 1.5 km from Helskloof gate (28.18S, 16.57E), 9.ix.1996 (F. W., S. K. and R. W. Gess) 1 female, 1 male (male on white flowers *Pelargonium klinghardtense* Knuth, Geraniaceae) [all AMG].

*Discussion.—J. codoni* is a very distinct, small, predominantly black-bodied and black-legged species, lacking clypeal and supraclypeal markings (latter sometimes weakly indicated in male) and frontal spots and without any red on the pronotum, scutellum and gastral terga, but with narrow yellowish-white transverse posterior bands on terga I–IV in female and I–V in male.

*Etymology.*—The name *codoni*, genitive singular, is formed from the generic name of the plant, *Codon royenii* L. (Hydrophyllaceae), in the flowers of which the wasp was found foraging for nectar and pollen.

*Codon royenii* is endemic to Namaqualand and Namibia.

## Jugurtia koeroegabensis Gess sp. nov.

*Female.*—Black. The following are reddish-brown: mandible (other than base and apex); sometimes median spot on basal half of clypeal disc and a pair of smaller spots on lateral angles; pair of large supraclypeal spots; spots in ocular sinuses; pair of small spots on frons adjacent to eyes above ocular sinuses (sometimes fused with spots in ocular sinuses to form a continuous band); sometimes pair of minute spots adjacent to eyes at level of hind ocelli; streaks on upper tempora behind eyes; pronotum (other than for anterior face); median streak on posterior half of mesoscutum; spot on axilla; disc of scutellum; large spot on prepectus; tegula; dorso-lateral parts of propodeum; whole metasoma (except sometimes lowermost third of declivity of tergum I); apical third of all femora; entire tibiae and tarsi. Underside of flagellomeres IX–X is yellow. In some specimens the following may be yellow rather than reddish-brown: very bottom of ocular sinus; dorso-lateral corners of pronotum; lateral margins of scutellum; diffuse narrow transverse posterior bands on terga II–V. Wings hyaline, not infuscated.

Length 6.9–8.1 mm (average of 7: 7.5 mm); length of front wing 4.8–5.1 mm (average of 7: 5.0 mm); hamuli 7–9.

Antenna short, abruptly and strongly clavate; scape (with radicle) 2.8 × as long as greatest width and 1.7 × as long as combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [the length of flagellomere I being taken as 1.0]—1.0 (0.85), 0.54 (1.57), 0.62 (1.38), 0.54 (2.00), 0.5 (2.43), 0.92 (1.92), 1.15 (1.87), 1.31 (1.76), 1.15 (1.87), 1.0 (end rounded). Clypeus, frons and vertex finely reticulate punctate; vertex behind ocelli not depressed and with preoccipital carina narrow.

Dorsal surface of pronotum, mesoscutum and scutellum coarsely punctured, with interspaces micro-sculptured; mesoscutum in posterior half (that is lacking carinate depression); scutellum moderately raised above mesoscutum and falling steeply onto it; scuto-scutellar furrow wide, crossed by about 12 well-defined carinae; scutellar disc not depressed centrally; angles of propodeum with bluntly rounded projections. Tegula with a few scattered punctures in posterior half, in basal half with sides subparallel, in apical half with outer margin slightly expanded before curving smoothly and obliquely to acutely and narrowly rounded inner posterior corner. Spurs of middle tibiae of average length, straight.

Gastral terga shiny, with microscopical punctures interspersed with larger, shallow, well separated punctures that become progressively smaller on apical terga). Sterna shiny, sparsely punctured.

*Male.*—Black. The following are lemon-yellow: mandible (except extreme base and apex); disc of clypeus; most of frons from fronto-clypeal suture to just below level of anterior ocellus (at which level marking is tri-lobed) but excluding an area broadly margining the lower part of eyes from antennal insertion to partially within ocular sinuses (however, not extending as far as bottom of latter); underside of antennal scape (but not radicle); underside of pedicel and flagellomeres I–IV or V; pronotum (other than for anterior face and dorso-lateral areas); lateral margins of scutellum; tegula anteriorly; broad diffuse areas on median third of terga I–III. Reddish-brown (grading through orange to the lemon-yellow delimited above) are: flagellomeres VI–X (other than for longitudinal black band); narrow streak on tempora behind eyes; dorso-lateral areas of pronotum; large spot on prepectus; posterior two-thirds of tegula; median streak on posterior half of mesoscutum; spot on axilla; scutellar disc posteriorly; dorso-lateral parts of propodeum;

entire metasoma (except lowermost third of declivity of tergum I and for diffuse yellow areas described above); apical third of femora, entire tibiae and tarsi. Wings hyaline, not infuscated.

Length 6.6–7.2 mm (average of 7: 6.8 mm; length of front wing 4.4–4.7 mm (average of 7: 4.5 mm); hamuli 7–8.

Antenna short, strongly clavate; flagellomeres VII–X enlarged and together forming a smoothly curved hook; flagellomeres VIII–X markedly excavated ventrally to form a continuous (that is single) oblique depression with rounded margins; scape (with radicle) 2.8 × as long as its greatest width and 1.5 × as long as combined length of pedicel and flagellomere I; flagellomeres I–X, respectively, with the following relative lengths (and breadths) [the length of flagellomere 1 being taken as 1.0]—1.0 (0.71), 0.53 (1.30), 0.59 (1.30), 0.59 (1.50), 0.59 (1.80), 1.0 (1.41), 0.94 (1.88), 1.24 (1.67), 1.12 (1.89), 1.53 (end rounded).

Tergum VII with posterior margin rounded except for a small semi-circular emargination medially. Punctures larger, somewhat sparser than in female (especially on pronotum and mesoscutum), with shiny, smooth (not microsculptured) interspaces.

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995, (F. W., S. K. and R. W. Gess) (on small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond., Zygophyllaceae) [AMG]. Paratypes (15 females, 16 males): Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995, (F. W., S. K. and R. W. Gess) 5 females, 1 male (2 females on small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond., Zygophyllaceae; 1 female on yellow flowers of *Zygophyllum* sp.; 1 female on yellow flowers of *Osteospermum* sp., Asteraceae; male on floor of dry watercourse); Na-

maqualand, Richtersveld National Park, Pootjiespram (28.05S, 16.57E), 16.ix.1995 (F. W., S. K. and R. W. Gess), 1 female on yellow flowers of *Cleome paxii* (Schinz) Gilg & Ben., Capparaceae); same locality, 7.ix.1996 (F. W., S. K. and R. W. Gess), 9 females, 15 males (1 female in deep violet flowers of *Peliostomum leucorrhizum* E. Mey. ex Benth., Scrophulariaceae; 2 females on flowers of *Ferraria* cf. *divaricata*, Iridaceae; 6 females, all 15 males on ground in dry drainage channel) [all AMG].

*Discussion.*—The species is easily recognizable in both sexes by the body coloration in conjunction with the hyaline, non-infuscated wings, and in the male by the characteristically modified antennae.

*Etymology.*—The name *koeroegabensis*, an adjective derived from the Nama word *koeroegab*, "plenty of flintstone," refers to the white quartz which outcrops all over the Richtersveld. Koeroegab is applied specifically to a mountain and to the adjacent Koeroegabvlakte (vlakte, "plain" in Afrikaans), the latter being the locality where most specimens collected during the 1995 expedition were found in and about a dry watercourse.

## *Masarina* Richards, 1962

*Masarina* Richards 1962 was listed as a junior subjective synonym of *Jugurtia* Saussure 1854 by van der Vecht and Carpenter (1990), a view which was confirmed by Carpenter (1993) in his cladogram of masarine genera. In the former publication reference was made to a paper in preparation by Carpenter on the phylogenetic system of the Masarinae in which would be given the rationale for this and other synonymies, arrived at by means of cladistic analyses. Though this paper has yet to be published Carpenter has very kindly allowed access to a manuscript copy. From a study of this manuscript and from personal communications it is evident that Carpenter had identified autapomorphies for both genera. Of these

he found most useful the character states regarding the form of the antennal club and the number of spurs of the middle tibiae. He did not, however, regard the features by which *Jugurtia* and *Masarina* differ to be as significant as those which they share. Strongly influencing his decision to sink *Masarina* into synonymy was the fact that the name is identical with that of a subtribe, which he considered could result in a nomenclatural tangle. The small number of species of *Masarina* known at the time and the wish to eliminate generic fragmentation in the Vespidae were further considerations.

The present author, following his discovery and study of six additional species assignable to *Masarina* (bringing the known species up to ten), had discussions with Carpenter who, as a result, has agreed that useful grounds for maintaining two genera have been provided.

Morphological differences between *Masarina* and *Jugurtia* are as follow.

Both genera have a preoccipital carina that runs posteriorly across the vertex. In *Jugurtia* (Fig. 17), however, the carina extends down the tempora whereas in *Masarina* (Fig. 18) it is effaced, the tempora being rounded, with at most a change in the sculpturing indicating the course taken by the carina in the former genus.

Species of *Jugurtia* are characterized by a marked sexual dimorphism which is manifested in the males not only by the elongated and variously modified antennae but by the generally long narrow abdomen. *Masarina* by contrast exhibits little sexual dimorphism, the males looking very like the females and requiring close scrutiny for separation.

Species of *Jugurtia* all exhibit a transverse furrow at the base of the second gastral sternum whereas this is absent in all species of *Masarina*.

The number of spurs of the middle tibiae has proved to be of only limited value as exceptions to the general rule occur in both genera. Whereas *Jugurtia* generally
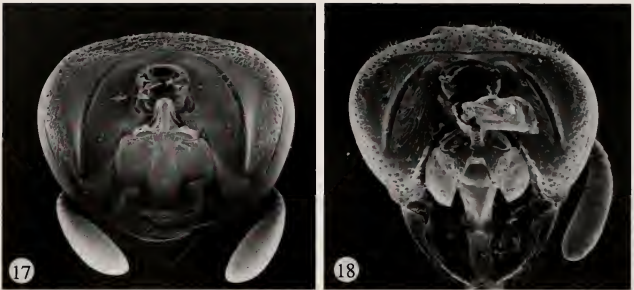
Figs. 17–18. 17. *Jugurtia braunsi*. Occipital view of head showing complete preoccipital carina (× 20). 18. *Masarina tylecodoni*. Occipital view of head showing incomplete preoccipital carina (× 20).

has two spurs, *J. eburnea* has only one. Conversely *Masarina* generally has only one spur but *M. ceres* and *M. peliostomi* each have two.

## Masarina strucki Gess

*Masarina strucki* Gess, 1988: 352, female (in Gess and Gess 1988). Holotype: female, South Africa: Goegap Nature Reserve near Springbok (AMG).

*Male.*—(Figs. 20–22). Males from Goegap Nature Reserve near Springbok (the type locality) and from Kamieskroon, Bakleikraal, are very similar to females (Fig. 19) from these localities. Sexual dimorphism is slight. The clypeus like that of the females is entirely black, differing from that of the males of many other species of *Masarina* in which it is partially or entirely pale coloured.

Tergum VII semi-circularly emarginate apically, angles of the emargination acute. Sterna VII + VIII transversely depressed, apically trilobed, median lobe produced ventrally.

Genitalia (Figs. 21 and 22): parameres long, apically rounded, gently curved inwards and ventrad.

Length: 6.0–7.1 mm (average of 9: 6.6 mm); wing length 4.1–4.6 mm (average of 9: 4.4 mm); tongue length 4.0 mm (average of 2). [Corresponding average lengths for females are 7.4 mm, 5.0 mm, and 4.2 mm.]

*Material examined.*—Cape Province, Namaqualand, Springbok, Hester Malan [now Goegap] Nature Reserve, 10-12.x.1988 (F. W. and S. K. Gess), 1 female; Namaqualand, [Springbok], Goegap [Nature Reserve], nr Kraaiwater (29.37S, 18.00E), 3–4.x.1994 (F. W. and S. K. Gess), 1 female (on sand in dry water course); same locality, at windmill site (29.37S, 17.59E), 4–8.x.1994 (F. W. and S. K. Gess), 12 females, 6 males (9 females on yellow flowers of *Hermannia disermifolia* Jacq., Sterculiaceae, 3 females, 6 males on ground beneath *H. disermifolia*); Namaqualand, Kamieskroon, Bakleikraal (30.13S, 18.03E), 9–11.x.1994 (F. W. and S. K. Gess), 16 females, 2 males (3 females on yellow flowers of *H. disermifolia* Jacq.; 12 females, 1 male on ground beneath *H. disermifolia*; 1 female, 1 male without further details); same locality, 28.ix.1995 (F. W., S. K. and R. W. Gess), 4 females, 4 males (4 females, 1 male on yellow flowers of *H. disermifolia*; 1 male on ground; 2 males without further details); Nieuwoudtville, Skuinshoogte Pass (31.16S, 19.08E), 23–30.ix.1994 (F. W. and S. K. Gess), 2 females (1 on dry river bed;

Figs. 19–22. *Masarina strucki*. 19, Frontal view of head of female (× 20). 20, Frontal view of head of male (× 20). 21, Dorsal view of genitalia of male (× 50). 22, Ventral view of genitalia of male (× 50).

1 on ground beneath *Hermannia* sp.); Clanwilliam Dam, E bank, 19.2 km S caravan park (32.17S, 18.56/7E), 5.x.1995 (F. W., S. K. and R. W. Gess), 3 females (in orange flowers of *Hermannia* (*Mahernia*) sp.) [all above records AMG]; Clanwilliam distr., Biedouw Valley (32.08S, 19.14E), 7.ix.1988 (C. D. Eardley), 1 female [NCP]; Ladismith, Buffelspoort (3320BD), 14.viii.1995 (V. B. Whitehead), 3 females (on *Herman-*

*nia* sp.) [SAM]; 6 km from Ladismith on road to Barrydale, 21.viii.1995 (F. W. and S. K. Gess), 3 females (visiting yellow flowers of *H. vestita* Thunb.) [AMG].

*Discussion.*—Since the description of this species from a single female from the Hester Malan [now Goegap] Nature Reserve near Springbok, many more specimens, including males, have been collected. They exhibit considerable geographic vari-

Figs. 23–24.  *Masarina ceres.* 23, Lateral view of male (× 10). 24, Frontal view of head of male (antennae missing) (× 25).

ation. Specimens from Namaqualand (Springbok and Kamieskroon) have fairly extensive yellowish-white markings. Those from the Clanwilliam district and from Ladismith, all females, are melanistic and lack the pale markings on the dorsal hind margin of the pronotum, the prepectus, the scutellum and the transverse posterior band on tergum V (also tergum IV in the specimen from Biedouw Valley). The specimens from Ladismith have the legs almost black instead of orange. In addition the non-Namaqualand specimens show some variation in the degree of concavity of the frons and clypeus, in the shape of the tegulae, and are somewhat more coarsely punctured. Those from the Clanwilliam district are also smaller (6.7–6.8 mm long).

#### Masarina ceres Gess, sp. nov.

*Masarina* sp. A. (Gess, S. K. 1996: Appendices 1 and 2)

*Male.*—(Figs. 23 and 24). Black. The following are yellow: disc of clypeus; labrum; mandible (except teeth); variously developed transverse supraclypeal marking on face and spot confluent with it above antennal sockets (these markings sometimes much reduced or absent); spot more or less filling ocular sinuses; streak

at top of tempora behind eyes; underside of scape; elongate transverse streaks on humeral angles and on pronotal dorsum medially; dorso-lateral posterior angles of pronotum adjacent to tegulae; large spot on prepectus; tegula (except for transparent central region); variously developed oval longitudinal spot on disc of scutellum; occasionally small transverse median streak on metanotum; small triangular median spots and larger, anteriorly convex lateral markings on distal half of terga I–VI (three markings on each tergum sometimes narrowly connected); sometimes a median longitudinal streak on tergum VII; sometimes a pair of small median spots and/or small lateral spots on anterior sterna; usually underside of middle and hind coxae, sometimes underside of front coxae distally; underside of front trochanters; distal portion of femora; and tibiae to variable extent. The following are reddish-brown: underside of distal flagellomeres; parts of tibiae; tarsi; occasionally diffuse area anterior to lateral yellow markings on terga I and II; sometimes sterna to variable degree. Wings subhyaline.

Length 5.7–6.3 mm (average of 5: 6.0 mm); length of front wing 3.3–3.8 mm (average of 6: 3.5 mm).

Head (Fig. 24). Mandible laterally widely and shallowly indented at base, apically with three strong pointed teeth of which subapical is only slightly smaller than apical. Clypeus steeply raised from sides; disc markedly broad and short, its width 1.69–1.81 × its length (average of 6: 1.74) (measured between lateral angles and from base to bottom of ventral emargination), flattened, slightly longitudinally depressed medially; ventral margin broadly bilobed and angularly emarginate, edentate, broadly lamellate; surface moderately coarsely but very shallowly punctured, shiny. Frons and vertex moderately coarsely and closely punctured, with interspaces finely punctured in parts and generally shiny. Preoccipital carina developed dorsally only, narrow.

Thorax (particularly pronotal dorsum, mesoscutum, and scutellum) coarsely, closely and deeply punctured, with interspaces very narrow and reticulate, and surface generally much less shiny than head. Scutellum raised above mesoscutum, falling almost perpendicularly into a wide, crenate anterior furrow, with lateral wings normal. Propodeal angles subtuberculate above. Middle tibia with two spurs; shorter hind tibial spur simple (not bifid); claws of all legs minutely toothed. Tegula short pyriform, only 1.5 × as long as broad.

Gastral terga I–VI with coarse shallow punctures (largest on tergum I, progressively smaller on II–VI), with entire surface (that is bottom of punctures and interspaces) microsculptured; tergum VII rounded at apex, closely and deeply punctured with interspaces reticulate. Sterna VII + VIII apically with large rounded lobe on each side but lacking a median lobe.

Material examined.—Holotype: male. Cape Province: 17 km N of Ceres, near top of Gydo Pass, 30.xi.1989 (F. W. and S. K. Gess) (on flowers of *Aspalathus* sp., Fabaceae) [AMG]. Paratypes: (5 males): same data as holotype [AMG].

Discussion.—The male of *ceres* is immediately recognizable by the coarse, close and deep puncturation of the thorax and by the distribution and form of the yellow markings on the otherwise black body. Closest in gross general appearance to the somewhat larger male of *strucki*, which like it has a yellow spot on the scutellum, it may readily be distinguished from it by the possession of yellow markings on the head and antennal scapes.

Etymology.—The name *ceres*, a noun in apposition to the generic name, is derived from the town Ceres which in its turn was named after the Roman goddess of agriculture. It indicates the provenance of the present specimens.

## Masarina mixtoides Gess, sp. nov.

Female.—(Fig. 32). Black. The following are yellowish-white: narrow streak at top of tempora behind eyes; transverse posterior bands on terga II–IV (on tergum II very narrow or interrupted medially but conspicuously expanded laterally, on III complete and moderately expanded laterally, on IV reduced laterally but slightly expanded medially). The following are various shades of reddish-brown: underside of flagellomeres V–VII; tegula (other than inner margin); axilla; terga I and II (except black extreme lateral margins and pale areas indicated above) and sometimes a small, diffuse area medially on tergum III anterior to pale band; knees of all legs; diffuse streak on front tibia; apex of front tarsomere I and whole of II–V. Wings lightly browned.

Length 6.8–8.2 mm (average of 9: 7.6 mm); length of front wing 5.1–5.7 (average of 9: 5.3 mm), hamuli 8–10. Length of tongue 3.5 and 3.6 mm (based on two specimens), average tongue length: average body length = 0.67.

Clypeus raised from sides; disc 1.6 × broader than long (measured between lateral angles and from base to bottom of ventral emargination), flattened but not depressed medially; ventral and lateral

margins lamellate; ventro-lateral corners rounded; ventral margin widely and shallowly emarginate, edentate; integument moderately coarsely and closely punctured, with punctures tending to run longitudinally. Frons evenly transversely curved, not depressed medially, similarly punctured to clypeus; vertex punctured like adjacent parts of frons; preoccipital carina developed only dorsally, lamellate, in length only 0.6 × interocular distance (measured across ocelli).

Dorsal surface of pronotum, mesonotum and scutellum with shallow, widely spaced punctures, interspaces micropunctured but shiny; scutellum evenly convex, fairly steeply raised above mesoscutum, separated from it by narrow, deep, shiny transverse depression, posteriorly widely rounded and only minimally indented. Tegula (Fig. 32) longer than broad, posteriorly narrowed, incurved and upturned. Middle tibia with one spur; shorter hind tibial spur simple (not bifid); claws of all legs minutely toothed.

Gastral terga with widely spaced, shallow punctures, interspaces micropunctured but shiny.

*Male.*—Coloration similar to that of female but differing in the presence of yellowish-white transverse streaks on the pronotum (mediodorsally and on humeral angles) and of a minute spot on the prepectus, and in the absence of any markings of this colour on the metasoma.

Length 6.3 mm; length of front wing 4.9 mm; hamuli 8.

Structurally similar to the female.

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995, (F. W., S. K. and R. W. Gess), (on small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond., Zygophyllaceae) [AMG]. Paratypes (26 females, 1 male): Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995, (F. W., S. K. and R.

W. Gess), 8 females (2 on small cream flowers of *Zygophyllum prismatocarpum*; 4 on yellow flowers of *Zygophyllum* sp.); 1 on yellow flowers of Asteraceae; 1 in purplish-violet flowers of *Wahlenbergia* sp., Campanulaceae); Richtersveld National Park, bet[ween] hills, at 28.08S, 17.01E and at 28.10S, 17.02E, NW Koeroegabvlakte, 14.ix.1996 (F. W., S. K. and R. W. Gess) 3 females (one from first locality, two from second locality, all on yellow flowers of *Zygophyllum meyeri* Sond.); Namaqualand, Richtersveld National Park, 1.5 km from Helskloof Gate (28.18S, 16.57E), 8 and 9.ix.1996 (F. W., S. K. and R. W. Gess) 15 females, 1 male (all females on white flowers of *Pelargonium klinghardtense* Knuth, Geraniaceae; male on ground) [all AMG].

*Discussion.*—Females of *mixtoides* differ from those of *mixta* in possessing yellowish-white transverse posterior bands on the abdominal terga and males differ in lacking any yellow markings on the clypeus and supraclypeus; both sexes, when viewed with the naked eye from above, differ in the blacker and more shiny appearance of the thorax. Under magnification this difference is seen to be due to *mixtoides* having smaller, shallower and less close punctures separated by smoother far less densely micropunctured interspaces. The scutellum is shorter, posteriorly much more widely rounded and only minutely indented. The tegula is of different shape and much longer (compare Figs. 31 and 32).

*Etymology.*—The name *mixtoides* serves to draw attention to the general similarity of this species to *M. mixta* Richards.

## Masarina namaqua Gess, sp. nov.

*Female.*—Black. The following are yellowish-white: small frontal spot near eyes above ocular sinus; narrow streak at top of tempora behind eyes, and occasionally lateral streaks on clypeus. The following are various shades of reddish-brown: labrum, lamellate ventral margin of clypeus; mandible, underside of flagellomeres V–

IX or X, tegula except for inner margin; occasionally propodeal angles; terga I–IV mostly and tergum V laterally; sterna to various degrees (only I and II or I–III and hind margins of IV, V and even VI); apices of femora, and all tibiae and tarsi. Wings subhyaline.

Length 6.8–7.9 mm (average of 9: 7.4 mm); length of front wing 4.8–5.2 mm (average of 12: 5.1 mm); hamuli 7–9.

Clypeus steeply raised from sides; disc 1.3–1.4 × broader than long (measured between lateral angles and from base to bottom of ventral emargination), flattened, only minimally depressed medially; ventral and lateral margins markedly lamellate; ventro-lateral corners smoothly rounded, obtuse; ventral margin shallowly and widely emarginate, edentate; integument moderately coarsely and closely punctured (except medially over proximal three quarters where punctures are few and interspaces are wide, smooth and shiny), with punctures tending to run longitudinally. Frons slightly depressed medially, with faintly impressed median line; frons and vertex moderately coarsely and closely punctured throughout (except sometimes medially on frons); preoccipital carina developed only dorsally, narrowly lamellate. Mandible over basal two-thirds with lamellate upper margin, smoothly widened and strongly outwardly bent. Antenna simple; flagellomeres somewhat depressed (therefore oval rather than round in cross section), gradually thickened, not forming distinct club; eighth flagellomere only slightly wider than scape, less than twice width of first two flagellomeres.

Thorax shiny under low magnification; mesoscutum and scutellum with punctures coarse but shallow and diffuse, with interspaces only moderately closely and not very noticeably micropunctured. Scutellum with disc bun-shaped, smoothly convex, anteriorly falling smoothly but steeply to meet mesoscutum (furrow between them smooth, narrow and deep),

posteriorly falling smoothly but steeply, slightly overhanging metanotum; lateral wings of scutellum produced, overhanging and therefore covering metanotum laterally; hind and lateral margins of scutellum forming an almost parabolic curve except that in the middle (that is posteriorly) it is slightly flattened or, in some specimens, even very weakly indented. Angles of propodeum slightly tuberculate above.

Front tarsomeres II–IV produced into inwardly directed lobes, that of II short, those of III and IV much longer, flattened, narrow and subparallel-sided, that of IV reaching beyond middle of V; middle tibia with one spur; shorter hind tibial spur simple (not bifid); claws of all legs minutely toothed. Tegula 1.4 × as long as wide, outer margin of its posterior half describing a mostly flat arc to the inner posterior angle (that is tegula markedly narrowed posteriorly).

Gastral terga with moderately sized shallow punctures, moderately spaced anteriorly, closer posteriorly.

*Male.*—(Figs. 25–27 and 33). Black. The following are yellowish-white: disc of clypeus; large sub-quadrate supraclypeal marking on face; entire labrum; mandible; entire underside of scape; variously sized spot in ocular sinus; narrow streak at top of tempora behind eyes; elongate transverse streak on humeral angles; occasionally spot or elongate transverse streak medially on pronotal dorsum; streaks on dorsal aspects of tibiae and front tarsomeres. The following are various shades of reddish-brown: underside of flagellomeres IV–X; tegula (except broad inner margin); terga I–III or I–IV generally, and tergum V and anterior sterna partially and to various degrees; apices of femora, and all tibiae (partially) and tarsi (partially). Wings subhyaline.

Length 5.8–6.3 mm (average of 8: 6.0 mm); length of front wing 4.1–4.5 mm (average of 8: 4.3 mm); hamuli 6–8.

Head (Fig. 25). Clypeus steeply raised from sides; disc 1.2–1.3 × broader than
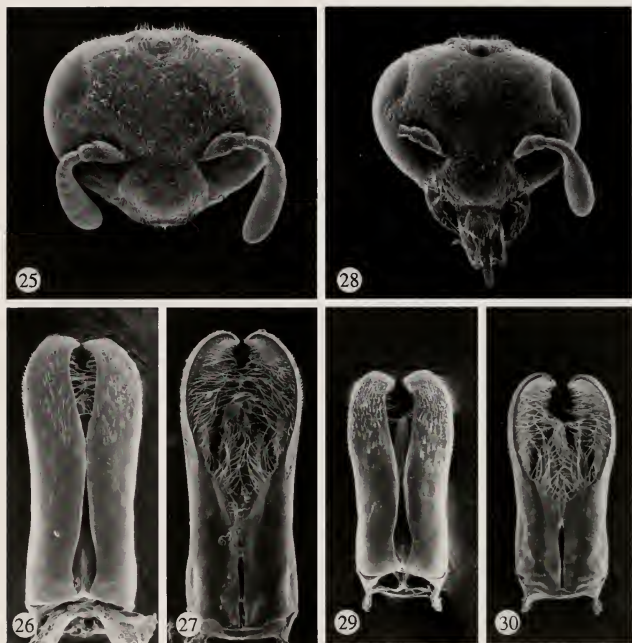
Figs. 25–30. *Masarina namaqua*. 25, Frontal view of head of male (× 25). 26, Dorsal view of genitalia of male (× 50). 27, Ventral view of genitalia of male (× 50). 28–30. *Masarina parvula*. 28, Frontal view of head of male (× 25). 29, Dorsal view of genitalia of male (× 50). 30, Ventral view of genitalia of male (× 50).

long (measured between lateral angles and from base to bottom of ventral emargination), smoothly convex (not depressed); ventral margin weakly bilobed and shallowly and widely emarginate, edentate, broadly lamellate.

Tergum VII rounded to subtruncate at apex. Proximal sterna unmodified; sterna VII + VIII trilobed apically with lateral lobes large and median lobe small.

Genitalia (Figs. 26 and 27).

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess) [AMG]. Paratypes (11 females, 8 males): Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess), 1 male (Malaise trap) [AMG]; Namaqualand, Klipfontein (29.51S, 12.47E), 14.x.1989 (F. W. and S. K. Gess),
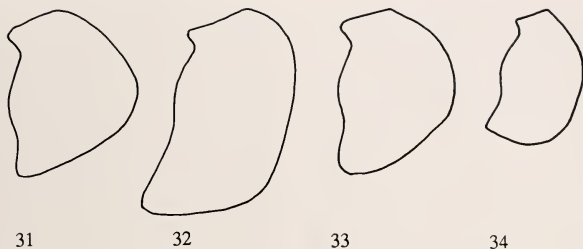
Figs. 31–34. Right tegula. 31. *Masarina mixta* (× 60). 32. *Masarina mixtoides* (× 60). 33. *Masarina namaqua* (× 60). 34. *Masarina parvula* (× 60).

1 female (visiting flowers of *Wahlenbergia* cf. *prostrata*) [AMG]; same locality and date (D. W. Gess), 2 females [AMG]; Namaqualand, Kamieskroon, Sors Sors, 11.x.1994 (F. W. and S. K. Gess), 1 female (on/in light violet flowers of *Wahlenbergia oxyphylla* A.DC. Campanulaceae) [AMG]; Namaqualand, Farm Arkoep, 6 km N Kamieskroon (30.19S, 17.56E), 1–2.x.1990 (C. D. Eardley), 7 females and 7 males [NCP].

*Discussion.*—In both sexes the species is somewhat reminiscent of *C. mixta* Richards but may immediately be distinguished by the different shape of the tegula (compare Figs. 31 and 33) and by differences in the puncturation of the thorax.

*Etymology.*—The name *namaqua*, a noun in apposition to the generic name, is derived from the Namaqua people of Namaqualand and refers to the provenance of the specimens.

### Masarina parvula Gess, sp. nov.

*Female.*—Black. The following are yellowish-white: minute frontal spot near eyes above ocular sinus and a narrow streak at top of tempora behind eyes; streaks on dorsal aspects of front tibia, basal half of middle tibia and basal quarter of hind tibia. The following are various shades of reddish-brown: underside of fla-

gellomeres IV–IX, mandible (if not dark brown); outer margin of tegula; terga I–IV generally and tergum V laterally; sterna to various degrees (mainly hind margins). Legs other than parts mentioned and most of sterna dark brown. Wings subhyaline.

Length 5.8 mm; length of front wing 4.0 mm; hamuli 7.

Clypeus moderately raised from sides; disc 1.6–1.7 × broader than long (measured between lateral angles and from base to bottom of ventral emargination), flattened, only minimally depressed medially; ventral and lateral margins weakly lamellate; ventro-lateral corners narrowly rounded, almost right-angular; ventral margin widely and shallowly emarginate, edentate; integument moderately coarsely and closely punctured (except medially over proximal three quarters where punctures are few and interspaces are wide, smooth, shiny), punctures tending to run longitudinally. Frons somewhat depressed medially, with distinct, finely impressed median line; moderately coarsely and closely punctured laterally, more finely so medially and ventrally, impunctate and shiny on either side of median impressed line; vertex punctured like adjacent parts of frons; preoccipital carina developed only dorsally, narrowly lamellate. Mandi-

ble over basal two-thirds with upper margin lamellate, smoothly widened and strongly outwardly bent. Antenna progressively thickened, especially from flagellomere IV onwards; flagellomere VIII markedly wider than scape and slightly more than twice width of flagellomeres I and II.

Thorax almost matt under low magnification; mesoscutum and scutellum with punctures only moderately coarse but well defined, interspaces very closely and noticeably micropunctured. Scutellum with disc bun-shaped, smoothly convex, anteriorly falling smoothly but steeply to meet mesoscutum (furrow between them smooth, narrow and deep), posteriorly falling smoothly but steeply and slightly overhanging metanotum; lateral wings of scutellum produced, overhanging and therefore covering metanotum laterally; hind and lateral margins of scutellum forming an almost parabolic curve except that in the middle (that is posteriorly) it is slightly flattened or, in some specimens, is even very weakly indented. Angles of propodeum slightly tuberculate above.

Front tarsus with tarsomeres II–IV produced into inwardly directed lobes, that of II very short, those of III and IV short, somewhat flattened, bow-sided, that of IV not attaining middle of V; middle tibia with one spur; shorter hind tibial spur simple (not bifid); all claws distinctly dentate.

Tegula 1.5 × as long as wide, outer margin of its posterior half describing a quarter circle to inner posterior angle (that is, tegula evenly rounded and not at all narrowed posteriorly).

Gastral terga with moderately sized and spaced punctures.

*Male.*—(Figs. 28–30 and 34). Black. The following are yellowish-white: disc of clypeus; occasionally narrow transverse marking above fronto-clypeal suture; sometimes labrum (if not testaceous); mandible (except apex); small spot on underside of scape; small spot in ocular si-

nus; narrow streak at top of tempora behind eyes; streaks on dorsal aspects of front and middle tibiae and front tarsomeres; basal third to half of hind tibia. The following are various shades of reddish-brown: underside of flagellomeres VI–IX (or fewer); tegula (except for broad inner margin); terga I–IV generally, V or V and VI occasionally; anterior sterna partially and to various degrees. Legs other than parts mentioned and most of sterna dark brown. Wings subhyaline.

Length 4.8–5.5 mm (average of 9: 5.3 mm); length of front wing 3.5–3.8 mm (average of 7: 3.7 mm); hamuli 5–7.

Head (Fig. 28). Clypeus steeply raised from sides; disc 1.4–1.5 × broader than long (measured between lateral angles and from base to bottom of ventral emargination), smoothly convex (not depressed); ventral margin weakly bilobed and widely emarginate, edentate, broadly lamellate. Tergum VII rounded to subtruncate. Proximal sterna unmodified; sterna VII + VIII trilobed apically, lateral lobes large and median lobe small.

Genitalia (Figs. 29 and 30).

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess) (Malaise trap) [AMG]. Paratypes (2 females, 9 males): Cape Province: Namaqualand, Springbok, Hester Malan [now Goegap] Nature Res[erve], 15–21.x.1987 (F. W. and S. K. Gess) 3 males (2 Malaise trap; 1 on ground); same locality, 10–12.x.1988 (F. W. and S. K. Gess), 2 males (in flowers of *Wahlenbergia* sp.); same locality, 10–11.x.1989 (F. W. and S. K. Gess), 1 male; same locality and date (D. W. Gess), 3 males; Namaqualand, Kamieskroon, Sors Sors, 11.x.1994 (F. W. and S. K. Gess), 1 female (on/in light violet flowers of *Wahlenbergia oxyphylla* A. DC. (Campanulaceae); Namaqualand, Sors Sors/Taaibos-kraal (30.08/9S, 18.01E), 3.x.1995 (F. W., S. K. and R. W. Gess), 1 female (in violet flowers of *Wahlenbergia* sp.) [all AMG].

*Discussion.*—Similar, though somewhat smaller, to *namaqua*, sharing with it and *mixta* a black thorax (including the scutellum) and an abdomen with at least the anterior segments reddish-brown but lacking yellow markings. It differs from both in the shape of the tegula (compare Figs. 31, 33 and 34), and from *namaqua* in the proportions of the clypeus, in the puncturation of the thorax, in the presence of yellow streaks on the tibiae and, in the male, in the less extensive yellow markings on the head and scape.

*Etymology.*—The name *parvula*, a Latin female adjective meaning rather small refers to the size of the species.

### Masarina peliostomi Gess, sp. nov.

*Female.*—(Figs. 35 and 36). Black. The following are pale yellowish-white: very small crescent-shaped mark occupying very bottom of ocular sinus, variably sized streak at top of tempora behind eyes, narrow streak on humeral angles, very occasionally small spot on upper part of prepectus, postero-dorsal angles of pronotum, sometimes posterior third or less of tegula, lateral margins of scutellum, propodeal angles, narrow but laterally slightly widened transverse posterior bands on terga I–V (that on tergum I sometimes interrupted medially and that on V frequently fragmented into a number of small spots), occasionally a small spot apically on front tibia. The following are various shades of reddish-brown: underside of flagellomeres VI–IX, mandible medially, tibiae and tarsi of all legs (except sometimes yellow spots proximally on tibiae), translucent spot on tegula. Wings light brown.

Length 6.3–6.8 mm (average of 5: 6.6 mm); length of front wing 4.1–4.2 mm; hamuli 8–12. Length of tongue 4.9–5.0 mm (based on 5 specimens); average tongue length: average body length = 0.75.

Head (Fig. 35) 1.25 × wider than long. Clypeus steeply raised from sides; disc 1.7 × wider than long, evenly convex; ventral margin widely and smoothly emarginate, edentate, lamellate; surface coarsely reticulate punctate. Frons on each side with pronounced smooth subtransverse carina; the two carinae laterally downcurved before reaching middle of upper part of eyes and ending near upper margin of ocular sinuses, together for most of their length forming an extremely flat V but each on approaching midline strongly downcurved to converge with the other and to meet in a very narrow V; surface sculpturing below carinae like that of clypeus, above carinae composed of larger and sparser punctures separated by shiny interspaces; vertex and tempora more closely and finely sculptured; preoccipital carina short, hardly exceeding distance between outer margins of posterior ocelli, very narrow and not at all lamellately produced.

Thorax (Fig. 36). Pronotum with dorsum similarly punctured to upper part of frons, shiny, contrasting with finely and closely punctured, dull lateral aspects. Mesoscutum impunctate and very shiny (except for a few sparse moderately sized punctures on anterior and lateral borders and a microsculptured area postero-medially), with a fine but clear median impression in anterior half and very clear, fine parapsidal furrows in posterior half. Scutellum microsculptured, slightly raised above mesoscutum, gently convex, posteriorly rounded, minimally depressed postero-medially. Propodeum microsculptured, with angles well developed but rounded. Middle tibia with two spurs; shorter spur of hind tibia simple (not bifid); claws of all legs minutely toothed.

Gastral terga microsculptured and with some sparse small punctures; tergum VI smoothly, transversely depressed in apical half.

*Male.*—(Figs. 37–39). Coloration very similar to that of female with none of the males examined having any additional pale markings on the head.

Length 5.6–6.9 mm (average of 5: 6.2
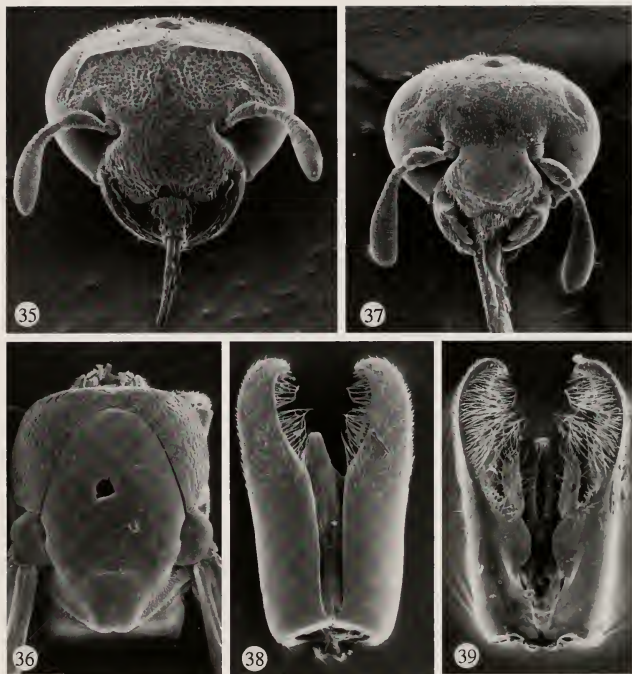
Figs. 35–39. *Masarina peliostomi*. 35, Frontal view of head of female (× 25). 36, Dorsal view of mesosoma of female (× 20). 37, Frontal view of head of male (× 25). 38, Dorsal view of genitalia of male (× 60). 39, Ventral view of genitalia of male (× 60).

mm); length of front wing 3.7–3.9 mm (average of 5: 3.8 mm); hamuli 8–9. Length of tongue 4.3–4.6 mm (average of 5: 4.4 mm); average tongue length: average body length = 0.71.

Structurally similar to female but differing in the following respects. Frons (Fig. 37) without carinae; sculpturing undiffer-

entiated, consisting throughout of small close punctures with shiny interspaces. Mesoscutum though shiny, sparsely punctate, punctures small to moderately sized. Tergum VII with hind margin more broadly rounded than tergum VI of female.

Genitalia (Figs. 38 and 39).

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995, (F. W., S. K. and R. W. Gess) (in deep violet flowers of *Peliostomum* sp., Scrophulariaceae) [AMG]. Paratypes (49 females, 7 males): Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17–21 and 24.ix.1995, (F. W., S. K. and R. W. Gess), 48 females, 5 males (all in deep violet flowers of *Peliostomum* sp.); same locality, 6.ix.1996 (F. W., S. K. and R. W. Gess), 2 males (1 in deep purple flowers of *Peliostomum* sp.; 1 on ground nr same) [AMG].

*Discussion.*—*M. peliostomi* differs from all other species of the genus in the possession of frontal carinae in the female and in the largely impunctate and very shiny mesoscutum in both sexes.

*Etymology.*—The name *peliostomi*, genitive singular, is formed from the generic name of the plant, *Peliostomum* sp. (Scrophulariaceae), in the flowers of which the wasp was found foraging for nectar or nectar and pollen.

**Masarina tylecodoni** Gess, sp. nov.

*Female.*—(Fig. 40). Black. The following are yellowish-white: usually small to minute spot on either side of frons, narrow streak at top of tempora behind eyes, very occasionally narrow interrupted transverse band medially on pronotal dorsum, usually small streak on humeral angles, small spots (sometimes extinguished) postero-laterally on tergite I, narrow entire or medially interrupted transverse posterior bands on terga II–IV (those on terga II and III laterally expanded), occasionally narrow transverse posterior band medially on tergum V. The following are reddish-brown: terga I and II to a variable extent, tegula to variable extent, knees of all legs, and front tibia and front tarsus to variable extent. Wings light brown.

Length 7.7–8.8 mm (average of 6: 8.3 mm); length of front wing 5.5–5.8 mm (average of 6: 5.7 mm); hamuli 10. Length of tongue 6.6–6.8 mm (average of 6: 6.7 mm); average tongue length: average body length = 0.80.

Head (Fig. 40) elongate, 1.1 × wider than long, in profile with frons and clypeus forming two distinct arcs—that of frons low and that of clypeus higher and nose-like. Antenna and mandible elongate. Clypeus gradually and evenly raised from sides, evenly but strongly convex transversely, elongate, 1.38 × wider than long; ventral margin widely emarginate, edentate, lamellate and somewhat upturned (especially at narrowly rounded sub-rectangular lateral angles); integument with large, shallow punctures separated by wide, smooth, shiny interspaces, and bearing fairly long, coarse, curved setae. Frons almost flat, barely convex transversely, with sculpture and setation similar to that of clypeus; vertex markedly flattened; preoccipital carina very pronounced, lamellate, extending over a distance = 0.9 × interocular distance (measured across ocelli), minimally curved over most of its length but abruptly inturned at its ends (viewed from above, the tempora appear to bulge out on either side of the carina).

Dorsal surface of pronotum, mesoscutum and scutellum with large shallow punctures (those on anterior half of mesoscutum particularly large and widely spaced), interspaces smooth and shiny, except on posterior third of mesoscutum and on scutellum where closely and finely micropunctured. Setation on pronotum and on adjacent parts of mesoscutum like that on head. Median line on anterior two-thirds of mesoscutum and parapsidal furrows fine but distinct. Scutellum evenly convex, fairly steeply but smoothly raised above mesoscutum and separated from it by a narrow, deep, shiny transverse depression, posteriorly weakly emarginate. Propodeum with angles strongly produced. Middle tibia with single bifid spur;

Figs. 40–43. *Masarina tylecodoni.* 40, Frontal view of head of female (× 20). 41, Frontal view of head of male (× 20). 42, Dorsal view of genitalia of male (× 50). 43, Ventral view of genitalia of male (× 50).

shorter spur of hind tibia bifid; all claws distinctly toothed.

Gastral terga with moderately sized shallow punctures and micropunctured interspaces; tergum VI slightly transversely depressed in apical half.

*Male.*—(Figs. 41–43). Similarly coloured to the female. Black. The following are yellowish-white: mandible to variable extent,

markings on clypeus (varying from almost entire disc or large central spot and smaller spot on each antero-lateral lobe, through reduction of these spots to their total extinction), narrow streak at top of tempora behind eyes; transverse band (sometimes interrupted or extinguished) medially on pronotal dorsum, humeral angles, narrow transverse streaks postero-

laterally on terga II–V (occasionally II–IV or II–VI). The following are reddish-brown: terga I and II to variable extent, tegula to variable extent, all knees, and front tibia and front tarsus to variable extent. Wings light brown.

Length 6.1–8.8 mm (average of 5: 7.6 mm); length of front wing 4.3–5.9 mm (average of 5: 5.3 mm); hamuli 10. Length of tongue 5.0–7.5 mm (average of 5: 6.4 mm); average tongue length: average body length = 0.84.

Structurally similar to female but differing in the following respects. Antenna even more elongate, equalling length of head (Fig. 41) (measured from vertex to middle of ventral emargination of clypeus). Median impression on frons below anterior ocellus much deeper (barely indicated in female). Tergum VII with hind margin more broadly rounded than tergum VI of female, not transversely depressed. Preoccipital carina not abruptly inturned laterally (viewed from above, the tempora do not appear to bulge out on either side of the carina).

Genitalia (Figs. 42 and 43).

*Material examined.*—Holotype: female. Cape Province: Namaqualand, Richtersveld National Park, Koeroegabvlakte (28.11S, 17.03E), 17-21 and 24.ix.1995, (F. W., S. K. and R. W. Gess) (in yellow flowers of *Tylecodon hallii* (Tölken) Tölken, Crassulaceae) [AMG]. Paratypes (22 females, 18 males): same data as holotype [AMG].

*Discussion.*—A very distinct species characterized by the elongate head and antennae, the nose-like clypeus, and the strongly produced propodeal angles.

*Etymology.*—The name *tylecodoni*, genitive singular, is formed from the generic name of the plant, *Tylecodon hallii* (Tölken) Tölken, (Crassulaceae), in the flowers of which the wasp was found foraging for nectar or nectar and pollen. *T. hallii* is endemic to the northern Richtersveld and the adjacent part of southern Namibia.

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KEY TO SPECIES OF *MASARINA* RICHARDS

Note that the female of *ceres* is as yet unknown and has been included in the key using presumed characters for which reason it is given in [ ].

FEMALES

X1. Head, mandibles and antennae elongated; clypeus markedly convex transversely, raised, bulbous and nose-like . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *tylecodoni* Gess sp. nov.
– Head, mandibles and antennae not as above; clypeus either longitudinally depressed or, if convex, not raised, bulbous and nose-like . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Metasoma black with white or yellow markings . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
– Metasoma partially or wholly red, with or without white or yellow markings . . . . . . . . . . 5

3. Frons with subtransverse, medially downcurved and converging carinae; clypeus convex; mesoscutum in greater part impunctate and very shiny; middle tibia with two spurs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *peliostomi* Gess sp. nov.
– Frons lacking carinae; clypeus longitudinally depressed; mesoscutum closely punctured; middle tibia with one or two spurs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4. Clypeus and adjacent part of frons markedly longitudinally aciculate; middle tibia with one spur . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *strucki* Gess
– [Clypeus and adjacent part of frons moderately coarsely punctured; middle tibia with two spurs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *ceres* Gess sp. nov.

5. Large (8.5–11.5 mm) species with longitudinally depressed clypeus and with red, pyriform tegulae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
– Small to medium (5.8–8.2 mm) species with convex clypeus and variously shaped red or black tegulae (if clypeus is weakly longitudinally depressed then tegula is black, broad and triangular) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

6.   Frons on each side above ocular sinus with a large yellow spot; metasoma with yellow markings in addition to reddish ones; puncturation of head, thorax and metasoma coarse; propodeal angles tuberculate; scutellum with a narrow smooth anterior furrow . . . . . . .
     . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***familiaris*** Richards
–    Frons on each side above ocular sinus with a small to minute reddish spot; metasoma with reddish markings only; puncturation of head, thorax and metasoma moderate; propodeal angles almost rounded. Scutellum with a wide coarsely crenulate anterior furrow
     . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .
     . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***hyalinipennis*** Richards
7.   Terga I and II predominently red, contrasting with predominently black terga III–VI; frons immaculate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
–    Terga I–V predominently red; frons on each side above ocular sinus with a small yellowish-white spot . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
8.   Terga II–IV without any yellowish-white markings; tegula short and broad, as in Fig. 31 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***mixta*** Richards
–    Terga II–IV with variously developed yellowish-white transverse posterior bands; tegula elongate, as in Fig. 32 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***mixtoides*** Gess sp. nov.
9.   Tibia and tarsus of all legs light reddish brown; tegula markedly narrowed posteriorly, as in Fig. 33; clypeal disc 1.3–1.4 × broader than long . . . . . . . . . . . ***namaqua*** Gess sp. nov.
–    Tibia and tarsus of all legs dark brown with variously developed yellowish white dorsal streaks; tegula evenly rounded posteriorly, as in Fig. 34; clypeal disc 1.6–1.7 × broader than long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***parvula*** Gess sp. nov.

## MALES

1.   Head, mandibles and antennae elongated; clypeus markedly convex transversely, raised, bulbous and nose-like . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***tylecodoni*** Gess sp. nov.
–    Head, mandibles and antennae not as above; clypeus either longitudinally depressed or, if convex, not raised, bulbous and nose-like. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2.   Metasoma black with white or yellow markings . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
–    Metasoma partially or wholly red, with (*familiaris* only) or without white or yellow markings . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
3.   Clypeus and adjacent part of frons convex; mesoscutum shiny, sparsely punctate; tegula black; middle tibia with two spurs . . . . . . . . . . . . . . . . . . . . . . . . . ***peliostomi*** Gess sp. nov.
–    Clypeus and adjacent part of frons longitudinally depressed; mesoscutum closely punctate; tegula yellow or yellowish-white; middle tibia with one or two spurs. . . . . . . . . . . . . . . . . . . 4
4.   Clypeus and adjacent part of frons markedly longitudinally aciculate; scape, mandible, labrum, clypeus and face black; middle tibia with one spur. . . . . . . . . . . . . . . ***strucki*** Gess
–    Clypeus and adjacent part of frons moderately coarsely punctured; scape, mandible, labrum, clypeus, supraclypeal marking and ocular sinus yellow; middle tibia with two spurs. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***ceres*** Gess sp. nov.
5.   Large (8.5–11.5 mm) species with longitudinally depressed clypeus and with red, pyriform tegulae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
–    Small to medium (5.8–8.2 mm) species with convex clypeus and variously shaped red or black tegulae (if clypeus is weakly longitudinally depressed then tegula is black, broad and triangular). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
6.   Frons on each side above ocular sinus with a large yellow spot; clypeal disc and supraclypeal marking yellow; metasoma with yellow markings in addition to reddish ones; puncturation of head, thorax and metasoma coarse; propodeal angles tuberculate; scutellum with a narrow smooth anterior furrow; sternum II unmodified; tergum VII emarginate apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***familiaris*** Richards
–    Frons on each side above ocular sinus immaculate; clypeal disc and supraclypeal marking pure white; metasoma with reddish markings only; puncturation of head, thorax and metasoma moderate; propodeal angles almost rounded; scutellum with a wide coarsely cren-

ulate anterior furrow; sternum II with a bituberculate prominence; tergum VII rounded
apically . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **hyalinipennis** Richards
7. Terga I, II (and sometimes III) predominently red, contrasting with terga III (or VI)–VII
which are predominently black; scape entirely black; mandible, labrum and clypeal disc
either black or yellowish-white . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
– Terga I–IV (at least) predominently red, not contrasting with terga V–VII but rather grad-
ing from red to reddish-brown to blackish; scape with yellow mark; mandible, labrum and
clypeal disc always yellowish-white . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
8. Mandible, labrum, clypeal disc and broad supraclypeal marking yellowish-white; tegula
short and broad, as in Fig. 31 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**mixta** Richards
– Mandible, labrum, clypeal disc and supraclypeus black; tegula elongate, as in Fig. 32. . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **mixtoides** Gess sp. nov.
9. Frons with large, sub-quadrate, yellowish-white supraclypeal marking; entire hind tibia
and basitarsus pale; tegula markedly narrowed posteriorly, as in Fig. 33; clypeal disc 1.2–
1.3 × broader than long. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **namaqua** Gess sp. nov.
– Frons with at most a narrow, transverse, yellowish-white supraclypeal marking; only prox-
imal half of hind tibia pale; tegula evenly rounded posteriorly, as in Fig. 34; clypeal disc
1.4–1.5 × broader than long . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **parvula** Gess sp. nov.

## ACKNOWLEDGMENTS

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# Update on the Flower Associations of Southern African Masarinae with Notes on the Nesting of *Masarina strucki* Gess and *Celonites gariepensis* Gess (Hymenoptera: Vespidae: Masarinae)

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*Abstract.*—Flower visiting records are presented for seven newly described species of Masarinae from the Richtersveld and for *Masarina strucki* Gess. The potential of these wasps as pollinators is discussed. *Celonites gariepensis* Gess and *Masarina peliostomi* Gess are associated with *Peliostomum* and the former, at least, with *Aptosimum* (Scrophulariaceae), a preference shared with four other species of *Celonites*. *Masarina tylecodoni* Gess appears to be restricted to *Tylecodon hallii* (Tölken) Tölken (Crassulaceae) and is apparently the first recorded insect visitor to a *Tylecodon* species. *Jugurtia codoni* Gess is an abundant visitor to *Codon royenii* L. of the family Hydrophyllaceae, one of the preferred forage plant families of the North American masarines but otherwise not known to be visited by masarines. Records for *Masarina strucki* from a wide range of localities confirm its, for a masarine, unusual association with *Hermannia* spp. (Sterculiaceae). In the Richtersveld *Zygophyllum* spp. (Zygophyllaceae) were being visited, though not apparently favoured, by *Ceramius brevitarsis* Gess, two species of *Jugurtia*, *J. codoni* Gess and *J. koeroegabensis* Gess, and *Masarina mixtoides* Gess. These records are of interest as *Zygophyllum* has only otherwise been shown to attract one other species of Masarinae, a *Quartinioides* species, in the Central Namib Desert. Some aspects of the nesting of *C. gariepensis*, which constructs aerial mud cells, and of *M. strucki*, which nests in the ground, are presented and discussed.

Gess (S.K. 1996) presented a synthesis of the available data on the nesting and flower visiting of the Masarinae in southern Africa. Recent fieldwork in southwestern southern Africa, most notably in the previously under collected Richtersveld National Park in the extreme north of Namaqualand (Fig. 1) (16–24.ix.1995 and 5–18.ix.1996), has resulted in the discovery of new species, additional flower associations of particular interest, and a nest each of *Masarina strucki* Gess and *Celonites gariepensis* Gess. Descriptions of the new species are given in Gess (F.W. 1997) and the flower visiting and nesting data are presented and discussed in the present paper.

Some other masarines collected in the Richtersveld National Park, all extending the known distributions for the species, are: *Ceramius cerceriformis* Saussure, four species of *Jugurtia*, *J. braunsi* (Schulthess),

*J. braunsiella* (Schulthess), *J. calcarata* Richards, and *J. duplicata* Richards, two species of *Celonites*, *C. clypeatus* Richards and *C. peliostomi* Gess. Flower visiting records for these species of *Jugurtia* and *Celonites* confirm previously recorded flower family choices (Gess, S.K. 1996).

## Celonites Latreille

### Celonites gariepensis Gess

*Distribution.*—*Celonites gariepensis* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

*Flower visiting.*—On the Koeroegabvlakte (28.11S, 17.03E) (Figs. 2–5) *C. gariepensis* females and males were foraging only on flowers of a species of *Peliostomum* (Scrophulariaceae), together with *Celonites clypeatus* Brauns, *Celonites peliostomi* Gess (Fig. 6) and *Masarina peliostomi* Gess (Fig.
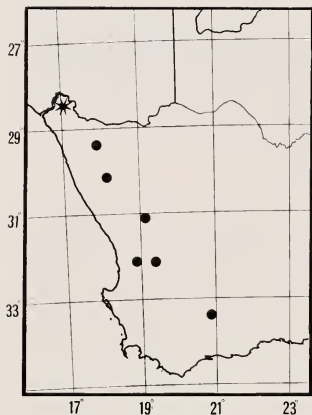
Figs. 1. Map of southwestern southern Africa. Dots mark areas from which *Masarina strucki* Gess has been collected. Star marks the position of the Richtersveld National Park.

7), and on *Aptosimum spinescens* (Thunb.) Weber (Scrophulariaceae), together with *C. peliostomi*. The plants were growing on the banks of a dry gravelly drainage channel (Figs. 4 and 5). *Celonites clypeatus* and *C. peliostomi* together with *Celonites andrei* Brauns and *Celonites tumidiscutellatus* Gess have previously been shown to be associated solely with *Peliostomum* and *Aptosimum* (Scrophulariaceae). Taking into account in addition size fit and behaviour, these species are considered to be, in the areas where they occur, the most dependable potential pollinators of the species which they visit (Gess and Gess 1989; Gess, S.K. 1996; Gess, F.W. 1997). Being of similar size and behaviour, *C. gariepensis* is considered to be an additional potential pollinator of the present two species of *Peliostomum* and *Aptosimum* visited by it in the Richtersveld.

The specific identity of the *Peliostomum*

species was not established. The much branched, rounded shrublets were up to 30 cm in height. The thicker stems, like those of *Peliostomum leucorrhizum* E. Mey. ex Benth., were strikingly pale. On the other hand the flowers were, in shape and markings, similar to those of *Peliostomum virgatum* E. Mey. ex Benth. (compare Fig. 7 and Gess, S.K. 1996, Fig. 24) not to those of *P. leucorrhizum* in which the narrow basal part of the tube is purple. However, unlike *P. virgatum* but like *P. leucorrhizum* the stems, leaves and flowers were not sticky.

*Nesting area.*—Only one nest of *C. gariepensis* was located. This nest was sited on the underside of a jutting edge in a rock crevice near the base of a slope in Paradise Kloof (28.19S, 17.01E) (Figs. 8–10).

*Provision.*—The provision was pale grey, very moist but, having a papillate surface (Fig. 12), barely touched the cell walls.

*Description of nest.*—The nest, which was still under construction, consisted of three earthen cells attached longitudinally to their horizontal rock substrate. Two cells were complete and attached to each other longitudinally and the third incomplete cell was being constructed with its closed end abutting the seal of one of the completed cells. The cells were 9 mm long and 4 mm wide at mid-length. Characteristic of *Celonites* cells is the distinct "fish scale" pattern on the outer surface of the constructed earthen-cell (Fig. 11) and the seal constructed just inside the cell opening (Gess, S.K. 1996). Like the cells of *Celonites abbreviatus* (Villers) described by Bellman (1984) the cell walls were incomplete, the cells being open to the substrate.

*Nest construction.*—As *C. gariepensis* was not found at water it is likely that, like other *Celonites* species, it does not use water in cell construction. The hard brittle nature of the cell walls suggests that nectar is probably the bonding agent as has been suggested for other *Celonites* species (Gess, S.K. 1996).
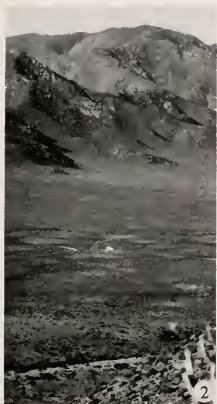
Figs. 2–5. Koeroegabvlakte, Richtersveld National Park. 2, looking north east from a hill, the *Masarina tylecodoni* Gess site, on the west flank of the flats. 3, the flats. 4, dry drainage channel, *Zygophyllum prismatocarpum* E. Mey ex Sond (Zygophyllaceae) in foreground. 5, Dry drainage channel to the west of the flats from above.

## Ceramius Latreille

## Ceramius brevitarsis Gess

*Distribution.*—*Ceramius brevitarsis* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997). It belongs in *Ceramius* Group 2A together with *Ceramius cerceriformis* Saussure and *Ceramius perin-* *gueyi* Brauns. It is the most northern Namaqualand species of *Ceramius* having been found in the hills in the north of the Richtersveld National Park. The only other species of *Ceramius* recorded from the Park as yet is the relatively widely distributed (Gess, S.K. 1996) *C. cerceriformis* which was recorded from the hills to the

Figs. 6 and 7. *Peliostomum* sp. (Scrophulariaceae). 6, *Celonites peliostomi* Gess preparing to enter flower. 7, *Masarina peliostomi* Gess entering flower (length of flower approximately 20 mm).

south. To the north of the Richtersveld National Park there is a surprising hiatus in the known distribution of *Ceramius*, no species having been recorded between there and northern Namibia whence a single species from Group 4, *Ceramius damarinus* Turner, was described by Turner (1935) from females and a male from Ongandjera (1923) and a male from Kamanyab (1925), part of material collected by the staff of the South African Museum (Gess, F.W. 1965). Recently this species was recorded flying abundantly 10.3 km

NW on the road from Okaukuejo to Okondeka, 3.iv.1996, by D.W. and G.T. Gess. A sample of twelve females was taken.

*Water visiting.*—*C. brevitarsis* was found to be abundant at a trickle of water crossing the road in a rocky pass (28.10S, 17.02E) immediately to the north of Koeroegabvlakte. Whilst imbibing water the wasps stood on wet sand or rock at the edge of the water. One further female was observed imbibing water from the edge of an isolated pool of water in a hollow on a steeply sloping rock. In this instance the surface on which the wasp stood was dry, indicating that water is imbibed directly from the pool and not from wet sand as has been observed for *Ceramius bicolor* (Thunberg) (Gess, S.K. 1996) and *Ceramius socius* Turner (Gess and Gess 1986). In no case did one of these wasps alight on the water surface.

*Flower visiting.*—All plants in flower in the vicinity of the water were sampled for flower visitors throughout the day, however, only one female and one male of *C. brevitarsis* were taken. Both were visiting the small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond. (Zygophyllaceae). This is the first record of *Ceramius* visiting flowers of Zygophyllaceae. The records are, however, too few for an association to be suggested as instances of casual visiting of flowers other than those preferred has occasionally been recorded for some species of *Ceramius* (Gess, S.K. 1996). Aizoaceae: Mesembryanthema would be the expected plant taxon to be favoured by *C. brevitarsis*, it being a member of Group 2A and there being consistency of flower family choice within *Ceramius* species groups in southern Africa (Gess, S.K. 1996).

## Jugurtia de Saussure
### Jugurtia codoni Gess

*Distribution.*—*Jugurtia codoni* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

Figs. 8–12. Paradise Kloof, Richtersveld National Park. 8, Approach to kloof. 9, Nesting site of *Celonites gariepensis* Gess marked with arrow. 10, Nest of *C. gariepensis* on underside of jutting edge in rock crevice (outer cell broken during capture of builder). 11, Cell of *C. gariepensis*. 12, Cell of *C. gariepensis* opened to show papillate provision mass and position of egg.

*Water visiting.*—Two females of *J. codoni* were collected at the edge of a pool of water in Paradise Kloof. This suggests that it is probable that *J. codoni*, like the other species of *Jugurtia* for which nesting is known, uses water in nest construction.

*Flower visiting.*—Females of *J. codoni* were found foraging abundantly on the flowers of the spiny, metre high herb *Codon royenii* L. (Hydrophyllaceae) growing in the gravelly bed of a dry watercourse, where it emerged from the hills before

crossing the Koeroegabvlakte (Fig. 5). The flowers of *C. royenii* are 35 mm high, erect and campanulate (Figs. 13–15). The many lobed corolla is white. There are 10–12 stamens. The filaments are attached to the corolla tube about 5 mm from the base and are closely adpressed so that they close off the base of the flower (Fig. 15) presumably protecting the nectar from evaporation. *Jugurtia codoni*, when visiting a flower, alights on the outwardly curved corolla lobes and, when preparing to imbibe nec-

Figs. 13 and 14. *Codon royenii* L. (Hydrophyllaceae). 13, *Jugurtia codoni* Gess imbibing nectar. 14, *J. codoni* collecting pollen.

tar, walks down the side of the flower (Fig. 13) and inserts its long tongue between the filaments. When collecting pollen, the wasp either reaches over from the corolla or moves across onto a filament and ingests the pollen directly from the anther (Fig. 14). Although apparently preferring *C. royenii*, *J. codoni* was found less commonly visiting the flowers of *P. leucorrhizum* (Scrophulariaceae) and of *Hermbstaedtia glauca* (Wendl.) Reichb. ex

Steud. (Amaranthaceae). At other sites in the Park it was found uncommonly visiting flowers of *Zygophyllum meyeri* Sond. (Zygophyllaceae), *Senecio arenarius* Thunb. (Asteraceae) and *Pelargonium klinghardtense* Knuth (Geraniaceae).

Due to the smallness in size of *J. codoni* compared with *Codon royenii* it is possible for *J. codoni* when obtaining nectar to enter and leave the flowers without coming into contact with either the anthers or the stigmas and to collect pollen from the anthers without coming into contact with the stigmas. It is therefore probable that, whereas *C. royenii* is clearly an important forage plant for *J. codoni*, *J. codoni* is not a potential pollinator of *C. royenii* but is rather a pollen and nectar thief. A more likely potential pollinator is the relatively large bee *Xylocopa lugubris* Gerstaecker (Apidae: Xylocopinae) which, although it is a less common visitor and not restricted to *Codon*, in behaviour and fit is ideally suited to act as a pollinator.

## *Jugurtia koeroegabensis* Gess

*Distribution.*—*Jugurtia koeroegabensis* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

*Flower visiting.*—Only seven females of *J. koeroegabensis* were collected from flowers. On the banks of a dry watercourse crossing the Koeroegabvlakte (28.11S, 17.03E) (Figs. 2–5) two females were taken from the small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond. (Zygophyllaceae) and one female was taken from a yellow rayed capitulum of *Osteospermum* sp. (Asteraceae). At Pootjiespram (20.05S, 16.57E), in a broad sandy drainage area, four females were taken visiting flowers, one from the yellow petalled flowers of *Cleome paxii* (Schinz) Gilg. & Benth. (Capparaceae), one from the flowers of *Peliostomum leucorrhizum* (Scrophulariaceae) and two from the green and brown flowers of *Ferraria* cf *divaricata* Sweet (Iridaceae). These records are too
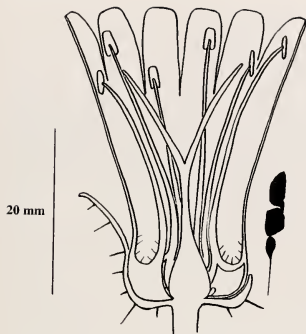
Fig. 15. *Codon royenii* L. (Hydrophyllaceae), Diagrammatic representation of flower cut longitudinally and of *Jugurtia codoni* Gess (wings and legs omitted).

20 mm

few to establish a particular preference, however, it is clear that *J. koeroegabensis* is not restricted to visiting flowers of a single plant family.

## Masarina Richards

### Masarina mixtoides Gess

*Distribution.*—*Masarina mixtoides* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

*Flower visiting.*—*Masarina mixtoides* is not restricted to a single family of plants. At a site 1.5 km from the Helskloof Gate (28.18S, 16.57E), the abundant white flowers of an isolated plant of *Pelargonium klinghardtense* Knuth (Geraniaceae) growing on the edge of a dry, stoney drainage channel on a hillside were clearly attractive to this wasp, a sample of 15 females and one male having been taken in under an hour. However, on the Koeroegabvlakte, where flowers associated with a dry, gravelly drainage channel crossing the flats (Figs. 2–5) were sampled, three females were taken from the small cream flowers of lax,

shrubby *Zygophyllum prismatocarpum* (Zygophyllaceae) (Fig. 4), and four from the larger yellow flowers of compact, shrubby *Zygophyllum meyeri*. In addition one female was collected from the flowers of a species of *Wahlenbergia* (Campanulaceae) and one from a yellow rayed capitulum of Asteraceae.

### Masarina peliostomi Gess

*Distribution.*—*Masarina peliostomi* has been recorded from only the Richtersveld National Park (Gess, F.W. 1997).

*Flower visiting.*—Both females and males of *M. peliostomi* were foraging abundantly on the flowers of *Peliostomum leucorrhizum* (Scrophulariaceae) (Fig. 7) growing along the banks of the upper reaches of a dry watercourse crossing the Koeroegabvlakte (Figs. 2–5). This is the first record of an association between a species of *Masarina* and a species of *Peliostomum*. However, five species of *Celonites* are known to be associated with plants of this genus (see above). *Masarina peliostomi* being of similar size and behaviour to the *Celonites* species should, like them, be considered a potential pollinator of *Peliostomum* in the Richtersveld. Although not collected from flowers of *Aptosimum spinescens*, which was growing further down the watercourse, it is probable that *M. peliostomi* would visit these flowers.

### Masarina strucki Gess

*Distribution.*—*Masarina strucki* has been recorded from Namaqualand (Goegap Nature Reserve, Springbok and the western side of the Kamiesberg), the Olifants River Valley to the south (east bank of the Clanwilliam Dam), immediately east of the Western Escarpment (Skuinshoogte Pass between Nieuwoudtville and Louriesfontein and Biedouw Valley in the Cederberg) and in the western Little Karoo (Ladismith) (Gess, F.W. 1997).

*Flower visiting.*—The first record was for a single female collected by Michael Struck, 20.viii.1985, visiting the yellow

flowers of *Hermannia disermifolia* Jacq. of the subgenus *Hermannia* (Sterculiaceae) in Goegap Nature Reserve (formerly Hester Malan Nature Reserve) in the Springbok district, Namaqualand. An intensive search by the Gesses for this masarine during six subsequent spring visits to Namaqualand yielded only one further female, from the same locality (10–12.x.1988, F.W. and S.K. Gess), until spring 1994 when they found females and males relatively abundant in association with *H. disermifolia* in the Goegap Nature Reserve (primarily at 29.37S, 17.59E) (3-8.x.1994, F.W. and S.K. Gess) and at Bakleikraal (30.13S, 18.03E) in the Kamiesberg (9-11.x.1994, F.W. and S.K. Gess) (Figs. 16 and 17). The following spring, 1995, they again found females and males at the Kamiesberg site (28.ix.1995, F.W., S.K. and R.W. Gess) but none were found at the Goegap site. The sites in the Goegap Nature Reserve and the Kamiesberg are level sandy areas at the base of rocky outcrops, in which *H. disermifolia* is the dominant plant.

In the Olifants River Valley on the east bank of the Clanwilliam Dam, 19.2 km south of the caravan park (32.17S, 18.56/7E) *M. strucki* was found by Robert Gess foraging on an orange flowered species of *Hermannia* subgenus *Mahernia* (3 females, 5.x.1995, F.W., S.K. and R.W. Gess) growing in sandy soil at the foot of a rocky slope.

At the Skuinshoogte Pass site (31.16S, 19.08E) only two females were collected (23-30.ix.1994, F.W. and S.K. Gess), one on the ground in a dry river bed and the other on the ground beneath a shrublet of a yellow flowered species of *Hermannia* subgenus *Hermannia*.

In the western Little Karoo two samples have been taken in the Ladismith district, one at Buffelspoort (3320BD) (3 females, 14.viii.1995, V.B. Whitehead) on a yellow flowered shrubby *Hermannia* sp. and the other 6 km from Ladismith on the road to Barrydale (3 females, 21.viii.1995, F.W.

and S.K. Gess) visiting yellow flowers of *Hermannia vestita* Thunb. of the subgenus *Hermannia* growing in level ground on the roadside halfway up a rocky slope.

It seems probable that *M. strucki* is always associated with *Hermannia* spp. as careful collecting by the Gesses from a wide range of flowering plants both in the vicinity of its collection sites and further afield has been undertaken. It also seems to be of note that the *Hermannia* plants with which it has been found have all been associated with rocky hill slopes.

The flowers of the *Hermannia* spp. recorded as being visited by *M. strucki* are all "bell-shaped" and 7–10 mm in length. *Masarina strucki*, of which the females are an average length of 7.4 mm and the males 6.6 mm, alights on the side of the downwardly hanging flowers, moves down, and curves around the lip to face upwards into the flower (Fig. 22h). When remaining in this position an individual is apparently ingesting pollen. When the individual enters into the flower leaving only its abdomen exposed it is undoubtedly imbibing nectar. The nectar held in the inrolled bases of the petals will be reached by the wasp's tongue which has an average length of 4.2 mm in the female and 4.0 mm in the male.

As a flower visitor *M. strucki* appears to be restricted to *Hermannia* and therefore to be dependant upon this genus for pollen and nectar. Its distribution is far more limited than that of *Hermannia* and within the areas where it does occur it seems to be restricted to rocky slopes and on these slopes to a limited range of *Hermannia* species. It is, however, not the sole visitor to these species of *Hermannia* (Table 1). Assemblages of visitors to the three species of *Hermannia* subgenus *Hermannia* with which it has been associated are characterized by the presence of, in addition, one or more species of *Anthophora* (*Pyganthophora*) (Apidae: Apinae: Anthophorini) and one or more species of Megachilidae—one or more species of *Plesianthidium*

Figs. 16–18. 16, Nesting area of *Masarina strucki* Gess, Kamiesberg, bushes in the foreground, *Hermannia disermifolia* Jacq. (Sterculiaceae). 17, Flowers of *H. disermifolia* (length of flower approximately 9 mm). 18, Cell of *M. strucki* opened to show papillate provision mass and position of egg.

(*Spinanthidium*) (Megachilidae: Megachilinae: Anthidiini) and/or a species of *Lasioglossum* (Halictidae). Though these bees are therefore also expected visitors to the flowers they are less constant as they are all known to visit in addition flower species of other genera belonging to other plant families occurring in close proximity to the *Hermannia* plants.

*Masarina strucki* and the bees all visit a considerable number of flowers in succession, and all while visiting flowers in the pollen-presenting stage receive a dusting of pollen which adheres to them. *Masarina strucki* in entering the flowers receives the pollen dorsally and the bees which are all too large to enter receive pollen on their hairy faces. Such pollen would be transferred to receptive stigmas by the wasps and the bees visiting flowers in the receptive phase. All can therefore be considered to be potential pollinators, but where they are present the masarines will be the more dependable.

The species of *Hermannia* subgenus *Mahernia* was sampled on one day only. On this day it was only visited by two masarines, *M. strucki* and *Masarina mixta* Richards. Both can be considered potential pollinators, however, *M. strucki* is more dependable than *M. mixta* which visits in addition flowers of plants of several other families which grow in close proximity to the *Hermannia* plants.

Table 1. Flower visitors to those species of *Hermannia* L. on which *Masarina strucki* Gess is known to forage. Number in brackets indicates the number of plant families in addition to Sterculiaceae which are known to be visited.

subgenus *Hermannia*
*Hermannia disermifolia* Jacq. and *Hermannia* cf. *disermifolia*

Vespidae: Masarinae

*Masarina strucki* Gess, Goegap, Kamiesberg, (Skuinshoogte) (0)

Vespidae: Eumeninae apparently hunting

Megachilidae: Megachilinae: Anthidiini

*Plesianthidium (Spinanthidium) callescens* (Cockerell), Skuinshoogte (1)

*Plesianthidium (Spinanthidium) trachusiforme* (Friese), Goegap (1)

Apidae: Apinae: Anthophorini

*Anthophora (Pyganthophora) abrochia* Eardley, Goegap, Kamiesberg (1)

*Anthophora (Pyganthophora) diversipes* Friese, Kamiesberg (3)

*Anthophora (Pyganthophora) krugeri* Eardley, Goegap (1)

*Anthophora (Pyganthophora) schultzei* Freise, Skuinshoogte (2)

*Amegilla (Micramegilla) niveata* (Friese), Kamiesberg, Skuinshoogte (16)

*Pachymelus peringueyi* (Friese) Goegap, Kamiesberg (3)

Apidae: Apinae: Apini

*Apis mellifera* L. (very many)

Scarabaeidae: Melalonthinae: Hopliini

A single species

*Hermannia* cf. *cuneifolia* Jacq.

Vespidae: Masarinae

*Masarina strucki* Gess, Goegap, (Skuinshoogte) (0)

Vespidae: Eumeninae apparently hunting

Halictidae

*Lasioglossum* sp., Skuinshoogte (?)

Megachilidae: Megachilinae: Anthidiini

*Plesianthidium (Spinanthidium) callescens* (Cockerell), Skuinshoogte (1)

Apidae: Apinae: Anthophorini

*Anthophora (Pyganthophora) schultzei* Freise, Skuinshoogte (2)

*Hermannia vestita* Thunb.

Vespidae: Masarinae

*Masarina strucki* Gess, Ladismith (0)

Halictidae

*Lasioglossum* sp., Ladismith (?)

Table 1. Continued.

Apidae: Apinae: Anthophorini

*Anthophora (Pyganthophora) krugeri* Eardley, Ladismith (1)

Nemestrinidae

*Prosoeca* sp.

subgenus *Mahernia*
*Hermannia* sp.

Vespidae: Masarinae

*Masarina mixta* Richards, Clanwilliam (3)

*Masarina strucki* Gess, Clanwilliam (0)

Vespidae: Eumeninae apparently hunting

*Nesting area.*—Unfortunately despite careful search only one nest has been located. This was at the Bakleikraal site in the Kamiesberg (Fig. 16). The nest entrance was between two stones in gently sloping ground in a bare area between the *Hermannia* bushes. The soil was sandy and friable.

*Provision.*—The provision from the single cell obtained was very moist but jelly-like, pale yellow ochre, and translucent. The longitudinal surface was regularly papillate, each papilla ending in a nipple (Figs. 18 and 19b). At the inner end of the provision was a larger central papilla which supported the egg. The outer end
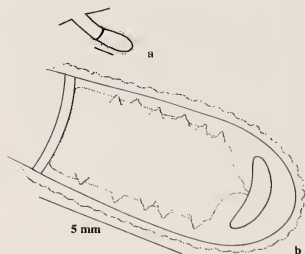


Fig. 19. Diagrammatic representations of longitudinal section of nest and cell, papillate provision mass and egg of *Masarina strucki* Gess.

of the provision was adpressed to the cell closure.

Samples of pollen were taken from the provision and examined microscopically. The pollen was all of one kind, 0.03 mm in diameter, and matched pollen from *H. disermifolia.*

*Description of nest.*—The single nest investigated consisted of a sloping burrow (3.5 mm in diameter and 6.5 mm in length) terminating in a cell (Fig. 19a). The cell which was rounded at the inner end and sealed with a seal, 0.5 mm in thickness, concave on the outside and convex on the inside, had an inner length of 7.9 mm and an inner diameter of 3.7 mm. The walls of the cell were smoothed on the inside and the surrounding earth was cemented to a depth of 0.5 mm so that the cell could be removed from the surrounding soil as an entity. There was no entrance turret.

*Method of construction, oviposition and provisioning.*—The nest was discovered after the burrow had been excavated and the cell walls were being smoothed and stabilized. The friable nature of the soil, the lack of any form of turret, the lack of discarded mud pellets, and the nature of the cell walls and seal suggest that excavation of the nest had taken place without the use of water but that some bonding agent other than water had been used for cementing the cell walls and constructing the seal. The extreme hardness of the cell walls akin to those of *Celonites* spp. and the pliable nature of the freshly completed seal suggest the use of nectar.

When observations commenced at 14h56 final smoothing of the cell walls was apparently in progress. The wasp was repeatedly moved backwards until half the body length protruded from the entrance and forwards again into the cell. By shining a light into the nest and using a dentist's mirror during the wasp's absence it could be seen that the cell walls were smooth and moist.

At 15h12 the builder, after an absence of eight minutes, returned to the nest and entered it head first. After apparently making an inspection she came out, turned around and reversed into the nest dorsum uppermost, emerged again eight minutes later, and then re-entered facing into the cell. Oviposition had apparently taken place. The egg which was obtained when the nest was later investigated was white, curved, and tapered somewhat towards the ends. It was 2.4 mm in length across the bow and 0.75 mm in diameter at midlength.

Provisioning then commenced. This took 85 minutes and was apparently accomplished with five loads as, during this phase, the wasp was away from the nest, apparently foraging, for five periods varying from 6–10 minutes and in the nest rotating (an average of four times), apparently depositing the provision, for five periods of 3–13.5 minutes.

Sealing of the cell commenced after an absence from the nest, apparently to collect nectar. Soil for sealing was seen to be taken from the walls of the entrance shaft. At 17h07 work for the day was over. On emerging from the nest the wasp was observed to groom for the first time. She was then away from the nest for seven minutes presumably feeding before settling for the night. On her return to the nest she went in head first, apparently to inspect the nest, and then came out, backed in, groomed her face, and then became still with her head blocking the nest entrance. The following morning she remained still in the same position, apparently sleeping, until 10h37 when she began to stir and look out of her nest. She, however, only left the nest at 10h56. After an absence of 13 minutes she was back in the nest continuing with the cell closure but not rotating as she had been when provisioning. Cell closure was completed by 11h30.

*Male behaviour.*—Males of *M. strucki* forage together with the females on the flowers of *Hermannia* spp. They were also observed on the ground beneath the *Herman-*

*nia* bushes. On the second day (whilst nest construction was being observed), before the female emerged from her nest, a male was seen resting on the ground sunning himself about 2 m from the nest. No instances of mating were observed.

*Associated insects.*—A probable association between *Allocoelia quinquidens* Edney (Chrysididae) and *M. strucki* is noted. Female *A. quinquidens* were present on the ground between the *Hermannia* bushes at the Goegap and the Bovlei sites. Furthermore on the second day of nesting observations one was observed at 11h34 *ca.* 1 m from the nest, at 11h36 *ca.* ½ m from the nest, at 11h39 30 cm from the nest, at 11h46 *ca.* 1 ½ m from the nest and finally at 11h50 entering the nest and leaving it, at 11h52 *ca.* ½ m from the nest, at 12h02 inspecting and entering the nest, at 12h50, 13h34 and 13h50 inspecting the nest.

It is of note that *A. quinquidens* has also been observed by the Gesses inspecting a nest of *Masarina familiaris* Richards between Clanwilliam and Graafwater.

## Masarina tylecodoni Gess

*Distribution.*—*Masarina tylecodoni* has only been recorded from the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

*Flower visiting.*—Both females and males of *M. tylecodoni* were discovered by Robert Gess to be foraging on the yellow flowers of *Tylecodon hallii* (Tölken) Tölken (Crassulaceae) growing on rocky hills on the west flank of the Koeroegabvlakte (Figs. 2, 5 and 20). This masarine was foraging abundantly, and apparently exclusively, on these flowers. *Tylecodon hallii* was the only species of *Tylecodon* in flower, so it is not known whether the flowers of other species of *Tylecodon* are visited. As nothing is known of the insect visitors to the flowers of *Tylecodon* (G. Williamson pers. comm.) this is of particular interest.

*Tylecodon hallii* is a compact succulent shrublet which holds aloft an abundance of yellow erect campanulate flowers (Figs.





Figs. 20 and 21.  20, Slope of rocky hill on west flank of Koeroegabvlakte, rounded shrublet in middle distance *Tylecodon hallii* (Tölken) Tölken (Crassulaceae). 21, *Masarina tylecodoni* Gess entering flower of *T. hallii*.

20 and 21). The flowers are 22 mm in height. The corolla consists of five fused petals. Each of the ten stamens is fused to the corolla just above the "waist" (Fig. 22).
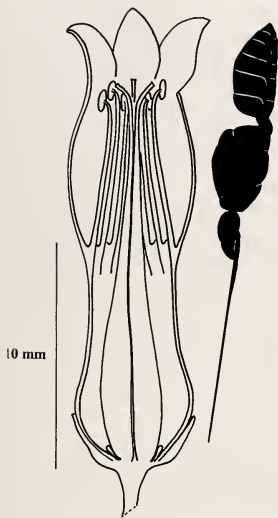
Fig. 22. Diagrammatic representations of half flower of *Tylecodon hallii* (Tölken) Tölken (Crassulaceae) cut longitudinally and of *Masarina codoni* Gess (wings and legs omitted).

*Masarina tylecodoni*, when visiting a flower for nectar, alights on the outwardly curved petal lobes and enters between the corolla and the filaments of the stamens which being closely adpressed form a barrier to the wasp which inserts its tongue between two filaments to reach the nectar at the base of the flower. In forcing its way into a flower the wasp pushes against the anthers and therefore when the anthers are ripe the wasp receives a load of pollen dorsally. When visiting a flower to collect pollen a wasp alights on the outwardly curved corolla lobes and standing thus ingests the pollen directly from the anthers.

*Masarina tylecodoni* should be consid-

ered as a potential pollinator of *T. hallii*. When coming from imbibing nectar from a flower in the pollen presenting phase and entering a flower with receptive stigmas which are outwardly curved it would effectively wipe off pollen from its dorsum onto one or more of the stigmas. If it is indeed dependant solely on *Tylecodon* for pollen and nectar, even if it visits more than one species of *Tylecodon*, it would be a dependable potential pollinator as *T. hallii* is the earliest of the *Tylecodon* species to come into flower in the Richtersveld.

DISCUSSION

*Flower visiting.*—The association between *Jugurtia codoni* and *Codon* is the first record of an association between a southern African masarine and Hydrophyllaceae, however, the Nearctic masarine genus *Pseudomasaris* shows a strong preference for flowers of this family. Flower visiting records are available for 13 of the *ca.* 15 described species of *Pseudomasaris* and of these 92% have been recorded from the genera *Phacelia* Juss. and *Eriodyction* Benth. (Gess, S.K. 1996).

The preference shown by *Masarina tylecodoni* for *Tylecodon* (Crassulaceae) is of interest as the only other record of a masarine visiting a species of Crassulaceae is that for *Celonites wahlenbergiae* Gess, which is primarily associated with *Wahlenbergia* (Campanulaceae), but has been recorded in addition from plants of several other genera and families, including *Crassula dichotoma* L. (Crassulaceae) (Gess and Gess 1992). The association with Crassulaceae (Rosales) is not so surprising if one considers that Rosales is considered to be basal in the Rosidae which includes the Fabales and therefore Papilionaceae with which are associated at least two species of *Masarina*.

That the flowers of *Zygophyllum* spp. (Rosidae: Sapindales: Zygophyllaceae) in the Richtersveld are visited, although apparently not favoured, by *Ceramius brevitarsis*, two species of *Jugurtia*, *J. codoni* and

*J. koeroegabensis*, and *Masarina mixtoides* is of interest. Although the Gesses have sampled *Zygophyllum* species in other areas where masarines have been present they have not encountered them visiting these flowers. The only other records of masarines visiting *Zygophyllum* are for a species of *Quartinioides* from *Zygophyllum simplex* L. at Gobabeb (23.34S, 15.03E) in the central Namib Desert (Wharton 1980). Indeed the only other record of a masarine visiting flowers of Zygophyllaceae seems to be that to *Larrea* Cav. by *Pseudomasaris wheeleri* Bequaert, a Nearctic species more typically associated with Scrophulariaceae, Hydrophyllaceae and Asteraceae (Richards 1966).

The association of *Masarina strucki* with *Hermannia* (Dilleniidae: Malvales: Sterculiaceae) is the first recorded association of a masarine with Sterculiaceae. Indeed an association with a member of the Dilleniidae as a whole is unusual for the Masarinae worldwide. Of the 164 other species of masarines for which flower visiting records are available only 13 have been recorded from Dilleniidae and most of these are species which are generally closely associated with plants of other classes so that the visits to Dilleniidae are casual in nature. Classes most favoured are Asteridae 104 species, Caryophyllidae 52 species (47 being from southern Africa), and Rosidae 41 species. Visits to other classes are for 3 species to Magnoliidae, 2 species to Liliidae and 1 species to Zingiberidae (classes *sensu* Cronquist 1988).

When taking into account the form of the flowers visited by southern African species it is of note that a masarine visiting the flowers of the favoured families Aizoaceae, Asteraceae, Campanulaceae, Scrophulariaceae and Papilionaceae is immediately in position for reaching the nectar and pollen supplies (Fig. 23 a–g). The same holds true for the erect campanulate flowers of *T. hallii* (Crassulaceae) and *C. royenii* (Hydrophyllaceae). By contrast when *M. strucki* alights on the outside of

the downwardly directed bell flower of *Hermannia* it is not immediately in position for reaching these resources but must move down, pass around the lip of the corolla, and then turn upwards to be positioned for reaching them (Fig. 23h).

*Discussion of nesting.*—The nesting of *M. strucki* is remarkably different from that of *M. familiaris* the only other *Masarina* for which nesting has been recorded (Gess and Gess 1988) and from the nests known for the closely related genus *Jugurtia*, that is those of *J. confusa* Richards (Gess and Gess 1980) and *J. braunsi* (Schulthess) (Gess, S.K. 1996).

In nest construction *M. strucki* unlike the other three species apparently excavates the burrow without the use of water and does not construct an entrance turret. Excavation of a nest with the use of water and the construction of a turret are considered to be basal for the masarines, and excavation without the use of water and without the construction of an entrance turret to be derived (Gess, S.K. 1996). Such a change has occurred independantly several times having been recorded for two species of *Rolandia* (Gess *et al.* 1995 and Houston 1995), and for *Celonites latitarsis* Gess (Gess and Gess 1992). Excavation of the nest without the use of water has also been recorded for *Quartinia vagepunctata* Schulthess (Gess and Gess 1992), however, this species does construct a turret but using self-generated silk not water as a bonding agent.

The cell of *M. strucki* like that of *Masarina familiaris* is an excavated cell with the walls impregnated with a bonding substance unlike those of the two *Jugurtia* species, in which distinct earthen cells are constructed within excavated cells. However, the bonding substance used by *M. strucki* is apparently nectar whereas that used by *M. familiaris* is water. Furthermore, the cells of the two *Masarina* species differ in shape. The cell of *M. strucki* has the inner end rounded like those of all other masarines for which cells are known

Fig. 23. Diagrammatic representations to show how masarines position themselves when preparing to utilize flowers of the types visited by them. a, Stamen carpet flower (Aizoaceae: Mesembryanthema). b, Cone flower ((Aizoaceae: Mesembryanthema). c, Capitulum (Asteraceae). d, Campanulate flower (Campanulaceae). e, Gullet flower (Scrophulariaceae). f and g, Papilionate flower (Papilionaceae). h, Bell flower (Sterculiaceae).

other than that of *M. familiaris* which is distinctly truncate (Gess, S. K. 1996). The use of nectar as a bonding agent has been recorded for *Pseudomasaris* (Torchio 1970) and suggested for *Celonites* (Gess and Gess 1992).

That *M. strucki* lays the egg free from the cell wall is usual for ground nesting masarines. In this *M. strucki* again differs from *M. familiaris* which, like the aerial nesting *Gayella eumenoides* Spinola (Claude-Joseph 1930) and *Pseudomasaris edwardsi* (Cresson) (Torchio 1970), attaches the egg to the cell wall.

The preparation of a very moist provision mass is common to both *M. strucki* and *M. familiaris*. In this they differ from *J. confusa* which prepares a firm provision mass. The construction of papillae seems to be a recurring feature of very moist pollen masses having been recorded also for that of *Pseudomasaris edwardsii* (Cresson) (Torchio 1970) but not for the less moist pollen masses of *Pseudomasaris maculifrons* (Fox) (Parker 1967) and *Pseudomasaris phaceliae* Rohwer (Parker 1967 and Torchio 1970) and in the present paper for *Celonites gariepensis*.

## ACKNOWLEDGMENTS

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# Mating Behaviour of an Undescribed Species of *Coccophagus*, Near *C. gurneyi* (Hymenoptera: Aphelinidae)

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*Abstract.*—We detail the mating behaviour of an undescribed species of *Coccophagus* that resembles *C. gurneyi* Compere anatomically, and which is also an Australian parasitoid of mealybugs. The pattern of the male-female interaction was complex and protracted, which is typical of many species in the genus. All three principal behavioural categories, namely precoital courtship, coitus and postcoital mount behaviour, were expressed. The postcoital aspect was longest, which is common in the genus and family. Wing flicking during coitus and head nodding movements during postcoital behaviour were two distinct displays of the males that have not so far been reported in other *Coccophagus* species. Attraction of the males to virgin females in the field is demonstrated and is the first direct evidence of long distance pheromonal attraction of mates in the genus *Coccophagus*, and which has been documented only occasionally in other hymenopterous parasitoids.

## INTRODUCTION

Cryptic species complexes exist in the genus *Coccophagus* Westwood and the intergradation of structural traits complicates the resolution of species limits (Compere 1931; Annecke and Insley 1974; Walter 1993). Colour patterns vary intraspecifically within some species groups in the genus and cannot be used alone in classification (Annecke and Insley 1974; Walter 1993). In contrast, observations on mating behaviour have sometimes provided a good taxonomic tool for accurate diagnosis of the *Coccophagus* species that have elaborate and protracted behaviour associated with mating (Battaglia *et al.* 1988; Walter 1993).

Chalcidoid mating behaviour is typically divided into three phases, the precoital phase, coitus and postcoital mount behaviour (Gordh and DeBach 1978). This division, though arbitrary, has been useful in conceptualising the mating behaviour of two closely-related *Coccophagus* species, *C. bartletti* Annecke and Insley and *C. lutes-*

*cens* Compere (Walter 1993). So far, the mating behaviour of only eight *Coccophagus* species has been described in any detail (Table 1). The sequences of many others (e.g., *C. capensis* Compere and *C. ochraceus* Howard), although reported, are still incompletely known. Long-distance pheromonal attraction of males by virgin females of *Coccophagus* species may initiate sexual communication (Walter 1993), but controlled tests have never been conducted.

Here we report the mating behaviour and role of sex pheromones in an undescribed species of *Coccophagus* that is anatomically similar to *C. gurneyi* Compere, but which differs in head colour, ratio of ovipositor length to middle tibial length (G.L. Prinsloo, South African National Collection of Insects, *in litt.*, 15. *vii.* 1994), and in aspects of its host relationships (Abeeluck 1995). Voucher specimens have been deposited in the Queensland Museum, Brisbane.

The male eggs of *C. gurneyi* reputedly follow one of two quite different devel-

Table 1. Summary of published analyses of mating behaviour of *Coccophagus* species. Mating is divided into precoital courtship, coitus and postcoital courtship, and the duration (seconds) of each is presented. Signals and appendages used in precoital and postcoital display are differentiated. Females of those species with an asterisk are known to be monandrous.

| Species | Duration (secs) | | | Signals and appendages used | | | | Author(s) |
|---|---|---|---|---|---|---|---|---|
| | Precoital courtship | Coitus | Postcoital courtship | Phero-mones | Wings | Anten-nae | Legs | |
| *C. atratus* | | | | | | | | |
| Compere | 2–10 | 0 | 0 | Pre | ? | Pre | ? | Donaldson et al. 1986 |
| *C. bartletti* | | | | | | | | |
| Annecke & Insley | 15 | 4 | 90 | Pre | Post | Pre | ? | Walter 1993 |
| C. capensis | | | | | | | | |
| Compere | <1 | ? | ? | ? | ? | ? | ? | Flanders 1937 |
| *C. lutescens* | | | | | | | | |
| Compere | 5 | 3 | 48 | Pre | Post | Pre | Post | Walter 1993 |
| C. matsuyamensis | | | | | | | | |
| Ishii | 7 | 4 | 22 | ? | Post | Pre | Post | Battaglia et al. 1988 |
| C. obscurus | | | | | | | | |
| Westwood | 6 | 15 | 0 | ? | ? | Pre | ? | Battaglia et al. 1988 |
| C. ochraceus | | | | | | | | |
| Howard | Few secs | Few secs | 0 | — | ? | ? | ? | Cendaña 1937 |
| C. varius | | | | | | | | |
| Silvestri | Reported to be the same as that for *C. matsuyamensis* (see above) | | | | | | | Battaglia et al. 1988 |

opmental pathways, depending on whether the mealybug that will host the male egg already contains a parasitoid larva or pupa at the time of oviposition (Flanders 1964). Conceivably, however, Flanders made observations on wasps from more than one unrecognised sibling species whose males differ from each other in their host relationships (Walter 1983). Our general aim is, therefore, to help resolve the question of species limits and host relationships in the *gurneyi* "group" of *Coccophagus* species.

## MATERIALS AND METHODS

Females of *Coccophagus* sp. nr *gurneyi* were collected from *Phenacoccus parvus* Morrison on *Lantana montevidensis* (Sprengel) Briq. on the St Lucia Campus of The University of Queensland. To determine whether long distance pheromonal attraction is involved in the sexual communication of this species, two cages with 15 virgin females in each and two with 15 mated females in each (all females were one day old) and one control cage without

females were placed one meter apart, at ground level, in *L. montevidensis* patches infested with *P. parvus*. The cages were observed continuously for 60 minutes, between 1000h to 1100h, and all small wasps that landed on them were captured. The position of the cages was then interchanged for a further 60 minutes of observation. The procedure was followed for three consecutive days. Each captured insect was stored alone in a vial with honey. All vials were kept cool in an insulated box for transport to the laboratory, where each male *Coccophagus* individual that had been captured was placed with a virgin *Coccophagus* female to check if they would mate.

For detailed behavioural observations, each virgin female (n =17) was released into a vial (35 mm × 10 mm diameter) containing a male of unknown age and mating status. (The usual hosts of the males of this species of *Coccophagus* are not known, so laboratory reared individuals were not available.) Observations were made at 25±2°C under a dissecting

microscope (40× magnification) with a heat-filtered tungsten light and were recorded on video tape. Following copulation, the male was discarded. To confirm successful insemination, each female was killed in 70% alcohol and transferred to a drop of 1% saline. The spermatheca was detached, covered with a coverslip in a drop of 1% saline, and examined under phase contrast for the presence of sperm. The spermathecal capsule was rated 100% full when sperm occupied the entire cavity within the capsule (Abeeluck 1995).

Females were also tested to establish whether, after first insemination, they remained receptive to males that attempted to mate. One-day old females (n = 11) were each exposed to a single male in a vial. After mating, the females were isolated with a drop of undiluted honey and the males were discarded. After 24 hours each female was again exposed to a male and observed for 20 minutes, a procedure that was followed for seven days. Most mated females (60%) died on the eighth day, when observations were stopped.

To determine whether males could mate with more than one female, single males (n = 7) were each placed in a vial (35 mm × 10 mm) with three virgin females. When each male had mated with all three females, he was isolated and the females were dissected to assess the sperm content of their spermathecal capsule. A further set of three virgin females was exposed to each of the males 30 minutes later; the females were dealt with as before.

## RESULTS

Cages with virgin females attracted males, whereas those with mated females and empty cages did not (Table 2), even when the position of the cages was changed. The mean time between initial exposure of cages and the arrival of the first male was 10 (±2.5) minutes (n = 12). Males flew in a zig-zag course, 10–20 cm above the cage, for 25 (±3.4) seconds before landing on the cage (n = 12). Once on

Table 2. Catches of *Coccophagus* sp. nr *gurneyi* males at cages that held virgin or mated females or that had no wasps (controls) (n = 2 cages for each treatment).

| Day | Trap type | Number of males caught | |
| | | 0–60 minutes | 60–120 minutes |
|---|---|---|---|
| 1. | Virgin female* | 18 & 21 | 11 & 10 |
| 2. | | 19 & 16 | 10 & 12 |
| 3. | | 17 & 19 | 9 & 11 |
| | Mean (± S.E.) | 18.3 (± 0.7) | 10.5 (± 0.4) |
| 1. | Mated female | 0 & 0 | 0 & 0 |
| 2. | | 0 & 0 | 0 & 0 |
| 3. | | 0 & 0 | 0 & 0 |
| 1. | Control cages | 0 & 0 | 0 & 0 |
| 2. | | 0 & 0 | 0 & 0 |
| 3. | | 0 & 0 | 0 & 0 |

* Catches were not significantly different between replicates and among days (P > 0.05, Chi Square Test; Statview 1992), so replicates have been pooled. Catches made during the first period of exposure were significantly higher than those made during the second exposure (Wilcoxon Signed Ranks Test, P = 0.028, Statview 1992).

the cage, males walked around, antennating the substrate.

All field-collected males that were tested mated readily with virgin females. Successful insemination was confirmed by all mated females having their spermathecal capsules 100% full (n = 57).

Mating behaviour followed a consistent pattern (n = 17) made up of several behavioural categories and is represented diagrammatically in Fig. 1. The precoital phase comprised five categories, but was relatively brief overall. Postcoital mount behaviour was more protracted than the precoital phase, but was not as diverse behaviourally.

### Precoital Courtship

Following introduction into a vial, males and females ran around, apparently at random. The time until the male was first stimulated by the presence of the virgin female, characterised by his faster pace and rapid upward and downward questing movements of his antennae, was 49.8 (±0.7) seconds. He then approached the

BEHAVIOURAL STEP　　　CAT. NO.　SILHOUETTE　MEAN (± 1 S.E.)
　　　　　　　　　　　　　　　　　　　　　　　　　　　(SECS)

POSITIVE ORIENTATION BY ♂　　1　　　　　　　┐

↓　　　　　　　　　　　　　　　　　　　├→ Combined
　　　　　　　　　　　　　　　　　　　　　　Duration = 2.6 (± 0.3)

ANTENNAL CONTACT　　　　　　2　　　　　　　┘

♀ WALKS AWAY　　♂ MOUNTS ♀　　3　　　　　┐

↓　　　　　　　　　　　　　　　　　　　│

ANTENNAL TOUCH　　　　　　　4　　　　　　├→ Combined
　　　　　　　　　　　　　　　　　　　　　Duration = 1.4 (± 0.3)

♂ SHIFTS BACK & CURLS ABDOMEN　5　　　　┘

AEDEAGUS
INSERTED　　　　　　　　　　6　　　　Duration　　= 3.0 (± 0.3)
♂ FLICKS WINGS　　　　　　　　　　　　Number of
　　　　　　　　　　　　　　　　　　　flicks　　= 1.5 (± 0.3)

♂ REMOUNTS ♀　　　　　　　　7　　　　Duration　　= 49.2 (± 14.2)

FLICKS WINGS
& NODS HEAD　　　　　　　　　　　　　Number of
(MOUTH PARTS ON PEDICEL)　　　　　　flicks　　= 24.5 (± 5.5)

♀ RESTLESS　　♀ STILL

♂ MOVES LEG　　BOTH STILL　　8
ON HEAD OF ♀

♀ DISLODGES ♂　　　　　　　TOTAL DURATION (SECS) = 56.2 (± 18.8)

Fig. 1.　Diagrammatic representation of the mating behaviour of *Coccophagus* sp. nr *gurneyi* (n=17).

female in a zig-zag pattern (category 1; Fig. 1). The male touched the female's antennae, either from the front or from the side, with his own antennae and then briefly touched her dorsal thorax with them (category 2). Unreceptive females walked away after initial contact with a male. Rejected males continued walking as they had when first introduced into the vial.

Receptive females stood still and allowed the male to mount her (category 3). Once on the female, the male moved forward to her head and touched her antennae with his own. Recognition was stimulated with a single touch and the male then moved back and curled his abdomen (category 5). Behavioural categories 1 to 5 were brief, their combined duration being only about four seconds on average (Figure 1).

## Coital Phase

The copulatory period was short ($3.0 \pm 0.3$ seconds). The male inserted his aedeagus into the female's gonopore and at the same time flicked his wings ($1.5 \pm 0.3$ flicks), but never more than four times. In three of 17 observations, males did not flick their wings. During coitus, the female remained quiescent with her antennae held in a geniculate posture and she maintained this copulatory position even when the male did not succeed in inserting his aedeagus at the first attempt. She allowed subsequent attempts to achieve intromission.

## Postcoital Mount Behaviour

After insemination, all males remounted the dorsum of their partner to stand on her. He placed his forelegs on her vertex and, with rhythmic head movements, moved his mouthparts along the antennal pedicel of the female. Simultaneously he flicked his wings, as detailed in Fig. 1. His head movements were not quantified but he continued with them until the female dislodged him. The period of postcoital mount was comparatively long (Fig. 1).

Throughout, the male flicked his wings and moved his head, as described above, in protracted or momentary bouts. Males also stood still for short periods.

In most observations, postcoital mount was terminated by the female. She either twisted her head, groomed her eyes with her forelegs, kicked the male's hind legs with hers or ran, which shook the male from her back. In response to each attempt to dislodge him, the male changed the position of his fore- and hind legs. Movements of his fore legs were thus conspicuous and gave the impression that the male either searched for a better hold for them or tried to "pacify" the female when she attempted to dislodge him. Both the female and male, when separated, walked away and preened. Females, once inseminated, were unreceptive if the male attempted to copulate a second time.

In the laboratory, males and females copulated at any time of the day and even at night, but this was not quantified. All males (n = 7) mated with the two sets of three virgin females (all of which had spermathecal capsules 100% full of sperm). Females, after their first mating, were no longer receptive to males that attempted to mate, at least not for seven days (n = 11). The mated females either flew or ran to elude an approaching male.

## DISCUSSION

Males of *Coccophagus* sp. nr *gurneyi* are polygynous, whereas the females are monandrous. Use of field-collected males for the observations reported is therefore unlikely to have influenced the recorded behaviour significantly.

Pheromones undoubtedly serve as distance attractants because males are attracted to caged virgins exposed in the field (Table 2). When males are close to females (< 35 mm), the zig-zag pattern of the male's approach indicates that olfaction is used for close range mate attraction and location, as suggested also for other *Coccophagus* species (Donaldson *et al.* 1988; Walter

1993). Whether the same pheromone operates for both close-up and distance attraction is not certain, but close range (about 1.5 cm) communication between the sexes by means of cuticular volatiles has been recorded in the braconid *Diachasmimorpha kraussii* (Fullaway) (Rungrojwanich 1994). Distance attraction of mates has been little studied in parasitic wasps (Powell and King 1984; Godfray 1994), and our demonstration of this phenomenon is apparently the first for any species of *Coccophagus*. In lepidopterous species the long-distance upwind orientation behaviour in responding insects may be elicited by one pheromone component whereas another component may evoke close-range responses (Roelofs *et al.* 1977). Visual orientation may also be involved when male moths, and perhaps parasitoids, get close to calling females.

Male antennation, either on the female's antennae (categories 2 and 4) or on her body (category 2), possibly indicates chemotactile mediated communication by means of cuticular compounds. The males of *Coccophagus* sp. nr *gurneyi* flick their wings during coitus, which is the first record for the genus. Its function has yet to be determined, but it is not necessary for successful insemination in species of *Aphytis* (Rao and DeBach 1969).

Males spend comparatively longer in postcoital mount than in the precoital or coitus phases. Protracted postcoital mounting has been described in six species of *Coccophagus*. In none of these do males touch the female's antennae with his mouthparts, as recorded for *C. sp.* nr *gurneyi*. In yet other species, postcoital mounting never occurs (e.g., *C. atratus* (Donaldson *et al.* 1986); *C. hemera* (Walker) (Zinna 1961); *C. obscurus* (Battaglia *et al.* 1988). The possible functions of postcoital mount behaviour in aphelinids have been discussed by Kajita (1986) and Walter (1993).

The possibility that *C. gurneyi* comprises a complex of species has been expressed

by Walter (1983), based on Flanders' (1964) description of the "dual ontogeny" of *C. gurneyi* males. That *Coccophagus* sp. nr *gurneyi* goes through a series of postures and behaviours that are complex, stereotyped and easily visible suggests that observations on mating behaviour should help to resolve possible species problems in the taxon *C. gurneyi*. However, the mating behaviour of *C. gurneyi* remains undescribed.

## ACKNOWLEDGMENT

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# A Review of the Host Ranges of Aphidophagous Aphelinidae (Hymenoptera: Chalcidoidea)

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*Abstract.*—The genera *Protaphelinus* and *Aphelinus* (the latter divided into three subgenera) comprise all known aphidophagous Aphelinidae. A literature review indicates that these four formal superspecific taxa are largely restricted to hosts in different families: *Protaphelinus* on Pemphigidae, *Aphelinus* (*Indaphelinus*) on Greeneidae, *Aphelinus* (*Mesidia*) on Drepanosiphidae, and *Aphelinus* (*Aphelinus*) on Aphididae.

## INTRODUCTION

Until 1972, the aphidophagous species of Aphelinidae (Hymenoptera: Chalcidoidea) were divided into three genera, *Aphelinus* Dalman, *Mesidia* Foerster and *Mesidiopsis* Novicky. Records of *Marietta* Motschulsky reared from aphids (Viggiani 1984) refer to incidences of hyperparasitism only. Species from *Aphelinus* are recorded from Aphididae, Drepanosiphidae, Lachnidae, Pemphigidae, Thelaxidae (all Homoptera), plus several non-homopteran hosts (Peck 1963, Ferrière 1965, Nikol'skaya and Jasnosh 1966, Kalina and Stary 1976). Lagace (1969a) noted that *Mesidia* was apparently restricted to the Phyllaphidini (Homoptera: Drepanosiphidae), while the sole species in *Mesidiopsis*, *M. subflavescens* (Westwood) was known only from arboreal Drepanosiphidae (Ferrière 1965).

Mackauer (1972) erected *Protaphelinus*, in which he placed *A. nikolskajae* Jasnosh, known only from Pemphigidae. *Mesidiopsis* and *Mesidia* were synonymized with *Aphelinus* by Boucek and Graham (1978) and Hayat (1983) respectively. Hayat (1990) divided *Aphelinus* into three subgenera: *Indaphelinus* (for a single yellow-bodied species), *Mesidia* (for the remaining yellow-bodied species), and *Aphelinus* (for the dark-bodied species).

I have reared several *Aphelinus* species from aphids in northern California (Zuparko 1983, Zuparko and Dahlsten 1993, Zuparko and Dahlsten 1995, Appendix). Most of these species are sympatric and share the same general ecological habitat (deciduous urban shade trees), but I found species assigned to *A.* (*Mesidia*) tended to attack drepanosiphids, and those classified in *A.* (*Aphelinus*) preferred aphids. This led me to conduct a literature review of the aphidophagous aphelinids to determine if a similar pattern occurred on a larger scale.

The two most extensive listings of *Aphelinus* host records previous to this are found in Peck's (1963) catalog of Nearctic Chalcidoidea and in Kalina and Stary's (1976) review of the hosts of European *Aphelinus*. Both studies predate the synonymization of *Mesidia* and *Mesidiopsis*, and do not include taxa from Africa and Asia. Additionally, at least 11 new species have been described in *Aphelinus* since these works.

## METHODS

I used only host records that could be assigned to a specified family of aphids,

excluding records such as "aphis" or "aphids" and specific names of questionable taxonomic status. I consider records of non-aphid hosts doubtful, and excluded them as well. I used Heie's (1980) system of aphid classification, and followed Eastop and Hille Ris Lambers (1976) and Smith and Parron (1978) for aphid synonymies and placement.

This work is not meant to validate any aphelinid at the specific level: I largely accepted the taxa defined by Mackauer (1972), Graham (1976), Kalina (1976), Gordh (1979), Wharton (1983), Polaszek and Hayat (1989), Hayat (1990) and Prinsloo and Neser (1994). The only exception is my consideration of *A. asychis* Walker. The synonymization of this species with *A. semiflavus* Howard (Ferrière 1965) tends to confuse records of populations that were disjunct until the mid-1900's, when Old World material was imported to North America in a series of biological control programs (van den Bosch 1957, Simpson et al. 1959, Jackson et al. 1971). Although *A. asychis* and *A. semiflavus* may be conspecific, I treat this group as three taxa based on their separation before these introductions: 1). *A. asychis* "NA", endemic to North America (= *A. semiflavus* in pre-1970 literature), 2). *A. asychis* "Eur", native to Europe and imported to North America for control of *Schizaphis graminum* (Rondani) and other Aphididae in the 1970's, and 3). *A. asychis* "Israel" (= *A. semiflavus* in early reports), imported to North America from Israel and the Middle East for control of a drepanosiphid, *Therioaphis maculata* (Buckton), in the 1950's.

RESULTS

Host records are summarized in Table 1. The two described species in *Protaphelinus* and *A.* (*Indaphelinus*) are known only from Pemphigidae and Greeneidae, respectively. Of the 55 host records for *A.* (*Mesidia*), 50 (91%) were from Drepanosiphidae, and 5 from Aphididae.

Of the 302 host records for *A.* (*Aphelinus*), 273 (90%) were from Aphididae. The remaining were from Drepanosiphidae (16), Pemphigidae (10), Hormaphididae (1), Lachnidae (1) and Thelaxidae (1). Of the 35 taxa with recorded hosts in this subgenus, 27 (77%) are known exclusively, and 5 (14%) primarily, from Aphididae.

DISCUSSION

The taxonomy of *Aphelinus* is not yet well elucidated. Zehavi and Rosen (1988) discussed an "*A. mali* group" whose members share similar morphological characters, but proposed no formal subdivisions of the genus. Hayat's (1990) concept of subgenera is based primarily on the Nearctic and western Palearctic fauna; only four species of *Aphelinus* have been described from Africa and three from eastern Asia (two of which are unplaced to subgenus).

Flanders (1953) stressed the importance that biological characters can provide with regard to the taxonomy of aphelinids. Hagen and van den Bosch (1968) speculated on the relationship of aphid morphology with parasitoid host selection, while Mackauer (1965) proposed using aphid/parasitoid host records of Aphidiinae (Hymenoptera: Braconidae) to help elucidate aphid phylogeny. Haardt and Holler (1992) reported differences in rates of parasitism and development in six European isofemale lines of *A. abdominalis* (Dalman), and found three groups that appeared to be reproductively isolated.

The results of this survey form a pattern of host specificity which supports the superspecific classifications proposed by Mackauer (1972) and Hayat (1990): each superspecific taxon is largely restricted to a different host family—*Protaphelinus* to Pemphigidae, *Aphelinus* (*Indaphelinus*) to Greeneidae, *A.* (*Mesidia*) to Drepanosiphidae and *A.* (*Aphelinus*) to Aphididae. Of the 69 taxa treated in this paper, 12 had unrecorded hosts, and a further three were *Aphelinus* species unplaced to sub-

genus, but of the remaining 54 species, 41 (76%) followed this pattern exactly.

Ten taxa largely conformed to this pattern, but had a total of 19 conflicting host records. Nine of these records (from *A. automatus* Girault, *A. fulvus* Jasnosh, *A. gilletti* (Howard), *A.* sp. nr. *perpallidus* Gahan, *A. abdominalis*, *A. chaonia* Walker and *A. semiflavus*) were based on rearings of less than 10 specimens each, and a further five (of *A. asychis*) are known only from laboratory exposures.

Although these records document a physiological ability to reproduce in a variety of hosts, the rarity of the field rearings suggests they are atypical parasitizations and do not reflect a parasitoid's normal life history. The physiological restrictions on *Aphelinus* host ranges have not been clearly delineated. Wilbert (1964) reported that *A. asychis* would attack drepanosiphids and aphidids, but not a pemphigid or a phylloxerid, while Carver and Woolcock (1985) demonstrated that *A. asychis* parasitized several genera of Aphididae, but failed to successfully develop in several others due to encapsulation and host incompatibility. Jackson and Eikenbary (1971) and Raney et al. (1971) suggest morphological or behavioral characters may be important aphid defense mechanisms which could influence aphelinid host choices.

Previous lab studies generally support the noted pattern of host ranges. Mackauer and Finlayson (1967) remarked on the absence of *A. asychis* "NA" (= *A. semiflavus*) from *Therioaphis* species in the field, and were unable to transfer it to *T. riehmi* (Borner) in the lab. Another drepanosiphid, *Periphyllus negundinis* (Thomas), was accepted for oviposition, but all parasitoids died before emerging. Transfers to aphidid species were generally successful. Jackson and Eikenbary (1971) and Raney et al. (1971) found that *A. asychis* demonstrated a distinct non-preference for the drepanosiphid *Sipha flava* (Forbes); the latter group of workers doubted the ability

of *A. asychis* to survive on this aphid in the field. Wood (1958) reported *A. varipes* (Foerster) (as *A. nigritus*) attacked four species of Aphidiidae, but not a drepanosiphid or a fifth aphidid species.

I found only three taxa did not follow this pattern of host specificity: all are in *Aphelinus* (*Aphelinus*), and are relatively more host specific (apparently to a single species or genus) than are the majority of the species in their subgenus. *Aphelinus mali* has been recorded from many species of Aphididae, but is most often found on the pemphigid *Eriosoma lanigerum* (Hausmann). Howard (1929) thought *A. mali* was restricted to aphids with waxy coverings (mostly Pemphigidae) and that other records were misidentifications. Michel (1969) and Kalina and Stary (1976) considered *A. mali* was specific to *E. lanigerum*. In lab trials, Zehavi and Rosen (1988) found that *A. mali* attacked *E. lanigerum* and ignored *Aphis gossypii* Glover (an acceptable host according to Howard [1895]), whereas *A. paramali* Zehavi and Rosen (which closely resembles *A. mali*) exhibited exactly the opposite behavior. *Aphelinus prociphili* Carver has been recorded only from a pemphigid (Carver 1980). This species was placed in the "*A. mali* group" (Zehvi and Rosen 1988). In the field, *Aphelinus asychis* "Israel" has been reared only from *Therioaphis* species, though Finney et al. (1960) found it "readily attacked" *Myzus persicae* (Sulzer) (Aphididae) in the lab. Manglitz and Schalk (1970) reported very low parasitism rates (3%) on *M. persicae*, versus 94% on *T. riehmi*.

Five described *Aphelinus* species have not been placed in Hayat's subgeneric scheme. Hayat (1991b) described *A. nepalensis* without referring it to a subgenus, but noted that it was the most distinctive species in the genus; its host is unknown. *Aphelinus ceratovacunae* Liao was described from eastern Asia (Liao et al. 1987), but its subgeneric placement is unknown. Its rearing from the Hormaphididae (Ho-

Table 1. Number of recorded host aphid species for *Protaphelinus* and *Aphelinus*.

| Genus (subgenus) | Species | Aphid host family* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Unk | Pem | Hor | The | Dre | Gre | Aph | Lac |
| *Protaphelinus* | *nikolskajae* | | 5 | | | | | | |
| | sp. | X | | | | | | | |
| *Aphelinus* (*Indaphelinus*) | *ancer* | | | | | | 1 | | |
| *Aphelinus* (*Mesidia*) | *annulipes* | | | | | 3 | | | |
| | *argiope* | | | | | 3 | | | |
| | *aureus* | | | | | 3 | | | |
| | *automatus* | | | | | 3 | | 1 | |
| | *fulvus* | | | | | 1 | | 1 | |
| | *gilletti* | | | | | | | 1 | |
| | sp. nr. *gilletti* | | | | | 1 | | | |
| | *maculatus* | X | | | | | | | |
| | *paoliellae* | | | | | 1 | | | |
| | *perpallidus* | | | | | 6 | | | |
| | sp. nr. *perpallidus* | | | | | 1 | | 1 | |
| | *subflavescens* | | | | | 17 | | 1 | |
| | sp. nr. *subflavescens* | | | | | 4 | | | |
| | *thomsoni* | | | | | 4 | | | |
| | *tetrataenion* | X | | | | | | | |
| | 4 unidentifed spp. | | | | | 4 | | | |
| *Aphelinus* (*Aphelinus*) | *abdominalis* | | | | 1 | | | 40 | |
| | sp. nr. *abdominalis* | | | | | | | 8 | |
| | *albipodus* | X | | | | | | | |
| | *asychis* "Eur" | | | | | 7 | | 35 | |
| | *asychis* "Israel" | | | | | 4 | | 1 | |
| | *asychis* "NA" | | | | | 2 | | 21 | |
| | sp. nr. *asychis* | | | | | | | 1 | |
| | *campestris* | X | | | | | | | |
| | *certus* | X | | | | | | | |
| | *chaonia* | | | | | 2 | | 40 | 1 |
| | *confusus* | | | | | | | 3 | |
| | *daucicola* | | | | | | | 11 | |
| | *desantisi* | | | | | | | 1 | |
| | *dies* | X | | | | | | | |
| | *flaviventris* | | | | | | | 3 | |
| | *gossypii* | | | | | | | 10 | |
| | *howardii* | | | | | | | 8 | |
| | *humilis* | | | | | | | 10 | |
| | *hyalopteraphidis* | | | | | | | 1 | |
| | *jucundus* | | | | | | | 5 | |
| | *lapisligni* | | | | | | | 2 | |
| | *maidis* | | | | | | | 3 | |
| | *mali* | | 9 | 1 | | | | 16 | |
| | sp. nr. *mali* | | | | | | | 1 | |
| | *mariscusae* | | | | | | | 1 | |
| | *meridionalis* | | | | | | | 4 | |
| | *nox* | X | | | | | | | |
| | *paramali* | | | | | | | 8 | |
| | *prociphili* | | 1 | | | | | | |
| | *sanborniae* | | | | | | | 2 | |
| | sp. nr. *sanborniae* | | | | | | | 1 | |
| | *siphonophorae* | | | | | | | 1 | |
| | *subauriceps* | X | | | | | | | |

Table 1.  Continued.

| Genus (subgenus) | Species | Aphid host family* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Unk | Pem | Hor | The | Dre | Gre | Aph | Lac |
| | *toxopteraphidis* | | | | | | | 2 | |
| | 2 spp. nr. *toxopteraphidis* | | | | | | | 5 | |
| | *varipes* | | | | | 1 | | 18 | |
| | sp. nr. *varipes* | | | | | | | 2 | |
| *Aphelinus* "own group" | *japonicus* | X | | | | | | | |
| *Aphelinus* unplaced | *ceratovacunae* | | | 1 | | | | | |
| | *marlatti* | | | | | | | 1 | |
| | *nepalensis* | X | | | | | | | |
| | *nigra* | | | | | 2 | | | |

* Unk = Unknown; Pem = Pemphigidae; Hor = Hormaphididae; The = Thelaxidae; Dre = Drepanosiphidae; Gre = Greeneidae; Aph = Aphididae; Lac = Lachnidae.

moptera) is unusual among *Aphelinus* and suggests it may belong to a separate group. The Hormaphididae is primarily an Oriental family (mainly on bamboos and palms) (Blackman and Eastop 1984) with few other recorded parasitoids, providing a diverse potential host resource. Hayat (1990, 1991a) considered *A. japonicus* Ashmead (also from eastern Asia and its host unknown) did not belong in any of the three subgenera, and placed it in its own species-group.

*Aphelinus marlatti* (Ashmead) was unplaced to subgenus by Hayat (1990), although Polaszek and Hayat (1989) noted that it appeared to be closest to *A. asychis* and *A. mariscusae* (Risbec), both in the subgenus *Aphelinus*. The only specific host reference is in McLeod (1938), who noted that local populations obtained from an "unidentified species of aphis on cineraria" were successfully reared on *Myzus persicae*.

The placement of *A. nigra* (Lagace) is also problematic. It has been reared from two drepanosiphid genera (Lagace 1969a, Hennessey 1981 [N.B. the latter record should read *Sipha flava* instead of *Siphaflava* sp.]), allying it with *A. (Mesidia)*. This species was first described in *Mesidia* based on antennal characters, but differs from other members of this genus by col-

or, discal cilia, and shape of the funicular segments (Lagace 1969a). Additionally, its ovipositional habits are unique for the genus: females oviposit while standing on, instead of next to, the host (Lagace 1969b). This behavior is similar to that of members of the aphelinid genus *Aphytis*, whose separation from *Aphelinus* was based largely on the difference in metasomal morphological features and ovipositional habits (Timberlake 1924, Compere 1955). Kalina and Stary (1976) noted that such characters may have a significant effect in determining host selection. These morphological and biological characteristics may ultimately justify placement of *A. nigra* outside of *Aphelinus*.

Kalina and Stary (1976) argued that aphelinid host ranges are habitat dependent, and other workers have commented on the crucial roles environmental factors play in the survival and reproduction of *Aphelinus* species (Hagen and van den Bosch 1968, Michel 1969, Schlinger and Hall 1959, van den Bosch et al. 1964). The correlation of aphelinid taxa with different aphid families suggests these host ranges reflect a history of coevolution. The most primitive aphid group (Adelgoidea) has no record of aphelinid parasitoids. The Pemphigidae, Drepanosiphidae and Greeneidae represent successively more de-

rived groups (Heie 1987), and each is attacked by a different taxon of aphelinids. The Aphididae is the most recent and diverse aphid family, and is parasitized by the most diverse *Aphelinus* subgenus. This hypothesis may be tested by a phylogenetic analysis of the aphidophagous Aphelinidae. Although such information is not yet available, an analysis of the Aphelinidae is currently in progress (J. Woolley, pers. comm.).

## ACKNOWLEDGMENTS

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## APPENDIX

New *Aphelinus* spp. host records, 1990–94. (All collections made by R. L. Zuparko). All material deposited in the Essig Museum of Entomology, University of California, Berkeley.

### *Aphelinus automatus* Girault

CALIFORNIA. *ALAMEDA CO.*: Berkeley; *Myzocallis* sp. on *Quercus agrifolia* Nee, 27-VII-1994, 1 male.

### *Aphelinus howardii* Dalla Torre

CALIFORNIA. *ALAMEDA CO.*: Albany; *Macrosiphum* (*Sitobion*) *rhamni* (Clark) on *Rhamnus californica* Eschscholtz, 4-VIII-1994, 1 female, 1 male.

### *Aphelinus* sp. nr. *mali* (Haldemann)

LOUISIANA. *ST. HELENA PAR.*: Highway 38, 5 kms. west of Easleyville; *Illinoia liriodendri*

(Monell) on *Liriodendron tulipifera* L., 29-IV-1992, 4 females.

### *Aphelinus* sp. nr. *perpallidus* Gahan

CALIFORNIA. *ALAMEDA CO.*: Berkeley; *Periphyllus* sp. on *Acer* sp., 11-VIII-1990, 15 females and 14-VI-1991, 4 females. *SONOMA CO.*: Petaluma; *I. liriodendri* on *L. tulipifera*, 29-IV-1992, 1 female (reported as *Aphelinus* sp. in Zuparko and Dahlsten 1993).

### *Aphelinus* sp. nr. *sanborniae* Gahan

CALIFORNIA. *ALAMEDA CO.*: Berkeley; *Aphis pomi* DeGeer on *Cotoneaster pannosa* Franch, 26-VIII-1993, 1 male.

### *Aphelinus subflavescens* (Westwood)

CALIFORNIA. *ALAMEDA CO.*: Berkeley; *Euceraphis gillettei* Davidson on *Alnus* sp., 30-VI-1992, 1 female and 1 male.

# Mexican species of the genus *Omphale* Haliday (Hymenoptera: Eulophidae), a taxonomic study

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*Abstract.*—Mexican species of *Omphale* Haliday are presented, including a key for their identification. The interpretation of *Omphale* and of species groups follows Hansson (1996b). Fortyfour (44) species are included, of which 30 are described as new: *angusticornis* (female), *carinata* (female, male), *cherana* (female, male), *cumbrensis* (male), *dentata* (female, male), *flaviscutellum* (female, male), *fossata* (female), *foveata* (female, male), *fulgida* (female, male), *gracilis* (female), *indistincta* (female, male), *lanceolata* (female), *metallica* (female, male), *nita* (female), *notaula* (female, male), *obscura* (female, male), *oriampla* (female), *pallida* (female, male), *petatlana* (female, male), *petiolata* (male), *sola* (female, male), *stigmalis* (female), *tempora* (female, male), *tria* (female, male), *triangulata* (female), *uruapana* (female, male), *valida* (female, male), *whartoni* (female, male), *woolleyi* (female), *zolnerowichi* (male). Thirteen previously described species are newly recorded from Mexico. The genus is divided into seven species groups, two of which are newly created, in addition there are six unplaced species. The phylogeny of species groups found in North America (including Mexico) is hypothesized. The male genitalia is shown to be a valuable tool for the classification, as was the case with Nearctic species (Hansson 1996b). Nothing is known concerning the biology of the species.

## INTRODUCTION

Mexico holds a major part of the worlds' biodiversity, including many endemic species (McNeely *et al* 1990). The biological wealth is a result of the great habitat variation, complex topography, heterogeneity of soils and climate, geological history and location—being a pathway between two major zoogeographical regions: the Nearctic and Neotropical regions. The insect fauna of Mexico is poorly known, but when studied, e.g. certain groups of beetles (Whitehead 1973, Liebherr 1991) and parasitic wasps (Hansson 1996a), the diversity revealed is high.

*Omphale* Haliday is a large and fairly well known genus in temperate areas. In the Palearctic region Graham (1963) and Gijswijt (1976) have formed a base for the knowledge of *Omphale*. Species of Canada and the United States have been treated recently by Hansson (1996b). *Omphale* is also well represented in subtropical and

tropical areas of the Americas, but is practically unknown taxonomically, and otherwise, from these parts. Prior to this study only one species of *Omphale* was recorded from Mexico.

The biology of *Omphale*-species is very poorly known. The current, scanty knowledge stems mainly from European species, where gallmidges (Diptera: Cecidomyiidae) have been found to be the principal host group (Boucek and Askew 1968; Gijswijt 1976). The few host records from the Nearctic region (Hansson 1996b) support these findings. There are no host records from Mexico.

Compared to *Omphale* in the Palearctic the fauna of Nearctic region (including all of Mexico) has a higher diversity, being richer in both species and species groups. There are no species groups exclusively found in the Palearctic, all groups present in the Palearctic are also found in the Nearctic. The Nearctic region (including

Mexico) holds seven species groups not present in the Palearctic. Also when comparing the number of species, far more have been found in the Nearctic region (including Mexico) (87), than in the Palearctic (34), indicating a peak in diversity in the New World. In the Americas some groups appear only in temperate areas, i.e. species groups of *salicis*, *versicolor* and *acamas*, and these groups are also present in the Palearctic, while others only appear in subtropical to tropical areas, i.e. species groups of *cherana* and *notaula*.

The purpose of this study is to introduce the subtropical and tropical New World species of *Omphale* into the classification of this genus. No such study has ever been published.

This study is based mainly on material from Texas A & M University (TAMU), College Station, with additional material from Canadian National Collection of Insects (CNC), Ottawa and Natural History Museum (BMNH), London. Unless otherwise stated the material is from Mexico.

The method used when studying male genitalia is accounted for in Hansson (1996a). The terminology of male genitalia in *Omphale* is indicated in Fig A. The description of each species includes the bulk of specimens examined, not just the primary type, and the observed variation is included in the descriptive text. Ratios for the species are accounted for in Table 1. The descriptions of previously described species are to be found in Hansson (1996b).

PHYLOGENY AND CLASSIFICATION

The monophyly of *Omphale* was demonstrated by Hansson (1996b) through a single apomorphy, the possession of enlarged volsellar setae on the male genitalia, a unique feature within Entedoninae. These setae are like spears, pointing straight backwards (Figs 92–99, 103–110), occasionally bent (*salicis* group, not represented in Mexico, see figs 176, 177 in Hansson (1996b)). In other genera of Entedoni-
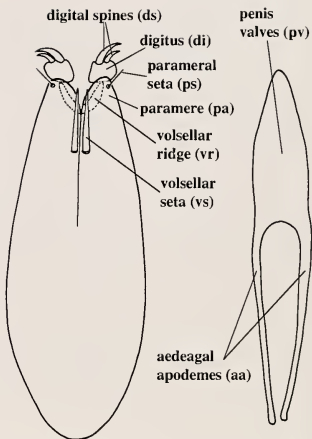


Fig. A.   Male genitalia of *Omphale erginnus* (Walker): phallobase (left) and aedeagus (right). For a discussion of the morphology of male genitalia in Entedoninae see Hansson (1996a).

nae the volsellar setae are thin, or missing (*Perditorulus* only (Hansson 1996a)).

The species groups used in this paper are the same as used in Hansson (1996b), but due to the addition of tropical elements, two species groups are newly created.

When autapomorphies of the species groups (Tab. 2) were excluded, apomorphies accounted for in Tab. 3 were available for analysis of the phylogeny of species groups of *Omphale* in North America (including Mexico). Due to the lack of sufficient number of characters unplaced species were excluded, otherwise the analysis could not be completed. The analysis was carried out using PAUP 3.0, and based on matrix in Tab. 4—character 1 weighted as 2, the others as 1. The analysis yielded two equally parsimonius trees (15 steps, CI=0.67, RI=0.76) (Figs 126, 127).

KEY TO MEXICAN SPECIES OF *OMPHALE*

1. Scape triangular (Fig. 30); forewing with characteristic pattern (Fig. 40) . . . . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 19. **O. triangulata** n.sp. (female)
— Scape not triangular; forewing hyaline, or with different pattern than in Fig. 40 . . . . . . 2
2. Mouth opening very wide (Fig. 85), 1.7× the height of eye in female, 1.5× in male . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 44. **O. tempora** n.sp. (female, male)
— Mouth opening narrower . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3. Frons pale nonmetallic between frontal cross-groove and antennal toruli (sometimes with
dark cross-stripes) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
— Frons with at least upper half between cross-groove and toruli dark and metallic . . . . . 12
4. Scutellum completely dark and metallic . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
— Scutellum completely or partly pale nonmetallic . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
5. Clypeus as long as wide, quadrate . . . . . . . . . . . . . . 20. **O. vinacea** Hansson (female, male)
— Clypeus transverse, or with different shape . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6. Clypeus poorly delimited dorsally (as in Fig. 51) . . . . . . . . . 28. **O. pallida** n.sp. (female)
— Clypeus distinctly delimited . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
7. Flagellomeres 2–4 about as long as wide (Fig. 28) . . . . . . . . . . . . . 18. **O. tria** n.sp. (female)
— Flagellomeres 2–4 longer than wide (Fig. 23) . . . . . 14. **O. divina** (Girault) . . . . . . (female)
8. Clypeus poorly delimited dorsally (as in Fig. 51) . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
— Clypeus distinctly delimited . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10
9. Male flagellum with a single proximal whorl of fine setae on each segment (Fig. 48);
female flagellomeres slender (Fig. 49), with proximal ventral setae from flagellomere 2
and following flagellomeres conspicuously long; 7th gastral tergite in female 3× as long
as wide at base . . . . . . . . . . . . . . . . . . . . . . 23. **O. acuminativentris** (Girault) (female, male)
— Male flagellum with some scattered setae (Fig. 47), setae stout and bent; female flagel-
lomeres stout (Fig. 46), ventral setae short; 7th gastral tergite in female at most 2.3× as
long as wide at base . . . . . . . . . . . . . . . . . . . . 27. **O. obscurinotata** (Girault) (female, male)
10. Clypeus transverse (Fig. 54), with rounded sides . . . . . . 29. **O. angusticornis** n.sp. (female)
— Clypeus as long as wide . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11
11. Mesoscutum and scutellum with strong reticulation, hence dull . . . . . . . . . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16. **O. petatlana** n.sp. (female, male)
— Mesoscutum and scutellum with weak reticulation, hence shiny . . . . . . . . . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 20. **O. vinacea** Hansson (female, male)
12. Notauli complete and deep throughout (Fig. 41) . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13
— Notauli at most delimited in posterior ⅔ . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15
13. Scutellum with two deep pits (Fig. 41) . . . . . . . . . . . . . . 21. **O. foveata** n.sp. (female, male)
— Scutellum without pits . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
14. Mesoscutum and scutellum with weak reticulation; digitus in male genitalia with 2 spines
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22. **O. notaula** n.sp. (female, male)
— Mesoscutum and scutellum with strong engraved reticulation; digitus in male genitalia
with 1 spine (Fig. 107) . . . . . . . . . . . . . . . . . . . . . . . . 43. **O. sola** n.sp. (female, male)
15. Midlobe of mesoscutum with 1 pair (posterior pair) of setae . . . . . . . . . . . . . . . . . . . . 16
— Midlobe of mesoscutum with 2 pairs of setae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17
16. Mouth opening as wide as height of eye in female, 1.3× as wide as height of eye in male;
temples large (Fig. 15) . . . . . . . . . . . . . . . . . . . . . . . . . . 10. **O. cherana** n.sp. (female, male)
— Mouth opening 0.7× as wide as height of eye in female, 1.0× as wide as height of eye
in male; temples small (Fig. 18) . . . . . . . . . . . . . . . 11. **O. flaviscutellum** n.sp. (female, male)
17. Head smooth and shiny, without reticulation; antennal scrobes join slightly below frontal
cross-groove (Fig. 87); male scape with a dent medioventrally (Fig. 79) . . . . . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 39. **O. dentata** n.sp. (female, male)
— Head at least with some reticulation; antennal scrobes join on frontal cross-groove or
meet cross-groove separately; male scape without ventral dent, or with apicoventral dent
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18

18. With pale spots below antennal toruli, or with entire frons below level of toruli pale
    (clypeus sometimes metallic) .......................................................... 19
—   Without pale spots below toruli, frons below level of toruli more or less metallic ..... 28
19. Clypeus poorly delimited, at least dorsally (Figs 51–52) ............................. 20
—   Clypeus distinctly delimited (Figs 54–56, 63) ....................................... 23
20. Clypeus dark and metallic; male flagellomeres with setae confined to a basal whorl (Fig.
    45) ........................................................... 24. *O. fulgida* n.sp. (female, male)
—   Clypeus pale nonmetallic; male flagellomeres with scattered setae (Fig. 83) ........... 21
21. Clypeus with distinct lateral borderlines (as in Fig. 89) ..... 41. *O. indistincta* n.sp. (male)
—   Clypeus poorly delimited throughout .................................................. 22
22. Forewing densely pubescent (Fig. 58) ............... 26. *O. masneri* Hansson (female)
—   Pubescense on forewing less dense (Fig. 57) ........ 28. *O. pallida* n.sp. (female, male)
23. Clypeus yellow to pale brown, nonmetallic .......... 29. *O. angusticornis* n.sp. (female)
—   Clypeus dark and metallic ........................................................... 24
24. Clypeus 8.5× as wide as long (Fig. 63) ............... 31. *O. oriampla* n.sp. (female)
—   Clypeus at most 2.5× as wide as long ................................................ 25
25. Clypeus large (Fig. 56); forewing speculum small (Fig. 64) ..........................
    ........................................................... 34. *O. zolnerowichi* n.sp. (male)
—   Clypeus smaller; forewing speculum larger ........................................... 26
26. Frons close to mouth opening pale nonmetallic; male scape widest medially .........
    ........................................................... 30. *O. cumbrensis* n.sp. (male)
—   Frons close to mouth opening dark and metallic; male scape widest below middle .... 27
27. Female mouth opening 1.2–1.4× the height of an eye; male inseparable from following
    species ............................................... 32. *O. scutellata* (Girault)
—   Female mouth opening as wide as height of an eye ........... 33. *O. vulgaris* Hansson
28. Frons with cross-ridge (Fig. 1) ..................................................... 29
—   Frons without cross-ridge ............................................................ 37
29. 7th gastral tergite in female 4.2× as long as wide at base; dorsellum hidden under scu-
    tellum, not visible in dorsal view ...................... 3. *O. lanceolata* n.sp. (female)
—   7th gastral tergite in female considerably shorter, usually shorter than width of base;
    dorsellum visible in dorsal view ...................................................... 30
30. Clypeus dark and metallic ........................................................... 31
—   Clypeus paler than surrounding frons ................................................ 33
31. Scutellum with strong and dense reticulation, meshes elongate and scutellum hence ap-
    pearing striate ....................................... 7. *O. stigmalis* n.sp. (female)
—   Scutellum with weak to strong reticulation, meshes not elongate and scutellum hence
    not appearing striate ................................................................ 32
32. Frons laterad of clypeus brownish with weak metallic tinge; male genitalia (Fig. 93): inner
    digital spine more curved, outer digital spine stout and straight ...................
    ........................................................... 9. *O. woolleyi* n.sp. (female, male)
—   Frons as dark and metallic as clypeus; male genitalia (Fig. 101): inner digital spine less
    curved, outer digital spine slender and slightly curved ............................
    ........................................................... 5. *O. metallica* n.sp. (female, male)
33. Male: petiole 1.0–1.3× as long as wide, scape elongate with narrow base (Fig. 5), 4.3×
    as long as wide ........................................ 6. *O. petiolata* n.sp. (male)
—   Male: petiole transverse, scape with about same width throughout, or if with narrow
    base then 3× as long as wide ........................................................ 34
34. Female forewing with infuscate area below marginal vein, infuscation reaching to hind
    margin of wing (Fig. 13); male scape widest at base (Fig. 4) ........................
    ........................................................... 8. *O. whartoni* n.sp. (female, male)
—   Female forewing never with just the area below marginal vein infuscate, either complete-
    ly hyaline, or with infuscate area below stigmal vein, or with infuscate area below stigmal
    and marginal veins; male scape widest at apex ...................................... 35

35. Reticulation on thoracic dorsum fine and weak ................................
.............................. 4. *O. marylandensis* (Girault) (female, male)
— Reticulation on thoracic dorsum strong ................................... 36
36. Clypeus comparatively wide, 2.3× as wide as long; female flagellomeres 1–4 compara-
tively short (Fig. 8) ..................... 2. *O. elevata* Hansson (female, male)
— Clypeus narrower, 1.6–1.7× as wide as long; female flagellomeres 1–4 long (Fig. 9) ...
................................ 1. *O. acuminaticornis* (Girault) (female, male)
37. Clypeus distinctly delimited ............................................ 38
— Clypeus poorly delimited, or without upper border ......................... 50
38. Midlobe of mesoscutum delimited from scutellum by a distinct and wide furrow (Fig.
66) ....................................... 35. *O. fossata* n.sp. (female)
— Midlobe of mesoscutum not delimited from scutellum by a furrow .............. 39
39. Flagellum with distinct 3-segmented clava (Figs 28–29), i.e. with apical three flagellom-
eres firmly attached to one another, flagellomeres less than 2× as long as wide ...... 40
— Flagellum without distinct clava, i.e. all flagellomeres with distinct constrictions, flagel-
lomeres usually longer ................................................. 41
40. Female frons predominantly pale nonmetallic; male genitalia (Fig. 95): digitus 9× as long
as wide, volsellar setae placed just below apex of paramera ......................
................................... 18. *O. tria* n.sp. (female, male)
— Female frons dark and metallic; male genitalia (Fig. 99): digitus 3.7× as long as wide,
volsellar setae placed at apex of paramera ......... 13. *O. carinata* n.sp. (female, male)
41. Antennal toruli situated in level with lower level of eyes ......................... 42
— Antennal toruli situated distinctly above lower level of eyes ...................... 45
42. Foretibia with a sharp edge along frontal margin (as in Fig. 71); thoracic dorsum with
raised and rather strong reticulation .............. 17. *O. poeta* (Girault) (female, male)
— Foretibia without edge along frontal margin; thoracic dorsum with engraved fine retic-
ulation ............................................................. 43
43. Females, i.e. gaster with an ovipositor visible in ventral view and reaching along major
part of gaster ...................................... 12. *O. australis* Hansson
— Males ................................................................ 44
44. Male genitalia (Fig. 97): volsellar setae distinctly curved at apex ... 14. *O. divina* (Girault)
— Male genitalia (Fig. 98): volsellar setae straight ............... 12. *O. australis* Hansson
45. Marginal vein as long as height of forewing ................................. 46
— Marginal vein 1.3–1.5× as long as height of forewing .......................... 47
46. Flagellomeres with about same width (Figs 24–25); body dark and metallic ..........
.................................... 15. *O. obscura* n.sp. (female, male)
— First flagellomere distinctly wider than following flagellomeres (Figs 31–32); body yellow
nonmetallic to infuscate ...................... 20. *O. vinacea* Hansson (female, male)
47. Vertex and thoracic dorsum with raised strong reticulation; foretibia with raised carina
along dorsal surface (Fig. 71) ...................... 38. *O. valida* n.sp. (female, male)
— Vertex and thoracic dorsum with weak reticulation; foretibia without raised carina .... 48
48. Mesoscutum and scutellum smooth and shiny, with weak traces of reticulation in some
places; antennal scrobes join below frontal cross-groove .... 42. *O. nita* n.sp. (female, male)
— Mesoscutum and scutellum reticulate; antennal scrobes join on frontal cross-groove ... 49
49. Mouth opening narrower than height of an eye; clypeus more or less quadratic, about
as long as wide .................................. 36. *O. semiglobosa* Hansson (female, male)
— Mouth opening 1.0–1.1 as wide as height of an eye; clypeus semicircular, 2× as wide as
long ........................................ 37. *O. uruapana* n.sp. (female, male)
50. Clypeus pale nonmetallic ......................... 25. *O. gracilis* n.sp. (female)
— Clypeus dark and metallic ............................................. 51
51. Setae on vertex and thoracic dorsum long (Figs 75, 88)—outermost seta on vertex as long

as distance between hind ocelli, hind pair of setae on mesoscutum longer than distance separating them  . . . . . . . . . . . . . . . . . . . . . . . . . . . 40. *O. erginnus* (Walker) (female, male)
— Setae on vertex and thoracic dorsum shorter  . . . . . . . . . . . 41. *O. indistincta* n.sp. (female)

## Omphale Haliday

*Diagnosis.*—Clypeus clearly delimited (in some species vaguely delimited (e.g. Fig. 51), or upper borderline missing (e.g. Figs 52–53)); pronotum reduced and hardly visible from above; reticulation on thoracic dorsum fine and engraved (raised or smooth in a few species); midlobe of mesoscutum with two pair of setae (one pair in species group *cherana*); petiole short and transverse. Volsellar setae in male genitalia enlarged (Figs 92–99, 103–110).

*Omphale* is differentiated from other genera with a delimited clypeus in Hansson (1996b:7).

*Literature.*—Hansson (1996b) revised the Nearctic species of *Omphale*.

### Species group bicincta

*Diagnosis.*—Head with frontal cross-ridge. Male flagellomeres with verticillate setae, i.e. with a single basal whorl of setae on each flagellomere (Figs 4, 5, 7). Male genitalia (Figs 92–93): volsellar setae long and strong and placed just below base of volsellar ridges; digitus long and slender, inner digital spine larger than outer, placed at different levels; paramere protruding with apex pointed, with two setae, one short at apex and one long below apex (not illustrated), or with only one seta at apex of paramere; aedeagus (Fig. 112) long and slender with median part of penis valves expanded, aedeagal apodemes 0.7–0.9× as long as penis valves. Flagellomeres with sensilla ampullacea short and asymmetric (type II sensu Hansson 1996b). Forewing usually with two fuscous spots or bands, one below stigmal vein and one below middle of marginal vein (infuscation lacking in some species, or with only one spot/band below marginal vein (Fig. 13)).

*Apomorphies.*—Head with frontal cross-ridge; male flagellomeres with verticillate setae. Male genitalia: aedeagus with median part of penis valves expanded; digital spines placed at different levels; digitus elongate.

### 1. Omphale acuminaticornis (Girault) (Figs 9, 12)

*Achrysocharella acuminaticornis* Girault, 1916b:50.
*Omphale acuminaticornis* (Girault), Yoshimoto 1978:716.

*Diagnosis.*—Thoracic dorsum with very strong and raised reticulation; clypeus narrow, 1.7× as wide as long, slightly paler than surrounding frons in female, pale nonmetallic in male; flagellomeres long and slender in female.

*Distribution.*—Campeche, Oaxaca, Veracruz. 9 females. New record for Mexico.

### 2. Omphale elevata Hansson (Figs 8, 92)

*Omphale elevata* Hansson, 1996b:27.

*Diagnosis.*—Thoracic dorsum with strong and raised reticulation; clypeus wide, 2.3× as wide as long, slightly paler than surrounding frons in female, pale nonmetallic in male; flagellomeres comparatively short in female.

*Distribution.*—Chiapas, Colima, Guerrero, Jalisco, Michoacan, Oaxaca, Puebla, Tamaulipas, Veracruz. 77 females, 48 males. New record for Mexico.

### 3. Omphale lanceolata n.sp.

*Type material.*——Holotype female labelled "Tamaulipas, 2mi W Gomez Farias, 5.vii.1986, G. Zolnerowich" (USNM).

*Etymology.*——Name referring to lanceolate gaster in females of this species.

*Diagnosis.*——Thoracic dorsum with strong and raised reticulation; clypeus dark and metallic in female (male un-

known); last tergite of female gaster elongate, 4.2× as long as wide at base; dorsellum hidden under scutellum, not visible in dorsal view.

*Description (female).*—Length of body = 2.4 mm.

Colour: Scape pale with apical tip infuscate; pedicel and flagellum dark. Frons and vertex metallic greenish-blue. Clypeus dark and metallic. Mesoscutum and scutellum with weak metallic bluish-purple tinges. Propodeum metallic bluish-green. Coxae dark and metallic; femora dark; tibiae and tarsi pale. Wings infuscate. Petiole pale. Gaster with 1st tergite metallic bluish-green, remaining tergites golden-green.

Head: Antenna as in *O. stigmalis* (Fig. 10). Frons and vertex with weak superficial reticulation. Clypeus transverse, 1.7× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove almost straight. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with strong reticulation. Forewing speculum open below; without stigmal hairline and with radial cell hairy.

Metasoma: Female gaster elongate, last tergite long, 4.2× as long as wide at base.

## 4. Omphale marylandensis (Girault)

*Rhicnopeltomyia marylandensis* Girault, 1916b:39.
*Achrysocharis athanasii* Girault, 1917c:3, syn. Hansson (1996b:28)
*Omphale marylandensis* (Girault), Schauff 1991:75.

*Diagnosis.*—Thoracic dorsum with weak and raised reticulation; clypeus distinctly to only slighter paler than surrounding frons in female, pale nonmetallic in male.

*Distribution.*—Guerrero, Michoacan. 2 females. New record for Mexico.

## 5. Omphale metallica n.sp.
(Figs 6, 7, 101)

*Type material.*—Holotype male labelled "Chiapas, Ocozocoautla, 8.viii.1990, 1800–2200', J.B. Woolley, 90/055B" (USNM). Paratypes: 6 females 4 males with same label data as holotype (3 females 2 males

LUZM, 3 females 2 males TAMU); 3 males "Chiapas, Municipal Tenejapa Paraje Yashanal, 5200–5800', 4.viii.1990, J.B. Woolley, 90/052" (1 male LUZM, 2 males TAMU); 1 female "Chiapas, 100km SE Palenque, Bonanpak, 9.vii.1983, 230m, M. Kaulbars" (CNC); 1 male "Chiapas, San Cristobal las Casas, 1–12.vii.1969, 7200'" (CNC); 1 female "Campeche, 10km W Xpujil, Chicanna, 12–14.vii.1983, 300m, M. Kaulbars" (CNC); 1 female 1 male "Colima, 9mi N Comala, 12.vii.1984, J.B. Woolley, 84/030" (TAMU); 1 male "Guerrero, 18.2mi S Iguala, 5.vii.1987, 3800', J.B. Woolley, 87/013" (TAMU); 2 females "Guerrero, 17mi E Tixtla, 11.vii.1985, J.B. Woolley and G. Zolnerowich, 85/050" (LUZM); 1 female 1 male "Guerrero, 7mi W Chilapa, 16.vii.1984, J.B. Woolley, 84/036" (TAMU); 1 male "Guerrero, 15mi SW Chichihualco, 15.vii.1984, J.B. Woolley, 84/034" (LUZM); 2 females "Guerrero, 6mi NE Tixtla de Guerrero, 16.vii.1984, J.B. Woolley, 84/035" (LUZM); 1 female "Guerrero, 2mi E Ocotito, 11.vii.1985, J.B. Woolley, 85/048" (TAMU); 1 female 1 male "Guerrero, 32mi SE Petatlan, 10.vii.1985, J.B. Woolley, 85/047" (TAMU); 1 female 5 males "Guerrero, 5mi NW El Ocotito, 7.vii.1987, 2500–3200', R. Wharton", 1 male gaster on slide (no. 271) (3 males LUZM, 1 female 2 males TAMU); 1 male "Guerrero, 2mi NE Cacahuamilpa, 4.vii.1987, 5300', R. Wharton" (TAMU); 1 male "Guerrero, 6mi E Xochipala, 5.vii.1987, 3500', J.B. Woolley, 87/014" (LUZM); 1 female 3 males "Jalisco, 16mi S Autlan, 8.vii.1984, J.B. Woolley, 84/025" (1 female 1 male LUZM, 2 males TAMU); 1 female "Jalisco, 5.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/022" (TAMU); 10 females 1 male "Oaxaca, 3.9mi NE San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley, 85/067" (5 females LUZM, 5 females 1 male TAMU); 2 females "Oaxaca, 15.1mi N San Gabriel Mixtepec, 11.vii.1987, 3850', J.B. Woolley and G. Zolnerowich, 87/031" (LUZM, TAMU); 9 females "Oaxaca, 4.4mi S San

Table 1. Ratios of Mexican *Omphale*. Abbreviations: HE = height of eye; HW = height of wing; LA = length of aedeagal apodeme; LD = length of digitus; LG = length of gaster; LM = length of marginal vein; LP = length of penis valves; LW = length of wing; MM = length of mesosoma; MS = malar space; OOL = shortest distance between compound eye and lateral ocellus; PM = length of postmarginal vein; POL = distance between lateral ocelli; ST = length of stigmal vein; WD = width of digitus; WH = width of head; WM = width of mouth opening; WT = width of thorax, measured across hind part of mesoscutum. Unless otherwise stated ratios are from both sexes.

| *Omphale* species | WM/HE ♀ | WM/HE ♂ | MS/HE ♀ | MS/HE ♂ | POL/OOL | WH/ST | PM/ST | LW/LM |
|---|---|---|---|---|---|---|---|---|
| *acuminaticornis* (Gir.) | 0.8–1.0 | 1.1 | 0.2–0.3 | 0.4 | 1.4–1.8 | 1.3 | 1.4–2.3 | 1.8–1.9 |
| *elevata* Hansson | 1.1 | 1.1–1.3 | 0.2–0.3 | 0.2–0.3 | 1.6–2.3 | 1.3 | 1.2–2.0 | 1.6–1.7 |
| *lanceolata* n. sp. | 0.8 | — | 0.3 | — | 1.4 | 1.2 | 1.9 | 1.7 |
| *marylandensis* (Gir.) | 0.8–1.2 | 1.0–1.1 | 0.2–0.3 | 0.3–0.4 | 1.6–2.0 | 1.3 | 1.1–2.0 | 1.7–1.9 |
| *metallica* n.sp. | 0.7 | 0.8 | 0.2 | 0.3 | 2.2 | 1.4 | 1.4 | 1.8 |
| *petiolata* n.sp. | — | 1.0 | — | 0.3 | 1.8 | 1.2 | 1.6 | 1.7 |
| *stigmalis* n.sp. | 1.0 | — | 0.4 | — | 1.3 | 1.2 | 0.8 | 1.7 |
| *whartoni* n.sp. | 0.8 | 1.2 | 0.2 | 0.2 | 1.8 | 1.3 | 1.2 | 1.8 |
| *woolleyi* n.sp. | 1.1 | 1.4 | 0.3 | 0.3 | 1.8 | 1.3 | 1.3 | 1.8 |
| *cherana* n.sp. | 1.0 | 1.3 | 0.2 | 0.3 | 1.5 | 1.1 | 1.1 | 1.7 |
| *flaviscutellum* n.sp. | 0.7 | 1.0 | 0.1 | 0.2 | 0.9 | 1.3 | 1.3 | 1.7 |
| *australis* Hansson | 1.0–1.1 | 0.8–1.3 | 0.2–0.3 | 0.3–0.4 | 1.6–2.3 | 1.1 | 0.6–0.7 | 1.9–2.1 |
| *carinata* n.sp. | 1.1 | 1.0 | 0.3 | 0.4 | 1.4 | 1.3 | 0.4 | 2.0 |
| *divina* (Gir.) | 0.7–1.0 | 0.8–1.1 | 0.3 | 0.2–0.5 | 1.5–2.8 | 1.2 | 0.4–0.8 | 1.9–2.0 |
| *obscura* n.sp. | 0.9 | 1.0 | 0.4 | 0.4 | 1.3 | 1.1 | 0.9 | 2.1 |
| *petatlana* n.sp. | 0.9 | 1.1 | 0.3 | 0.4 | 1.9 | 1.2 | 0.4 | 2.1 |
| *poeta* (Gir.) | 1.2–1.3 | 1.2–1.5 | 0.3–0.4 | 0.2–0.5 | 2.0–2.6 | 1.2 | 0.5–0.7 | 2.0–2.1 |
| *tria* n.sp. | 1.0 | 1.0 | 0.2 | 0.3 | 1.4 | 1.1 | 0.5 | 2.1 |
| *triangulata* n.sp. | 1.1 | — | 1.1 | — | 1.4 | 1.4 | 0.9 | 1.8 |
| *vinacea* Hansson | 0.6–0.9 | 0.9–1.1 | 0.3 | 0.3–0.5 | 1.1–1.7 | 1.3 | 0.5–0.7 | 1.9–2.1 |
| *foveata* n.sp. | 0.7 | 0.6 | 0.1 | 0.2 | 1.3 | 1.2 | 1.2 | 2.0 |
| *notaula* n.sp. | 0.6 | 1.2 | 0.1 | 0.2 | 1.8 | 1.2 | 1.0 | 1.6 |
| *acuminativentris* (Gir.) | 0.9–1.2 | 0.8–1.1 | 0.2–0.3 | 0.2–0.4 | 1.7–2.1 | 1.1 | 1.0–1.1 | 1.9–2.0 |
| *fulgida* n.sp. | 1.0 | 1.2 | 0.3 | 0.3 | 1.3 | 1.2 | 1.5 | 2.0 |
| *gracilis* n.sp. | 1.3 | — | 0.3 | — | 1.7 | 1.3 | 0.6 | 2.2 |
| *masneri* Hansson | 1.3–1.4 | 1.2 | 0.3 | 0.4 | 1.2–1.8 | 1.2 | 0.5–0.9 | 2.2 |
| *obscurinotata* (Gir.) | 1.1–1.4 | 1.3–1.5 | 0.3–0.4 | 0.3–0.4 | 1.4–2.8 | 1.1 | 0.6–0.8 | 2.0–2.1 |
| *pallida* n.sp. | 1.1 | 0.9 | 0.3 | 0.2 | 1.7 | 1.3 | 1.2 | 2.0 |
| *angusticornis* n.sp. | 1.2 | — | 0.3 | — | 1.6 | 1.1 | 0.7 | 1.9 |
| *cumbrensis* n.sp. | — | 1.1 | — | 0.4 | 2.0 | 1.2 | 1.1 | 1.9 |
| *oriampla* n.sp. | 1.3 | — | 0.3 | — | 1.4 | 1.3 | 0.8 | 1.9 |
| *scutellata* (Gir.) | 1.2–1.4 | 1.0–1.4 | 0.2–0.3 | 0.2–0.3 | 1.4–2.3 | 1.3 | 0.6–1.2 | 1.8–2.0 |
| *vulgaris* Hansson | 1.0 | 1.0–1.4 | 0.2–0.4 | 0.2–0.3 | 1.5–2.3 | 1.2 | 0.6–1.3 | 1.8–2.0 |
| *zolnerowichi* n.sp. | — | 1.0 | — | 0.2 | 2.0 | 1.4 | 0.9 | 1.8 |
| *fossata* n.sp. | 0.6 | — | 0.2 | — | 1.7 | 1.3 | 0.9 | 1.8 |
| *semiglobosa* Hansson | 0.7–0.8 | 0.7–0.9 | 0.1–0.2 | 0.1–0.2 | 1.2–1.6 | 1.4 | 1.7–2.5 | 1.7–1.8 |
| *uruapana* n.sp. | 1.0 | 1.1 | 0.2 | 0.3 | 1.2 | 1.2 | 1.4 | 1.7 |
| *valida* n.sp. | 0.9 | — | 0.2 | — | 1.2 | 1.1 | 1.0 | 1.6 |
| *dentata* n.sp. | 0.7 | 0.7 | 0.2 | 0.2 | 2.3 | 1.5 | 1.1 | 1.8 |
| *erginnus* (Walker) | 0.9–1.1 | 0.9–1.1 | 0.2–0.4 | 0.2–0.4 | 1.8–2.6 | 1.3 | 0.7–1.2 | 1.8–1.9 |
| *indistincta* n.sp. | 1.1 | 1.2 | 0.3 | 0.3 | 1.7 | 1.1 | 1.0 | 1.9 |
| *nita* n.sp. | 1.2 | — | 0.2 | — | 1.2 | 1.3 | 1.5 | 1.7 |
| *sola* n.sp. | 1.1 | 1.1 | 0.2 | 0.3 | 1.9 | 1.3 | 1.0 | 1.8 |
| *tempora* n.sp. | 1.7 | 1.5 | 0.2 | 0.3 | 1.1 | 1.3 | 2.0 | 1.7 |

Table 1. Extended.

| LW/HW | LA/LP | LD/WD | MM/LG ♀ | MM/LG ♂ |
|---|---|---|---|---|
| 1.7–1.9 | — | — | 0.9 | 0.9–1.0 |
| 1.7–1.8 | 0.8 | 5.8 | 0.8 | 0.8–0.9 |
| 2.1 | — | — | 0.4 | — |
| 1.8–2.1 | — | — | 0.5–0.8 | 0.7–1.0 |
| 1.7 | 0.7 | 5.8 | 0.6–0.8 | 0.7–0.9 |
| 1.9 | 0.9 | 4.9 | — | 0.7–0.9 |
| 1.9 | — | — | 0.5–0.6 | — |
| 1.8 | 0.8 | 3.8 | 0.6–0.7 | 0.7–1.0 |
| — | 0.8 | 5.8 | 0.5–0.6 | 0.8–0.9 |
| 2.4 | 1.0 | 1.2 | 0.6–0.7 | 0.6–0.8 |
| 2.3 | 0.9 | 1.2 | 0.5–0.6 | 0.6–0.7 |
| 1.7–1.9 | 0.5 | 5.5 | 0.6–0.8 | 0.7–0.9 |
| 1.8 | 0.8 | 3.7 | 0.6–0.7 | 0.8 |
| 1.8–2.0 | 0.7 | 7.0 | 0.5–0.7 | 0.7–0.8 |
| — | — | 2.8 | 0.4 | 0.7 |
| 1.8 | 0.9 | 2.8 | 0.6–0.7 | 1.0–1.2 |
| 1.7–1.8 | 0.9 | 2.0 | 0.5–0.7 | 0.7–0.9 |
| — | 0.6 | 9.0 | 0.6–0.7 | 0.7–0.8 |
| 1.8 | — | — | 0.5 | — |
| 2.0–2.1 | 1.0 | 2.7 | 0.6–0.7 | 0.8–0.9 |
| 1.9 | 0.9 | 2.0 | 0.7–0.9 | 0.7–0.8 |
| 1.3 | 0.8 | 3.0 | 0.7–0.9 | 0.8–1.0 |
| 1.6–1.9 | 1.0 | 0.5 | 0.4–0.5 | 0.8–1.0 |
| 1.8 | 1.0 | 0.5 | 0.7–0.9 | 0.7–0.8 |
| — | — | — | 0.7 | — |
| 2.2 | — | — | 0.6 | 0.8 |
| 1.6–1.8 | 1.0 | 0.4 | 0.4–0.7 | 0.7–0.9 |
| 1.9 | 0.9 | 0.5 | 0.6 | 0.8–1.2 |
| 1.8 | — | — | 0.6–0.7 | — |
| 1.9 | 0.8 | 1.5 | — | 0.8–0.9 |
| 1.7 | — | — | 0.7–0.9 | — |
| 1.6–1.7 | 0.8 | 0.7 | 0.5–1.0 | 0.7–1.0 |
| 1.5–1.8 | 0.8 | 0.7 | 0.4–0.8 | 0.7–1.0 |
| — | 0.6 | 2.3 | — | 0.8–0.9 |
| 2.2 | — | — | 0.6 | — |
| 1.9–2.6 | 0.8 | 2.9 | 0.5–0.6 | 0.7–0.9 |
| — | 0.8 | 4.0 | 0.5–0.7 | 0.7–0.8 |
| 2.3 | — | — | 0.5 | — |
| 1.9 | 1.1 | 1.0 | 0.5–0.7 | 0.7–0.8 |
| 1.8–2.0 | 1.3 | 1.0 | 0.5–0.6 | 0.7–0.9 |
| 2.2 | 0.9 | 1.0 | 0.5–0.8 | 0.7 |
| — | — | — | 0.4 | — |
| 1.7 | 0.7 | 2.8 | 0.6–0.8 | 0.7–0.9 |
| 2.4 | 0.6 | 1.5 | 0.6 | 0.6–1.0 |

Table 2. Autapomorphies for species groups of *Omphale*.

| Species group | Derived character states |
|---|---|
| *bicincta* group | Aedeagus with median part of penis valves expanded (Fig. 112) |
| *cherana* group | Midlobe of mesoscutum with 1 pair of setae; volsellar setae short and rather weak, placed close to apex of phallobase (Fig. 94) |
| *divina* group | Volsellar setae placed apically on phallobase (Figs 96–99) |
| *notaula* group | Notauli complete and deep throughout; digitus with concavity in basal outer half (Fig. 103) |
| *obscurinotata* group | Clypeus poorly delimited (Figs 51–53) |
| *scutellata* group | Inner apical corner of paramere drawn out (Fig. 105); clypeus with rounded sides (Figs 54–56) |
| *semiglobosa* group | Forewing long and narrow |

Table 3. Apomorphies within *Omphale*, excluding autapomorphies for the genus and the species groups.

| No | Character | Derived character state |
|---|---|---|
| 1 | Frontal cross-ridge | Present (Fig. 1) |
| 2 | Volsellar setae, placement | Placed at different levels (Figs 103–105, 109) |
| 3 | Digital spines, placement | Placed at different levels (Figs 92, 101, 106) |
| 4 | Digitus, shape | Elongate (e.g. Figs 93, 100–102) |
| 5 | Clypeus | Without upper border (Figs 51–53, 88, 89) |
| 6 | Sensilla ampullacea, shape | Elongate and asymmetric (type III sensu Hansson 1996b) |
| 7 | Arrangement of setae on male flagellomeres | Verticillate (i.e. with setae confined to a basal whorl on each flagellomere) (e.g. Fig. 5) |

Table 4. Character matrix for species groups of *Omphale*. 0 = plesiomorphic, 1 = apomorphic. Character 8 is size of volsellar setae: 0 is thin setae, 1 is enlarged setae. *Asecodes* Förster is used as outgroup.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| *Asecodes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *acamas* group | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *bicincta* group | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| *cherana* group | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *divina* group | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| *notaula* group | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *obscurinotata* group | 0 | 0 | 0 | 0 | 0 | 0 | 0,1 | 1 |
| *salicis* group | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *scutellata* group | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *semiglobosa* group | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *versicolor* group | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

Gabriel Mixtepec, 10–11.vii.1987, 2500′, J.B. Woolley and G. Zolnerowich, 87/027A″ (5 females LUZM, 4 females TAMU); 5 females 3 males "Oaxaca, 4.7mi S San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/066″ (2 females 2 males LUZM, 3 females 1 male TAMU); 2 females 8 males "Oaxaca, 2mi N Candelaria Loxicha, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/068″ (1 female 4 males LUZM, 1 female 4 males TAMU); 3 males "Oaxaca, 4.4mi NE San Pedro Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/065″ (1 male LUZM, 2 males TAMU); 1 female 4 males "Oaxaca, 8mi NE El Punto, 18,vii,1985, J.B. Woolley and G. Zolnerowich, 85/074″ (1 female 2 males LUZM, 2 males TAMU); 1 female 2 males "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80′, J.B. Woolley and G. Zolnerowich, 87/038″ (TAMU); 2 males "Puebla, 4.7mi SW La Cumbre, 23.vii.1987, 5100′, J.B. Woolley, 87/055″ (LUZM, TAMU); 1 female 2 males "Tamaulipas, Reserva El Cielo Gomez Farias, 28.vii.1993, 450m, J.B. Woolley, 93/025″ (LUZM); 1 male "Tamaulipas, Reserva El Cielo San Jose, 29.vii.1993, J.B. Woolley, 93/033″ (TAMU); 1 male "Tamaulipas, Reserva El Cielo Alta Cimas, 30.vii.1993, 3100′, J.B. Woolley and K. Wikse, 93/035″ (TAMU); 1 female 2 males "Veracruz, 3mi

E Huatusco, 23.vii.1984, J.B. Woolley, 84/049a″ (LUZM); 1 male "Veracruz, 11mi S Misantla, 24.vii.1984, J.B. Woolley, 84/051″ (TAMU); 1 female "Veracruz, 3mi NE Huatusco, 22.vii.1985, J.B. Woolley, 85/084″ (TAMU); 1 male "Veracruz, Catemaco, 31.vii.1983, M. Kaulbars" (CNC).

*Etymology.*—Name referring to metallic clypeus.

*Diagnosis.*—Thoracic dorsum with weak and superficial to strong raised reticulation; clypeus dark and metallic, as dark and shiny as frons in both sexes.

*Description.*—Length of body female= 1.2–1.6 mm, male= 0.9–1.3 mm.

Colour: Scape pale with apical ¼ infuscate; pedicel and flagellum dark. Female frons below cross-groove golden-red, above cross-groove golden-green; entire male frons metallic bluish-green or bluish-purple. Clypeus dark and metallic, as dark and shiny as frons. Vertex golden-red or golden-green. Mesoscutum and scutellum golden-green, golden-red, golden-purple or metallic bluish-green. Dorsellum golden-red. Propodeum golden-green or metallic bluish-green. Coxae dark and metallic, pale in a few specimens; femora infuscate to pale; tibiae pale; tarsi infuscate to pale. Wings hyaline, or with infuscate spot below stigmal vein, or with infuscate spot below stigmal vein and with infuscate stripe below median marginal vein reaching to hind margin of wing. Petiole pale to dark. Gaster with 1st tergite metallic bluish-green or golden-green, remaining tergites golden-purple.

Head: Antennae as in Figs 6, 7. Frons and vertex smooth and shiny or with weak superficial reticulation. Clypeus transverse, 1.4× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove V-shaped. Occipital margin with weak edge.

Mesosoma: Mesoscutum and scutellum with weak and superficial to strong reticulation. Dorsellum small, flat and smooth. Forewing speculum open below (closed in

Table 5. Mexican (M) and Nearctic (N) species of *Omphale*. Species also occurring in the Palearctic region is marked with a P.

| Species | Group | Distribution |
|---------|-------|-------------|
| *acamas* (Walker) | *acamas* | (N, P) |
| *acuminaticornis* (Girault) | *bicincta* | (M, N) |
| *acuminativentris* (Girault) | *obscurinotata* | (M, N) |
| *angusticornis* n.sp. | *scutellata* | (M) |
| *aureopurpurea* Hansson | *acamas* | (N) |
| *australis* Hansson | *divina* | (M, N) |
| *bicincta* Ashmead | *bicincta* | (N) |
| *brevicornis* Hansson | *acamas* | (N) |
| *carinata* n.sp. | *divina* | (M) |
| *cherana* n.sp. | *cherana* | (M) |
| *clavata* Hansson | *scutellata* | (N) |
| *clypealba* Hansson | unplaced | (N) |
| *clypeolata* Hansson | *scutellata* | (N) |
| *cumbrensis* n.sp. | *scutellata* | (M) |
| *dentata* n.sp. | unplaced | (M) |
| *deplanata* Hansson | unplaced | (N) |
| *divina* (Girault) | *divina* | (M, N) |
| *elevata* Hansson | *bicincta* | (M, N) |
| *elongata* n.sp. | *divina* | (N) |
| *erginnus* (Walker) | unplaced | (M, N, P) |
| *exodonta* Hansson | *scutellata* | (N) |
| *exserta* Hansson | *obscurinotata* | (N) |
| *filicornis* Hansson | unplaced | (N) |
| *flavicephala* Hansson | *divina* | (N) |
| *flavifacies* Hansson | unplaced | (N) |
| *flavifrons* Hansson | *divina* | (N) |
| *flaviscutellum* n.sp. | *cherana* | (M) |
| *fossata* n.sp. | *semiglobosa* | (M) |
| *foveata* n.sp. | *notaula* | (M) |
| *fulgida* n.sp. | *obscurinotata* | (M) |
| *gracilicornis* (Hansson) | *versicolor* | (N) |
| *gracilis* n.sp. | *obscurinotata* | (M) |
| *indistincta* n.sp. | unplaced | (N) |
| *laevigata* Hnasson | unplaced | (N) |
| *lanceolata* n.sp. | *bicincta* | (M) |
| *longiseta* Hansson | *versicolor* | (N) |
| *marginalis* Hansson | *bicincta* | (N) |
| *marylandensis* (Girault) | *bicincta* | (M, N) |
| *masneri* Hansson | *obscurinotata* | (M, N) |
| *mellea* Hansson | *obscurinotata* | (N) |
| *metallica* n.sp. | *bicincta* | (M) |
| *nita* n.sp. | unplaced | (M) |
| *nitida* Hansson | *divina* | (N) |
| *notaula* Hansson | *notaula* | (M) |
| *obscura* n.sp. | *divina* | (M) |
| *obscurinotata* (Girault) | *obscurinotata* | (M, N) |
| *ocelliparva* Hansson | *acamas* | (N) |
| *oculiparva* Hansson | *versicolor* | (N) |
| *oriampla* n.sp. | *scutellata* | (N) |
| *orilata* Hansson | *scutellata* | (N) |
| *pallida* n.sp. | *obscurinotata* | (M) |
| *pedicellata* Hansson | *scutellata* | (N) |

Table 5. Continued.

| Species | Group | Distribution |
|---------|-------|-------------|
| *petatlana* n.sp. | *divina* | (M) |
| *petiolata* n.sp. | *bicincta* | (M) |
| *pilosa* Hansson | *semiglobosa* | (N) |
| *poeta* (Girault) | *divina* | (M, N) |
| *prasina* Hansson | unplaced | (N) |
| *purpurea* Hansson | *versicolor* | (N) |
| *radialis* (Thomson) | *salicis* | (N, P) |
| *salicis* Haliday | *salicis* | (N, P) |
| *scutellata* (Girault) | *scutellata* | (M, N) |
| *semiglobosa* Hansson | *semiglobosa* | (M, N) |
| *setosa* Hansson | *bicincta* | (N) |
| *sola* n.sp. | unplaced | (M) |
| *speciosa* Hansson | *semiglobosa* | (N) |
| *stigmalis* n.sp. | *bicincta* | (M) |
| *straminea* Hansson | *salicis* | (N) |
| *sublaevis* (Boucek) | *scutellata* | (N) |
| *taborskyi* (Boucek) | *bicincta* | (N) |
| *tempora* n.sp. | unplaced | (M) |
| *theana* (Walker) | *salicis* | (N, P) |
| *triangulata* n.sp. | *divina* | (M) |
| *triclava* Hansson | *salicis* | (N) |
| *tria* n.sp. | *divina* | (M) |
| *uruapana* n.sp. | *semiglobosa* | (M) |
| *valida* n.sp. | *semiglobosa* | (M) |
| *varia* (Hansson) | unplaced | (N) |
| *versicolor* (Nees) | *versicolor* | (N, P) |
| *vinacea* Hansson | *divina* | (M, N) |
| *viridiscutellum* (Girault) | *versicolor* | (N) |
| *vulgaris* Hansson | *scutellata* | (M, N) |
| *wahli* Hansson | *bicincta* | (N) |
| *whartoni* n.sp. | *bicincta* | (M) |
| *woolleyi* n.sp. | *bicincta* | (N) |
| *zolnerowichi* n.sp. | *scutellata* | (M) |

2 males); without stigmal hairline and with radial cell hairy.

Metasoma: Female gaster ovate. Male genitalia (Fig. 101) with outer digital spine narrow and slightly curved; paramere with two setae.

### 6. Omphale petiolata n.sp.
(Figs 5, 102)

*Type material.*—Holotype male labelled "Guerrero, 6.6mi SW Filo de Caballo, 12.vii.1985, J.B. Woolley, 85/051" (USNM). Paratypes: 3 males with same label data as holotype, 1 gaster on slide (no. 270) (1 male LUZM, 2 males TAMU); 2 males "Guerrero, 5mi SW Filo de Caballo,
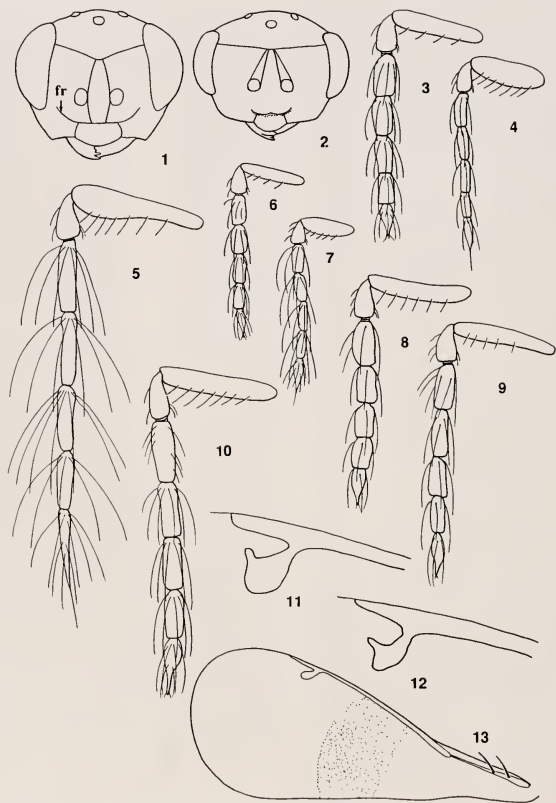
Figs. 1–13. 1–2. Head, frontal. 1, *woolleyi*, female (fr= frontal cross-ridge). 2, *whartoni*, male. 3–10. Antennae. 3, *whartoni*, female. 4, Ditto, male. 5, *petiolata*, male. 6, *metallica*, female. 7, Ditto, male. 8, *elevata*, female. 9, *acuminaticornis*, female. 10, *stigmalis*, female. 11–12. Stigmal vein. 11, *stigmalis*. 12, *acuminaticornis*. 13, Forewing, *whartoni*.

17.vii.1984, J.B. Woolley, 84/037a", 1 gaster on slide (no. 277) (LUZM, TAMU); 1 male "Guerrero, 6.2mi SW Xochipala, 13.vii.1985, J.B. Woolley, 85/056" (TAMU); 1 male "Chiapas, San Cristobal Reserva Huitepec, 7300–7500', 3.viii.1990, J.B. Woolley, 90/051A" (LUZM); 4 males "Oaxaca, 10.7mi N Guelatao de Juarez, 17.vii.1987, 8500', R. Wharton" (2 males LUZM, 2 males TAMU); 2 males "Oaxaca, Llano des Flores, 17.vii.1987, 8900', R. Wharton", 1 gaster on slide (no. 272) (LUZM, TAMU); 1 male "Oaxaca, 6.1mi NE Mitla, 20.vii.1985, J.B. Woolley, 85/077" (TAMU); 1 male "Oaxaca, 1.4mi NE La Cumbre, 18.vii.1985, J.B. Woolley and G. Zolnerowich, 85/075" (LUZM).

*Etymology.*—Name referring to elongate petiole in males of this species.

*Diagnosis.*—Thoracic dorsum with weak to strong raised reticulation; clypeus dark with weak metallic tinges to white, but always paler than surrounding frons; male scape long, narrow at base (Fig. 5); male petiole elongate, 1.0–1.3× as long as wide.

*Description (male).*—Length of body= 1.2–2.0 mm.

Colour: Scape pale with apical ½ dark and metallic; pedicel and flagellum dark. Frons metallic bluish-green or golden-green. Clypeus dark with weak metallic tinges, to white. Vertex golden-purple. Mesoscutum and scutellum golden-green or metallic bluish-green. Dorsellum golden-green. Propodeum golden-green. Fore and mid coxae dark and metallic, hind coxa pale with dark base, to all coxae pale; femora dark with pale stripes on either side, to completely pale; tibiae pale with dark stripe laterally; tarsi infuscate. Forewing with infuscate spot below stigmal vein and with infuscate stripe below median marginal vein reaching to hind margin of wing, to completely hyaline. Petiole pale to dark. Gaster with 1st tergite metallic bluish-green, remaining tergites golden-purple.

Head: Antenna as in Fig. 5. Frons and vertex smooth and shiny, inside ocellar

triangle with weak superficial reticulation. Clypeus transverse, 2.2× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove almost straight. Occipital margin with weak edge.

Mesosoma: Mesoscutum and scutellum with strong to weak reticulation. Dorsellum small, flat and smooth. Forewing speculum open or closed below; without stigmal hairline and with radial cell hairy.

Metasoma: Petiole elongate, 1.0–1.3× as long as wide. Male genitalia (Fig. 102) with outer digital spine stout; paramere with two setae.

### 7. **Omphale stigmalis** n.sp.
(Figs 10, 11)

*Type material.*—Holotype female labelled "Oaxaca, Llano de las Flores, 17.vii.1987, 8900', R. Wharton" (USNM). Paratypes: 2 females with same label data as holotype (LUZM, TAMU).

*Etymology.*—Name referring to enlarged stigmal vein in this species.

*Diagnosis.*—Thoracic dorsum with strong dense reticulation, on scutellum with elongate meshes which therefore appears striate; clypeus dark and metallic; stigmal vein enlarged.

*Description (female).*—Length of body= 2.0–2.9 mm.

Colour: Scape pale with apical tip infuscate; pedicel and flagellum dark. Frons metallic bluish-purple. Clypeus dark and metallic. Vertex metallic bluish-green. Mesoscutum and scutellum metallic bluish-green. Dorsellum metallic bluish-green. Propodeum golden-green. Coxae dark and metallic; femora pale, hind femur with apical ½ infuscate; tibiae pale; tarsi pale to infuscate. Forewing with infuscate spot below stigmal vein and with infuscate stripe below median marginal vein reaching to hind margin of wing (infuscation weak in one specimen). Petiole pale. Gaster with 1st tergite metallic bluish-green, remaining tergites golden-green.

Head: Antenna as in Fig. 10. Frons and

vertex with weak reticulation. Clypeus transverse, 1.7× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove almost straight. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with strong and dense reticulation, on scutellum with elongate meshes. Dorsellum small, flat and smooth. Forewing speculum open below; without stigmal hairline and with radial cell hairy; stigmal vein enlarged.

Metasoma: Female gaster elongate.

### 8. Omphale whartoni n.sp.
#### (Figs 2–4, 13, 100)

*Type material.*—Holotype female labelled "Guerrero, 2.1mi NE Cacahuamilpa, 4.vii.1987, 5250', J.B. Woolley, 87/011" (USNM). Paratypes: 1 female 2 males with same label data as holotype, 1 male gaster on slide (no. 274) (1 male LUZM, 1 female 1 male TAMU); 3 females "Guerrero, 2mi E Ocotito, 11.vii.1985, J.B. Woolley, 85/048" (1 female LUZM, 2 females TAMU); 1 female 1 male "Guerrero, 5mi NW El Ocotito, 7.vii.1987, 2500–3200', R. Wharton", male gaster on slide (no. 281) (LUZM); 1 female 1 male "Guerrero, 2mi NE Cacahuamilpa, 4.vii.1987, 5300', R. Wharton" (LUZM); 1 male "Guerrero, 2mi NE Cacahuamilpa, 19.vii.1984, 5000', J.B. Woolley, 84/043" (LUZM); 1 female "Jalisco, 5.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/022" (TAMU); 1 female 1 male "Jalisco, 8.3mi S Autlan on highway 80, 8.vii.1984, J.B. Woolley, 84/024" (TAMU); 1 male "Jalisco, 16mi S Autlan, 8.vii.1984, J.B. Woolley, 84/025", gaster on slide (no. 266) (LUZM); 1 male "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (TAMU).

*Etymology.*—Name referring to collector of some of the type material of this species.

*Diagnosis.*—Thoracic dorsum with strong raised reticulation in female, weak raised reticulation in male; clypeus trans-verse (2× as wide as long), distinctly convex, yellowish-brown in female, white in male; female forewing with an infuscate area below marginal vein, infuscation reaching to hind margin of wing (Fig. 13); male scape widest at base (Fig. 4), pedicel and flagellum metallic bluish-purple.

*Description.*—Length of body female= 1.3–2.0 mm, male= 1.1–1.5 mm.

Colour: Scape pale with apical ½ infuscate in female, pale with apical tip metallic in male; pedicel and flagellum dark. Frons metallic bluish-green, golden-green or golden-red in female, metallic bluish-green in male. Clypeus yellowish-brown in female, white in male. Vertex golden-red or golden-green. Mesoscutum and scutellum golden-purple in female, golden-green or golden-red in male. Dorsellum golden-purple in female, golden-red in male. Propodeum golden-green. Coxae dark and metallic in female, pale in male; femora dark in female, pale in male (some specimens with apical ⅓ of hind femur dark); tibiae and tarsi pale. Forewing with infuscate stripe below median marginal vein reaching to hind margin of wing in female, with weak median infuscate stripe or completely hyaline in male. Petiole pale. Gaster with 1st tergite metallic bluish-green or golden-green, remaining tergites golden-purple.

Head: Antennae as in Figs 3, 4. Frons and vertex with weak reticulation in female, smooth and shiny in male. Clypeus transverse, 2× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove almost straight. Occipital margin with weak edge.

Mesosoma: Mesoscutum and scutellum with strong reticulation in female, weak in male. Dorsellum small, flat and smooth. Forewing speculum open below; without stigmal hairline and with radial cell hairy.

Metasoma: Female gaster ovate. Male genitalia (Fig. 100) with outer digital spine stout; paramere with two setae.

## 9. **Omphale woolleyi** n.sp.
### (Figs 1, 93, 112)

*Type material.*—Holotype female labelled "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (USNM). Paratypes: 9 females with same label data as holotype (4 females LUZM, 5 females TAMU); 8 females "Guerrero, 2mi E Ocotito, 11.vii.1985, J.B. Woolley, 85/048" (4 females LUZM, 4 females TAMU); 1 female "Guerrero, 2mi NE Cacahuamilpa, 4.vii.1987, 5300', R. Wharton" (TAMU); 1 male "Guerrero, 15mi SW Chichihualco, 15.vii.1984, J.B. Woolley, 84/034", gaster on slide (no. 273) (TAMU); 3 male "Guerrero, 2.1mi NE Cacahuamilpa, 4.vii.1987, 5250', J.B. Woolley, 87/011" (2 males LUZM, 1 male TAMU); 1 female "Jalisco, 8.3mi S Autlan on highway 80, 8.vii.1984, J.B. Woolley, 84/024" (LUZM); 2 males "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (LUZM, TAMU); 1 male "Oaxaca, 10.8mi S El Punto, 19.vii.1987, 6100', R. Wharton", gaster on slide (no. 288) (LUZM).

*Etymology.*—Name referring to collector of some of the type material of this species.

*Diagnosis.*—Thoracic dorsum with strong raised reticulation in female, weak raised reticulation in male; clypeus dark and metallic, frons lateral of clypeus brownish with weak metallic tinge; forewing hyaline, with speculum closed below and with radial cell bare; inner digital spine more curved than in other males of this group (Fig. 93).

*Description.*—Length of body female= 1.3–1.7 mm, male= 1.0–1.5 mm.

Colour: Scape pale with apical tip infuscate, to completely infuscate; pedicel and flagellum dark. Frons metallic greenish-blue or bluish-purple, close to mouth opening lateral of clypeus brownish with weak metallic tinge in female, yellowish-white to infuscate in male. Clypeus dark and metallic. Vertex metallic greenish-blue or golden-green, inside ocellar triangle usually brownish in females, golden-red to golden in males. Mesoscutum, scutellum, dorsellum and propodeum metallic greenish-blue, bluish-purple, golden-green or golden-red. Coxae dark and metallic; femora dark; tibiae and tarsi pale in females, infuscate in males. Wings hyaline. Petiole pale. Gaster with 1st tergite metallic greenish-blue or golden-purple, remaining tergites golden-purple.

Head: Antennae as in *O. metallica* (Figs 6, 7). Frons and vertex with weak reticulation in females, weak and superficial reticulation in males. Clypeus transverse, 2× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with strong reticulation in female, weak in male. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster elongate. Male genitalia (Fig. 93) with volsellar ridges U-shaped; inner digital spine more curved than in other species of this group, outer spine stout; paramere with one seta at apex of paramere.

### Species group **cherana**

*Diagnosis.*—Clypeus with upper corners angulate and semicircularly protruding (Fig. 14). Head without frontal cross-ridge. Male flagellomeres with scattered setae (Figs 17, 20). Male genitalia (Fig. 94): volsellar setae short and rather weak, placed close to apex of phallobase; digitus 1.2× as long as wide, inner digital spine larger than outer; paramere with one seta at apex; aedeagus (Fig. 113) stout, aedeagal apodemes 0.9–1.0× as long as penis valves. Flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b). Midlobe of mesoscutum with one pair of setae (posterior pair).

*Apomorphies.*—Flagellomeres with sen-
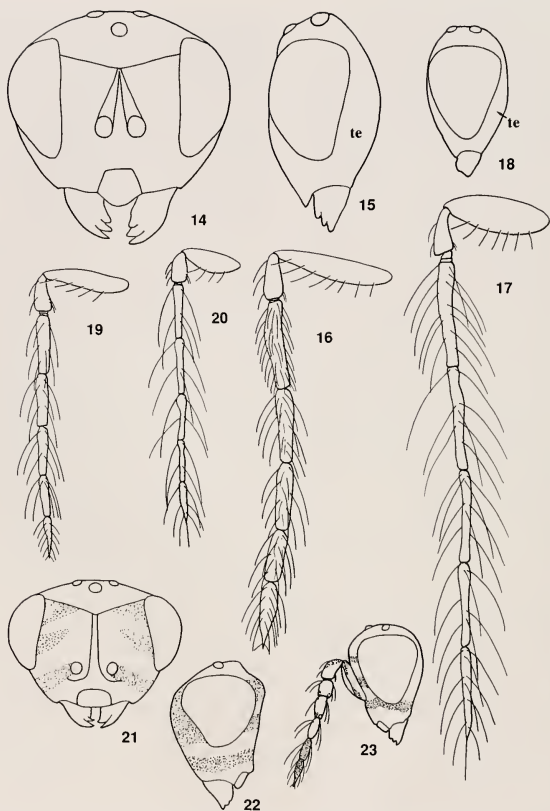
Figs. 14–23.    14–17. *cherana*. 14, Head, frontal. 15, Head, lateral. 16, Antenna, female. 17, Ditto, male. 18–20. *flaviscutellum*. 18, Head, lateral. 19, Antenna, female. 20, Ditto, male. 21–22. *triangulata*. 21, Head, frontal. 22, Head, lateral. 23, Head, lateral, *divina*, female. te= temple.

silla ampullacea elongate and asymmetric. Midlobe of mesoscutum with 1 pair of setae. Male genitalia: volsellar setae short and rather weak, placed close to apex of phallobase.

### 10. **Omphale cherana** n.sp.
(Figs 14–17, 94, 113)

*Type material.*—Holotype female labelled "Michoacan, 6mi N Cheran, 8.vii.1985, J.B. Woolley, 85/034" (USNM). Paratypes: 14 females 10 males with same label data as holotype, 1 male gaster on slide (no. 261) (7 females 5 males LUZM, 7 females 5 males TAMU); 2 males "Michoacan, 2mi S Carapan, 6.vii.1985, J.B. Woolley, 85/031" (LUZM, TAMU); 1 female "Guerrero, 6.6mi SW Filo de Caballo, 12.vii.1985, J.B. Woolley, 85/051" (TAMU).

*Etymology.*—"From Cheran".

*Diagnosis.*—Mouth opening as wide as height of eye in male, 1.3× wider than eye in male; temples large (Fig. 15); scutellum in female always dark metallic. Description.—Length of body female= 1.3–1.9 mm, male= 1.1–1.9 mm.

Colour: Scape pale with dorsal edge dark; pedicel and flagellum dark, 5th flagellomere partly to completely pale in female. Head golden-green or golden. Mesosoma golden-green, golden or metallic bluish-green. Legs pale, or pale with fore and hind coxae infuscate, femora dark brown, tibiae and tarsi infuscate. Wings hyaline. Petiole pale. Gaster metallic bluish-green.

Head: Antennae as in Figs 16, 17. Frons and vertex with weak engraved reticulation, male vertex sometimes smooth and shiny. Clypeus as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove slightly V-shaped. Occipital margin smoothly rounded.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation; notauli not delimited. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Petiole in male transverse, 0.6× as long as wide. Female gaster ovate.

*Remarks.*—*O. cherana* and *O. flaviscutellum* both look like species belonging to the *semiglobosa* group (head semiglobose, flagellomeres long and slender—in male with scattered setae—with sensilla ampullacea long and asymmetric, lacking frontal cross-ridge, antenna attached high up—in middle of frons, forewing long). However, the male genitalia of *O. cherana* and *O. flaviscutellum* is quite different from males in the *semiglobosa* group. Other separating characters are: notauli not delimited (delimited in posterior $^2/_3$ in *semiglobosa* group), midlobe of mesoscutum with only one pair of setae (two pairs in *semiglobosa* group).

### 11. **Omphale flaviscutellum** n.sp.
(Figs 18–20)

*Type material.*—Holotype female labelled "Oaxaca, 15.1mi N San Gabriel Mixtepec, 3850', 11.vii.1987, J.B. Woolley and G. Zolnerowich, 87/031" (USNM). Paratypes: 6 females with same label data as holotype (3 females LUZM, 3 females TAMU); 6 females "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (3 females LUZM, 3 females TAMU); 1 female "Oaxaca, 19mi S San Miguel Suchixtepec, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/069" (TAMU); 1 female "Oaxaca, 10.8mi S El Punto, 19.vii.1987, 6100', R. Wharton" (LUZM); 2 females "Oaxaca, 4.7mi S San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/066" (LUZM, TAMU); 2 females "Oaxaca, 4.4mi NE San Pedro Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/065" (LUZM, TAMU); 1 male "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038" (TAMU); 1 female "Campeche, 10km W Xpujil, Chicanna, 12–14.vii.1983, 300m, M. Kaulbars" (CNC); 6 females 1 male from Chiapas, Palenque (3 females 1 male CNC, 3 fe-

males LUZM); 3 females "Chiapas, San Cristobal las Casas, 26.5–3.6.1969" (2 females CNC, 1 female LUZM); 1 female "Guerrero, 2mi N Cacahuamilpa, 19.vii. 1984, 5000', J.B. Woolley, 84/043" (LUZM); 2 males "Guerrero, 18.2mi S Iguala, 5.vii.1987, 3000', J.B. Woolley, 87/013", 1 male gaster on slide (no. 259) (LUZM, TAMU); 1 female "Michoacan, 10mi S Uruapan, 7.vii.1985, J.B. Woolley and G. Zolnerowich, 85/037" (TAMU); 1 female "Puebla, 2km N Xicotepec de Juarez, 17.vi.1983, 1070m, M. Kaulbars" (CNC); 2 females "Quintana Roo, 68km SW Chetumal, Kohunlich, 14–17.vii.1983, 160m, M. Kaulbars" (CNC, LUZM); 1 female "Tamaulipas, Reserva El Cielo, Gomez Farias, 450m, 27–30.vii.1993, J.B. Woolley, 93/020" (TAMU); 1 female "Tamaulipas, Reserva El Cielo, Alta Cimas, 3100', 30.vii.1993, J.B. Woolley and K. Wikse, 93/035" (LUZM); 2 females "Veracruz, 3mi E Huatusco, 23.vii.1984, J.B. Woolley, 84/049a" (LUZM, TAMU); 1 female "Veracruz, 11mi S Misantla, 24.vii.1984, J.B. Woolley, 84/051" (TAMU); 1 male "Veracruz, 33km NE Catemaco, 160m, Tuxtlas Research Station, 1.vii.1983, M. Kaulbars" (CNC); 6 females "COSTA RICA: Guanacaste, Santa Rosa N.P., SE8C, 26.x-16.xi.1985, D. Janzen, I.D. Gauld" (BMNH, LUZM); 3 females from same locality as previous but collected 18.x-8.xi.1986 (BMNH, LUZM).

Etymology.—"Flaviscutellum" meaning "with yellow scutellum".

Diagnosis.—Mouth opening 0.7× as wide as height of eye in female, 1.0× in male; temples small (Fig. 18); scutellum in female usually yellow nonmetallic.

Description.—Length of body female= 1.1–1.8 mm, male= 0.7–1.1 mm.

Colour: Scape pale with dorsal edge dark; pedicel and flagellum dark, 4 and 5th flagellomeres partly to completely pale in female. Frons below cross-groove golden-green; frons above cross-groove and vertex metallic bluish-green or golden-green. Mesoscutum usually dark and metallic (bluish-purple or golden-purple), in a few female specimens partly to completely yellow nonmetallic. Scutellum usually yellow nonmetallic with median infuscate spot, in a few specimens dark and metallic (golden-green), always dark and metallic in male. Coxae white, remaining parts of legs weakly infuscate. Wings hyaline. Petiole pale. Gaster golden-purple to yellow nonmetallic.

Head: Antennae as in Figs 19, 20. Frons and vertex with weak engraved reticulation, vertex sometimes smooth and shiny. Clypeus as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove slightly V-shaped. Occipital margin with weak edge.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation; notauli not delimited. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Petiole in male transverse, 0.6× as long as wide. Female gaster ovate.

Species group divina

Diagnosis.—Clypeus quadrangular to semicircular, pale yellow non-metallic or dark and metallic. Head without frontal cross-ridge. Male flagellomeres with verticillate setae, i.e. with a single basal whorl of setae on each flagellomere (e.g. Figs 25, 27). Male genitalia (Figs 95–99): volsellar setae long and strong and placed at, or close to, apex of parameres, far above base of volsellar ridges; digitus elongate, at least 3× as long as wide, digital spines equally large, or with inner spine larger than outer spine; paramere with one or two setae; aedeagus (Figs 114–116) long and narrow, aedeagal apodemes 0.5–0.9× as long as penis valves. Flagellomeres with sensilla ampullacea short and asymmetric (type II sensu Hansson 1996b).

Apomorphies.—Male flagellomeres with verticillate setae. Male genitalia: volsellar setae placed apically on phallobase; digitus elongate.
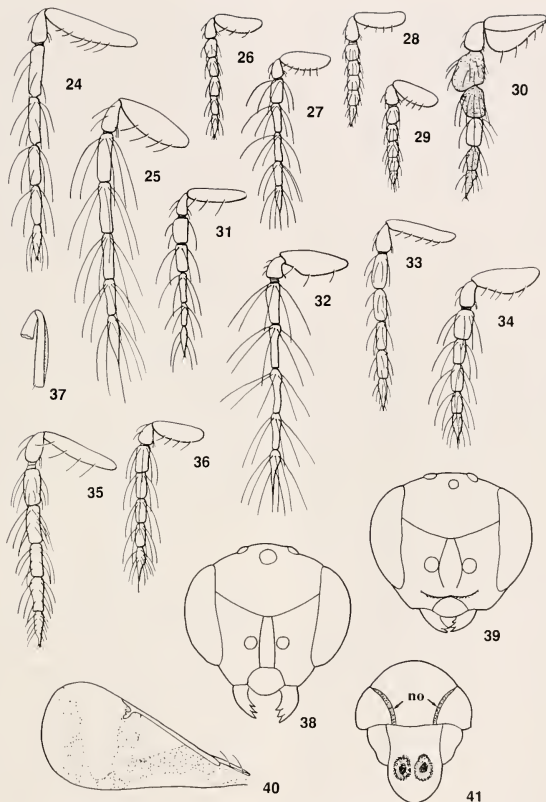
Figs. 24–41. 24–36. Antennae. 24, *obscura*, female. 25, Ditto, male. 26, *petatlana*, female. 27, Ditto, male. 28, *tria*, female. 29, Ditto, male. 30, *triangulata*, female. 31, *vinacea*, female. 32, Ditto, male. 33, *notaula*, female. 34, Ditto, male. 35, *foveata*, female. 36, Ditto, male. 37, Foretibia, lateral, *tria*. 38–39. Head, frontal. 38, *foveata*, female. 39, *notaula*, female. 40, Forewing, *triangulata*. 41, Mesoscutum+scutellum (no= notauli), dorsal, *foveata*.

## 12. **Omphale australis** Hansson
(Fig. 98)

*Omphale australis* Hansson, 1996b:34.

*Diagnosis.*—Head and mesosoma dark and metallic; thoracic dorsum with engraved fine reticulation; scutellum purple; head dark and metallic with large temples; male genitalia with digitus 5.3× as long as wide, volsellar setae almost straight.

*Distribution.*—Chiapas, Colima, Guerrero, Jalisco, Michoacan, Oaxaca (Hansson 1996).

## 13. **Omphale carinata** n.sp.
(Figs 99, 116)

*Type material.*—Holotype female labelled "Colima, 7mi SSW Colima, 9.vii.1984, J.B. Woolley, 84/026a" (USNM). Paratypes: 4 females 1 male with same label data as holotype, male gaster on slide (no. 249) (2 females LUZM, 2 females 1 male TAMU); 1 female "Guerrero, 6mi E Xochipala, 13.vii.1985, J.B. Woolley, 85/054" (TAMU); 1 female "Guerrero, 6mi E Xochipala, 6.vii.1987, J.B. Woolley, 87/016" (LUZM); 1 female "Guerrero, 11.2mi N Iguala, 5.vii.1987, 4300', J.B. Woolley, 87/012" (TAMU).

*Etymology.*—Name referring to carina along frontal edge of fore tibia.

*Diagnosis.*—Head and mesosoma dark and metallic; flagellum with 3-segmented clava (as in Figs 28, 29); flagellomeres 1 and 2 1.4× as long as wide; fore tibia with carina along frontal edge (as in Fig. 71); frons, including clypeus and mouth region, dark and metallic; thoracic dorsum with fine and weak reticulation; volsellar setae stout and sinuate, placed at apex of parameres (Fig. 99); digitus 3.7× as long as wide.

*Description.*—Length of body female= 0.9–1.1 mm, male= 0.8 mm.

Colour: Antenna infuscate, some specimens with antenna dark, except median part of scape, apical pedicel and flagellomeres 2 and 3 which are pale. Frons below cross-groove metallic greenish-blue; above cross-groove golden-green. Vertex golden-red. Mesoscutum golden-green; scutellum golden-green to golden-red; dorsellum and propodeum golden-red. Coxae dark and metallic; femora dark; tibiae infuscate with apex paler; tarsi infuscate. Wings hyaline. Petiole dark. Gaster with weak golden-red tinge.

Head: Without frontal cross-ridge. Antennae as in *O. tria* (Figs 28, 29), i.e. with a distinct 3-segmented clava. Frons and vertex with weak smallmeshed reticulation. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with weak and fine smallmeshed reticulation. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster ovate. Male genitalia (Fig. 99): volsellar setae long and strong, placed at same level at apex of parameres; inner digital spine larger than outer; paramere with one seta close to apex of paramere.

## 14. **Omphale divina** (Girault)
(Figs 23, 97)

*Achrysocharis divina* Girault, 1917b:22.
*Omphale divina* (Girault), Yoshimoto 1980:1047.

*Diagnosis.*—Female. Head pale yellow nonmetallic, frons usually with brown cross-stripes, mesosoma metallic (bluish-purple or bluish-green)—scutellum predominantly yellow nonmetallic in a few specimens; scape expanded with a ventral edge; temples small; thoracic dorsum with raised and strong reticulation. Male. Phallobase with digitus very elongate, 7× as long as wide and with volsellar setae curved.

*Distribution.*—Chiapas, Colima, Guanajuato, Guerrero, Jalisco, Michoacan, Oaxaca, Puebla, Tamaulipas, Veracruz, Zacatecas. 252 females 80 males. New record for Mexico.

*Remarks.*—A few specimens have entire frons dark and metallic (majority with frons yellow nonmetallic and usually with fuscous cross-stripes (Hansson 1996)).

### 15. Omphale obscura n.sp.
(Figs 24, 25)

*Type material.*—Holotype female labelled "Chiapas, Parque Nacional Lagunas de Montebello, 11.viii.1990, 5000', J.B. Woolley, 90/061" (USNM). Paratypes: 1 male with same label data as holotype (TAMU).

*Etymology.*—"Obscura" meaning dark, referring dark colouration of species (as opposed to the similar species *vinacea*, which usually is pale).

*Diagnosis.*—Head and mesosoma dark and metallic; flagellomeres equal in length and narrow in both sexes (1st flagellomere is always distinctly wider than following segments in the similar *O. vinacea* ); apical gastral tergite elongate in female, 2.4× as long as wide at base; clypeus as wide as long; body dark and metallic (yellow nonmetallic or infuscate in most specimens of *O. vinacea*); male genitalia as in *O. petatlana* (Fig. 96).

*Description.*—Length of body female= 2.2 mm, male= 1.4 mm.

Colour: Scape infuscate, slightly darker in male than in female, pedicel and flagellum dark. Female frons golden-green, pale nonmetallic close to mouth opening and below toruli, vertex golden; male frons and vertex golden-purple with pale nonmetallic spots below toruli. Mesoscutum and propodeum golden-green; scutellum golden-purplish. Coxae dark and metallic; remaining parts of legs pale, hind femur infuscate. Wings hyaline. Petiole pale. Gaster with golden tinges.

Head: Without frontal cross-ridge. Antennae as in Figs 24, 25. Frons and vertex with weak reticulation, smooth and shiny in some places. Clypeus quadratic, as wide as long. Frontal cross-groove straight. Occipital margin with sharp edge.

Mesosoma: Mesoscutum and scutellum with weak reticulation. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster elongate, final tergite elongate, 2.4× as long as wide at base. Male genitalia with volsellar setae long and strong, placed at apex of parameres; inner digital spine larger than outer; paramere with one seta below apex of paramere.

### 16. Omphale petatlana n.sp.
(Figs 26, 27, 96, 115)

*Type material.*—Holotype female labelled "Guerrero, 32mi SE Petatlan, 10.vii.1985, J.B. Woolley, 85/047" (USNM). Paratypes: 4 females 16 males with same label data as holotype, 1 male gaster on slide (no. 254) (2 females 8 males LUZM, 2 females 8 males TAMU); 1 female "Chiapas, Ocozacoautla, 8.viii.1990, 1800–2200', J.B. Woolley, 90/055B" (TAMU); 4 females "Michoacan, 3mi N Nueva Italia, 8.vii.1985, J.B. Woolley and G. Zolnerowich, 85/042" (2 females LUZM, 2 females TAMU); 1 female "Oaxaca, 4.4mi NE San Pedro Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/065" (TAMU); 4 females "Oaxaca, 4.7mi S San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/066" (2 females LUZM, 2 females TAMU); 1 male "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (TAMU); 1 female "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038" (LUZM); 1 male "Michoacan, 28.5mi S Nueva Italia, 9.vii.1985, J.B. Woolley and G. Zolnerowich, 85/045", gaster on slide (no. 255) (TAMU).

*Etymology.*—"From Petatlan".

*Diagnosis.*—Head and mesosoma pale nonmetallic; mesoscutum and scutellum with strong reticulation, hence dull; clypeus as wide as long.

*Description.*—Length of body female= 1.1–1.3 mm, male= 0.8–0.9 mm.

Colour: Scape and pedicel pale yellow with scape fuscous along dorsal edge and pedicel fuscous at base, or completely pale yellow; flagellum yellowish-brown, in female frequently with flagellomeres 4 and 5 dark. Head pale yellow with infuscate spots close to eyes and with antennal scrobes infuscate. Vertex pale yellow, setae dark. Thorax pale yellow, setae dark. Legs pale yellow. Wings hyaline, or forewing with fuscous spot below stigmal vein. Petiole pale yellow. Female gaster pale yellow, hind edge of tergites 1–5 dark, apical part of ovipositor sheaths dark; male gaster with pale subbasal spot and with apical ½ dark.

Head: Without frontal cross-ridge. Antennae as in Figs 26, 27. Frons and vertex with strong smallmeshed reticulation, hence dull. Clypeus quadratic, as wide as long. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum, scutellum, dorsellum and propodeum with strong smallmeshed reticulation; midlobe of mesoscutum with 2 pair of setae, occasionally with 5 setae (2 pair and an odd seta). Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster elongate. Male genitalia (Fig. 96) with volsellar setae long and strong, placed at apex of parameres; inner digital spine larger than outer; paramere with one seta below apex of paramere.

## 17. Omphale poeta (Girault)

*Rhicnopeltomyia carlylei var. poeta* Girault, 1920: 197.
*Omphale poeta* (Girault), Hansson (1996b:37).

*Diagnosis.*—Head and mesosoma dark and metallic; fore tibia with an edge along frontal margin; head dark and metallic with frons below antennal toruli pale, except partly to completely metallic clypeus; temples large; antennae with short setae;

mouth opening wide, 1.2–1.3× height of an eye in female, 1.2–1.5× in male; thoracic dorsum with raised rather strong reticulation; male genitalia with digitus 3× as long as wide, volsellar setae almost straight.

*Distribution.*—Guerrero, Jalisco. 28 females. New record for Mexico.

## 18. Omphale tria n.sp.
### (Figs 28, 29, 37, 95, 114)

*Type material.*—Holotype female labelled "Guerrero, 6.2mi SW Xochipala, 13.vii.1985, J.B. Woolley, 85/056" (USNM). Paratypes: 24 females 6 males with same label data as holotype, 1 male gaster on slide (no. 248) (12 females 3 males LUZM, 12 females 3 males TAMU); 2 females "Guerrero, 2mi N Cacahuamilpa, 19.vii. 1984, 5000', J.B. Woolley, 84/043" (LUZM, TAMU); 3 females "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038" (1 female LUZM, 2 females TAMU); 5 females "Michoacan, 3mi N Nueva Italia, 8.vii.1985, J.B. Woolley and G. Zolnerowich, 85/042" (2 females LUZM, 3 males TAMU); 1 female "Zacatecas, Tropic of Cancer marker on highway 54, 1958m, 4.vii.1984, J.B. Woolley, 84/016" (TAMU).

*Etymology.*—No specific derivation.

*Diagnosis.*—Head entirely pale nonmetallic (female) or with vertex metallic (male), mesosoma dark and metallic; flagellum pale with 3-segmented clava, flagellomeres 1 and 2 about as long as wide (Figs 28, 29); fore tibia with carina along frontal edge (Fig. 37); frons predominantly pale nonmetallic in female; digitus elongate, 9× as long as wide (Fig. 95); volsellar setae placed just below apex of parameres.

*Description.*—Length of body female= 0.9–1.3 mm, male= 0.9 mm.

Colour: Female antenna pale with base of pedicel and flagellomeres 4 and 5 infuscate, male antenna completely pale. Female frons pale nonmetallic with 3 transverse stripes (as in Fig. 123), stripes sometimes present only close to eyes, or absent;

male frons predominantly metallic greenish-blue except pale area around mouth opening. Female vertex pale non-metallic; male vertex metallic greenish-blue. Occiput golden-green in both sexes. Female thoracic dorsum golden-red or golden-green; male mesoscutum golden-green, scutellum, dorsellum and propodeum golden-red to golden-purple. Coxae dark and metallic; fore femur weakly infuscate, mid femur pale, hind femur infuscate; fore and mid tibiae pale, hind tibia infuscate; tarsi pale to weakly infuscate. Female forewing with small infuscate spot below stigmal vein, sometimes also with weak spot below median marginal vein; male forewing completely hyaline. Petiole dark. Gaster golden-purple.

Head: Without frontal cross-ridge. Antennae as in Figs 28, 29, i.e. with a distinct 3-segmented clava. Frons and vertex with strong smallmeshed reticulation. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum in female with strong, in male with weak, and smallmeshed reticulation. Dorsellum small, convex with weak reticulation. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster ovate. Male genitalia (Fig. 95) with volsellar setae long and strong, placed at same level, just below apex of parameres; inner digital spine larger than outer; paramere with one seta close to apex of paramere.

### 19. Omphale triangulata n.sp.
(Figs 21, 22, 30, 40)

*Type material.*—Holotype female labelled "Guerrero, 32mi SE Petatlan, 14.vii.1984, J.B. Woolley, 84/032" (USNM).

*Etymology.*—Name referring to shape of scape.

*Diagnosis.*—Head pale nonmetallic, mesosoma dark and metallic; scape triangular (Fig. 30), strongly flattened with a sharp ventral edge; 1st flagellomere flattened and distinctly wider than remaining flagellomeres (Fig. 30); antenna dark with 3rd flagellomere pale; head pale nonmetallic with 3 dark cross-stripes (Figs 21, 22); forewing with characteristic pattern (Fig. 40).

*Description (female).*—Length of body= 1.6 mm.

Colour: Entire antenna dark, except pale stripe on scape and pale 3rd flagellomere. Frons pale nonmetallic with 3 dark cross-stripes. Vertex pale nonmetallic. Midlobe of mesoscutum and median scutellum metallic bluish-green, sidelobes of mesoscutum and sides of scutellum metallic purple. Dorsellum and propodeum metallic bluish-purple. Coxae, femora and tibiae dark and metallic; tarsi pale. Forewing with infuscate pattern as in Fig. 40. Petiole dark. Gaster with 1st tergite metallic bluish-purple, remaining tergites golden-purple.

Head: Without frontal cross-ridge. Antenna as in Fig. 30, i.e. with a triangular and strongly flattened scape and with 1st flagellomere distinctly wider than remaining flagellomeres. Frons and vertex with strong smallmeshed reticulation. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with strong and smallmeshed reticulation, scutellum smooth and shiny laterally and along posterior margin. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster elongate, acuminate at apex.

### 20. Omphale vinacea Hansson
(Figs 31, 32)

*Omphale vinacea* Hansson, 1996b:37.

*Diagnosis.*—Yellow to pale brown, nonmetallic species—occasionally with head and mesosoma dark and weakly metallic; clypeus as high as wide; forewing usually with an infuscate spot below marginal vein; frontal cross-groove high up on frons.

*Distribution.*—Chiapas, Colima, Guerrero, Jalisco, Michoacan, Oaxaca, Puebla, Tamaulipas, Veracruz. 17 females 24 males. New record for Mexico.

## Species group notaula

*Diagnosis.*—Clypeus semicircular and semicircularly protruding (Figs 38, 39). Head without frontal cross-ridge in *foveata* (Fig. 38), with weak frontal cross-ridge in *notaula* (Fig. 39). Male flagellomeres with verticillate setae, i.e. with a single basal whorl of setae on each flagellomere (Figs 34, 36). Male genitalia (Fig. 103): volsellar setae long and strong and placed at different levels below base of volsellar ridges; digitus 2–3× as long as wide and with concavity in basal outer half, inner digital spine larger than outer; paramere with 1–2 setae at apex; aedeagus (Fig. 117) long and slender, aedeagal apodemes 0.8–0.9× as long as penis valves. Flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b). Notauli complete and deep throughout. Radial cell hairy.

*Apomorphies.*—Flagellomeres with elongate and asymmetric sensilla ampullacea; male flagellomeres with verticillate setae. Notauli complete and deep throughout. Male genitalia: volsellar setae placed at different levels; digitus elongate and with concavity in basal outer half.

## 21. Omphale foveata n.sp.
(Figs 35, 36, 38, 41, 103, 117)

*Type material.*—Holotype female labelled "Oaxaca, 2mi N Candelaria Loxicha, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/068", in USNM. Paratypes: 2 females 2 males with same label data as holotype, 1 male gaster on slide (no. 237) (1 female 1 male LUZM, 1 female 1 male TAMU); 1 female 1 male "Oaxaca, 15.1mi N San Gabriel Mixtepec, 3850', 11.vii.1987, J.B. Woolley and G. Zolnerowich, 87/031" (TAMU); 2 females 2 males "COSTA RICA: Alajuela, N slope Volcan Cacao, 650 m, 17.iii.1986, C. Hansson" (LUZM); 1 female "COSTA RICA: Turrialba, CATIE, Reventazon, 4.ix.1986, L. Masner" (CNC); 1 female "COSTA RICA: Puntarenas, Monteverde, St Luis Valley, 17.viii.1986, L. Masner" (CNC); 4 females 1 male "COSTA RICA: Limon, Hitoy-Cerere BR HQ, 14–18.i.1991, 100m, J.S. Noyes" (BMNH, LUZM); 1 female "ECUADOR: Pichin, Tinalandia, 2.xi.1983, 850 m, Masner and Sharkey" (CNC).

*Etymology.*—"Foveata" meaning "with pits", referring to pits on scutellum.

*Diagnosis.* Scutellum with two deep pits (Fig. 41); paramere with one seta at apex (Fig. 103).

*Description.*—Length of body female= 1.0–1.3 mm, male= 0.9–1.2 mm.

Colour: Scape pale yellow, pedicel and flagellum dark. Clypeus dark and metallic. Frons golden-purple to golden-green in female, metallic bluish-green in male. Vertex golden-purple. Mesoscutum and scutellum golden-purple. Dorsellum and propodeum golden-green. Female with fore coxa infuscate, remaining parts of fore leg, mid and hind legs pale; male with coxae dark and metallic, hind femur infuscate and remaining parts of legs pale. Wings hyaline. Petiole pale. Gaster with 1st tergite golden-green, remaining tergites golden-purple.

Head: Antennae as in Figs 35, 36. Frons and vertex with very weak reticulation. Antennal scrobes reach frontal cross-groove separately. Occipital margin with a sharp edge.

Mesosoma: Mesoscutum and scutellum with fine and engraved reticulation; setae on dorsum long and strong; scutellum with two deep pits. Dorsellum small, convex and smooth. Forewing speculum closed below.

Metasoma: Gaster elongate in female. Male genitalia (Fig. 103): paramere with one seta at apex of paramere.

*Remarks. Omphale foveata* resembles *O. erginnus* (lacking frontal cross-ridge and having elongate and asymmetric sensilla ampullacea on flagellomeres) but differs

as follows. Male flagellomeres with verticillate setae (i.e. with a single whorl of setae at base of each flagellomere) (scattered in *erginnus*), clypeus completely delimited (lacking upper border in *erginnus*), vertex with short setae (long setae in *erginnus*). The deep and complete notauli is very unusual, and the scutellar pits present in *O. foveata* is unique within genus *Omphale*.

## 22. Omphale notaula n.sp.
### (Figs 33, 34, 39)

*Type material.*—Holotype female labelled "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500′, J.B. Woolley and G. Zolnerowich, 87/027A" (USNM). Paratypes: 8 females 12 males with same label data as holotype (4 females 6 males LUZM, 4 females 6 males TAMU); 6 females 11 males "Oaxaca, 4.7mi S San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/066" (3 females 5 males LUZM, 3 females 6 males TAMU); 8 females 3 males "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80′, J.B. Woolley and G. Zolnerowich, 87/038" (4 females 1 male LUZM, 4 females 2 males TAMU); 1 male "Oaxaca, 3.9mi NE San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley, 85/067" (TAMU); 2 males "Oaxaca, 2mi N Candelaria Loxicha, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/068" (LUZM, TAMU); 1 male "Oaxaca, 3mi SE Matatlan, Microondas Road, 17.vii.1987, 6650′, J.B. Woolley and G. Zolnerowich, 87/049" (TAMU); 1 female "Chiapas, 12.1km S Palenque, 13.viii.1990, 1200′, J.B. Woolley, 90/063" (TAMU); 1 male "Chiapas, Parque nacional Lagunas de Montebello, 11.viii.1990, 5000′, J.B. Woolley, 90/061" (TAMU); 1 female 1 male "Chiapas, 3mi N Berriozabal, 8–9.viii.1990, 4000′, J.B. Woolley, 90/056" (LUZM); 1 female 3 males "Chiapas, Municipal Tenejapa, Paraje Yashanal, 5200–5800′, 4.viii.1990, J.B. Woolley, 90/052"; 1 female "Guerrero, 2mi N Cacahuamilpa, 19.vii.1984, 5000′, J.B. Woolley, 84/043" (TAMU); 2 females 7 males "Guerrero, 2mi NE Cacahuamil-

pa, 4.vii.1987, 5300′, R. Wharton" (1 female 3 males LUZM, 1 female 4 males TAMU); 1 male "Guerrero, 2.1mi NE Cacahuamilpa, 4.vii.1987, 5250′, J.B. Woolley, 87/011" (TAMU); 1 male 1 female "Guerrero, 32mi SE Petatlan, 10.vii.1985, J.B. Woolley, 85/047" (LUZM); 1 female "Guerrero, 7mi W Chilapa, 16.vii.1984, J.B. Woolley, 84/036" (TAMU); 3 females 4 males "Jalisco, 16mi S Autlan, 8.vii.1984, J.B. Woolley, 84/025" (1 female 2 males LUZM, 2 females, 2 males TAMU); 2 females 1 male "Jalisco, 5.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/022" (TAMU); 1 female 1 male "Jalisco, 8.3mi S Autlan on highway 80, 8.vii.1984, J.B. Woolley, 84/024" (LUZM); 2 females 1 male "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (TAMU); 1 female "Puebla, 4.7mi SW La Cumbre, 23.vii.1987, 5100′, R. Wharton" (TAMU); 1 female 4 males "Puebla, 4.7mi SW La Cumbre, 23.vii.1987, 5100′, J.B. Woolley, 87/055", 1 male gaster on slide (no. 264) (1 female 2 males LUZM, 2 males TAMU); 1 female "Tamaulipas, road from Alta Cimas to Rancho de Cielo, 6.vii.1986, R. Jones and P. Kovarik" (TAMU); 1 male "Tamaulipas, 2mi W Gomez Farias, 5.vii.1986, G. Zolnerowich" (LUZM); 1 female 4 males "Veracruz, 3mi NE Huatusco, 22.vii.1985, J.B. Woolley, 85/084" (1 female 2 males LUZM, 2 males TAMU); 1 male "Veracruz, 11mi S Misantla, 24.vii.1984, J.B. Woolley, 84/051" (TAMU).

*Etymology.*—Name referring to complete notauli in this species.

*Diagnosis.*—Scutellum without pits; paramere with two setae at apex.

*Description.*—Length of body female= 0.9–1.5 mm, male= 0.8–1.3 mm.

Colour: Scape pale to infuscate in female, male scape infuscate to dark with base pale; pedicel and flagellum dark. Female with frons below cross-groove golden-red, golden-green or golden; above cross-groove metallic bluish-purple, golden-purple or golden-green; vertex metallic bluish-purple, bluish-green or golden-

green. Male with frons and vertex metallic greenish-blue, vertex sometimes golden-purple. Midlobe of mesoscutum golden-purple or golden; sidelobes metallic bluish-green or golden-purple. Scutellum metallic bluish-green, bluish-purple or golden-green. Propodeum golden-green. Fore coxa dark and metallic, mid and hind coxae pale, to all coxae dark and metallic; remaining parts of legs pale yellow, femora sometimes dark. Wings hyaline to infuscate. Petiole pale to dark. Gaster with 1st tergite metallic bluish-green, remaining tergites golden-purple.

Head: Antennae as in Figs 33, 34. Frons and vertex with weak superficial reticulation, shiny, to smooth and shiny without reticulation. Antennal scrobes reach frontal cross-groove separately. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Midlobe of mesoscutum with weak reticulation, sidelobes and scutellum with weak superficial reticulation, shiny. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline and with radial cell hairy.

Metasoma: Female gaster ovate. Male genitalia: paramere with two setae at apex of paramere.

## Species group obscurinotata

*Diagnosis.*—Clypeus (Figs 51–53) poorly delimited, more or less semicircular and semicircularly protruding below lower edge of frons. Head without frontal cross-ridge. Male flagellomeres with verticillate, i.e. with a single basal whorl of setae on each flagellomere (Figs 45, 47, 48), or scattered (Fig. 42) arrangement of setae. Male genitalia (Fig. 104): volsellar setae laterally flattened and placed at different levels far below apex of parameres and below base of volsellar ridges; digitus as long as wide to transverse; paramere with one seta close to apex; aedeagus (Fig. 124) slender, sometimes expanded apically. Flagellomeres with sensilla ampullacea short and asymmetric (type II sensu Hansson

1996b). Forewing with radial cell bare but without hairline from stigmal vein; speculum closed below.

*Apomorphies.*—Clypeus poorly delimited. Male flagellomeres with verticillate setae (reversed in some species).

## 23. **Omphale acuminativentris** (Girault)
### (Figs 48, 49)

*Achrysocharella acuminativentris* Girault, 1917c:6.
*Omphale acuminativentris* (Girault), Yoshimoto 1978:716.

*Diagnosis.*—Entire frons pale nonmetallic in female, in male pale nonmetallic below frontal cross-groove, dark and metallic above cross-groove; flagellum with slender segments and with long setae in female, ventral setae especially long from 2nd segment and onwards; male scape widest in middle, flagellomeres long and slender with only a proximal whorl of thin setae; 7th tergite of female gaster long, $3\times$ as long as width of base.

*Distribution.*—Chiapas, Colima, Guerrero, Jalisco, Michoacan, Oaxaca, Tamaulipas, Veracruz. 104 females 5 males. New record for Mexico.

*Remarks.*—Some specimens from Mexico have head and mesosoma dark and metallic.

## 24. **Omphale fulgida** n.sp.
### (Figs 44, 45, 52, 119)

*Type material.*—Holotype male labelled "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (USNM). Paratypes: 1 male 3 females with same label data as holotype, male gaster on slide (no. 291) (1 female 1 male LUZM, 2 females TAMU); 1 female "Chiapas, Ocozacoautla, 8.viii. 1990, 1800–2200', J.B. Woolley, 90/055B" (TAMU).

*Etymology.*—"Fulgida" latin for shiny, referring to shiny clypeus.

*Diagnosis.*—Frons, including clypeus, metallic and shiny in both sexes; male flagellomeres with fine and verticillate setae (Fig. 45).
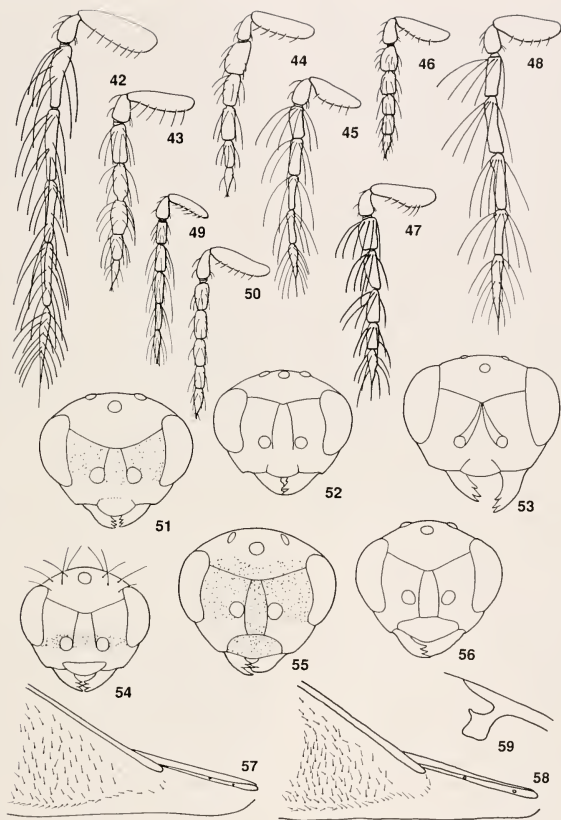
Figs. 42–59. 42–50. Antennae. 42, *pallida*, male. 43, Ditto, female. 44, *fulgida*, female. 45, Ditto, male. 46, *obscurinotata*, female. 47, Ditto, male. 48, *acuminativentris*, male. 49, Ditto, female. 50, *gracilis*, female. 51–56. Head, frontal. 51, *pallida*, male. 52, *fulgida*, male. 53, *gracilis*, female. 54, *angusticornis*, female. 55, *cumbrensis*, male. 56, *zolnerowichi*, male. 57–58. Base of forewing. 57, *pallida*. 58, *masneri*. 59, Stigmal vein, *pallida*.

*Description.*—Length of body male= 1.0–1.1 mm, female= 1.1–1.2 mm.

Colour: Entire antenna dark in male, scape in female pale with apical tip dark. Frons golden-green with pale spots below toruli, in one female entire frons below toruli (except metallic clypeus) pale. Vertex golden-purple in male, golden-green in female. Mesoscutum and scutellum with golden-green tinges. Fore and mid coxae infuscate, hind coxa dark and metallic; femora and tarsi infuscate; tibiae pale. Wings hyaline. Petiole dark. Gaster golden-purple, with pale subbasal spot in male.

Head: Antennae as in Figs 44, 45. Frons and vertex smooth and shiny. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with fine and weak reticulation, smooth in some places. Dorsellum small, flat and smooth. Forewing without stigmal hairline but with radial cell bare.

Metasoma: Female gaster ovate. Male genitalia (as in Fig. 104) with inner digital spine about twice as large as outer spine, spines placed wide apart.

### 25. **Omphale gracilis** n.sp.
### (Figs 50, 53)

*Type material.*—Holotype female labelled "Jalisco, 8.3mi S Autlan on highway 80, 5000', 8.vii.1984, J.B. Woolley" (USNM).

*Etymology.*—"Gracilis" latin for slender, referring to slender mesosoma.

*Diagnosis.*—Frons golden-green and clypeus pale in female (male unknown); antennae, legs and gaster pale; mesosoma elongate, 1.8× as long as wide.

*Description (female).*—Length of body= 1.2 mm.

Colour: Antenna pale. Clypeus pale. Frons and vertex golden-green. Thorax golden-green with reddish tinge. Legs pale. Wings hyaline. Petiole pale. Gaster pale, apical part of ovipositor sheaths dark.

Head: Without frontal cross-ridge. Antenna as in Fig. 50. Frons with very weak reticulation, almost smooth. Vertex with weak reticulation. Clypeus poorly delimited dorsally. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation. Dorsellum small, convex and smooth. Forewing without stigmal hairline but with radial cell bare.

Metasoma: Female gaster elongate.

### 26. **Omphale masneri** Hansson
### (Fig. 58)

*Omphale masneri* Hansson, 1996b:32.

*Diagnosis.*—Predominantly dark with weak metallic tinges; clypeus and frons below toruli pale brown in female, white in male; male flagellomeres with scattered setae; forewing densely pubescent; setae on thoracic dorsum long.

*Distribution.*—Oaxaca. 1 female. New record for Mexico.

### 27. **Omphale obscurinotata** (Girault)
### (Figs 46, 47)

*Achrysocharella obscurinotata* Girault, 1916a:306.
*Omphale obscurinotata* (Girault), Yoshimoto 1978:717.

*Diagnosis.*—Entire frons pale nonmetallic in female, in male pale nonmetallic below frontal cross-groove, dark and metallic above cross-groove; flagellum with short and stout segments and with comparatively short setae in female; male scape widest at base, flagellomeres short and stout with thick and bent setae—apart from a proximal whorl also with some setae apical to whorl.

*Distribution.*—Guanajuato, Guerrero, Jalisco, Michoacan, Oaxaca. 63 females 52 males. New record for Mexico.

### 28. **Omphale pallida** n.sp.
### (Figs 42, 43, 51, 57, 59, 104, 124)

*Type material.*—Holotype male labelled "Michoacan, 6mi N Cheran, 8.vii.1985, J.B.

Woolley, 85/034'' (USNM). Paratypes: 5 males 4 females with same label data as holotype, one male gaster on slide (no. 258) (2 males 2 females LUZM, 3 males 2 females TAMU); 1 female ''Michoacan, 2mi S Carapan, 6.vii.1985, J.B. Woolley, 85/031'' (TAMU); 1 female ''Chiapas, 4km W San Cristobal, San Felipe, 7200', 10–13.viii.1990, J.B. Woolley, 90/058'' (LUZM); 1 female ''Chiapas, San Cristobal Reserva Huitepec, 7300–7500', 3.viii.1990, J.B. Woolley, 90/051A'' (LUZM); 1 male ''Chiapas, San Cristobal Reserva Huitepec, 7700–7850', 3.viii.1990, J.B. Woolley, 90/051B'' (TAMU); 1 female ''Guerrero, 2mi E Ocotito, 11.vii.1985, J.B. Woolley, 85/048'' (LUZM); 4 males 2 females ''Guerrero, 17mi E Tixtla, 11.vii.1985, J.B. Woolley and G. Zolnerowich, 85/050'' (2 males 1 female LUZM, 2 males 1 female TAMU); 2 females ''Guerrero, 6.2mi SW Xochipala, 13.vii.1985, J.B. Woolley, 85/056'' (LUZM, TAMU); 1 female ''Guerrero, 6mi NE Tixtla de Guerrero, 16.vii. 1984, J.B. Woolley, 84/035'' (TAMU); 1 male ''Jalisco, 8.3mi S Autlan on highway 80, 8.vii.1984, J.B. Woolley, 84/024'' (TAMU); 1 male ''Oaxaca, Llano de las Flores, 17.vii.1987, 8900', R. Wharton'' (LUZM); 1 male 2 females ''Oaxaca, 3.2mi SW La Cumbre, 8.vii.1985, J.B. Woolley, 85/071'' (TAMU); 1 male 9 females ''Oaxaca, 8mi NE El Punto, 18.vii.1985, J.B. Woolley and G. Zolnerowich, 85/074'' (1 male 5 females LUZM, 4 females TAMU); 1 female ''Oaxaca, 6mi NE Mitla, 20.vii.1985, J.B. Woolley, 85/077'' (TAMU); 2 females ''Oaxaca, 19mi S San Miguel Suchixtepec, 17.vii. 1985, J.B. Woolley and G. Zolnerowich, 85/069'' (LUZM); 1 female ''Puebla, 4mi E Azumbilla, 22.vii.1984, J.B. Woolley, 84/047'' (TAMU); 2 females ''Puebla, 3.7mi S Zacapoaxtla, 23.vii.1985, J.B. Woolley, 85/085'' (LUZM, TAMU); 1 male 3 females ''Veracruz, 3mi NE Huatusco, 22.vii.1985, J.B. Woolley, 85/084'' (1 male 1 female LUZM, 2 females TAMU).

Etymology.—''Pallida'' is latin for pale, referring to pale frons below level of antennal toruli in male.

Diagnosis.—Male: frons below level of toruli pale (including clypeus) (Fig. 51), above this level dark and metallic; flagellomeres long and narrow, with strong and scattered setae (Fig. 42). Female: frons pale nonmetallic or pale below toruli and dark and metallic above. Both sexes: stigmal vein enlarged (Fig. 59).

Description.—Length of body male= 0.9–1.5 mm, female= 1.3–2.0 mm.

Colour: Male: Antenna dark, a few specimens with scape pale and apical tip dark. Frons below toruli and eyes pale, above golden-green (a few specimens pale up to frontal cross-groove). Vertex golden-green. Mesoscutum and scutellum golden-green or golden-purple, one male with sides of scutellum pale nonmetallic. Coxae and femora pale to dark; tibiae and tarsi pale to infuscate. Wings hyaline, forewing occasionally infuscate round stigmal vein. Petiole dark. Gaster golden-purple with pale subbasal spot, to completely dark and metallic. Female: Scape pale with apex and base dark to completely dark; pedicel pale brown to dark brown; flagellum dark. Head nonmetallic to pale with frons above toruli and vertex golden-green. Mesoscutum and scutellum yellowish-brown with weak metallic tinge to golden-green. Coxae yellowish-brown to dark and metallic; femora, tibiae and tarsi yellowish-brown to infuscate. Wings hyaline. Petiole dark. Gaster pale with posterior $\frac{1}{2}$ of tergites dark, to completely dark with weak metallic tinges.

Head: Antennae as in Figs 42, 43. Frons and vertex smooth and shiny. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with fine and weak reticulation. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline and with radial cell hairy.

Metasoma: Female gaster elongate. Male genitalia (Fig. 104) with inner digital

spine about twice as large as outer spine, spines placed wide apart.

*Remarks.* The female of *pallida* is very similar to the female of *acuminativentris*, the only difference being the enlarged stigmal vein and the metallic thoracic dorsum in *pallida* (thoracic dorsum nonmetallic in *acuminativentris*).

### Species group scutellata

*Diagnosis.*—Clypeus with rounded sides (Figs 54–56, 63), sides never straight and clypeus hence never quadrangular, metallic or partly metallic, never completely pale. Head with frontal cross-ridge (see Fig. 1) (weak or missing in newly described species below). Male flagellomeres with verticillate setae, i.e. with a single basal whorl of setae on each flagellomere (Fig. 61). Male genitalia (Fig. 105): volsellar setae long and strong and placed far below apex of parameres and base of volsellar ridges, and at different levels; digitus as long as wide to transverse, digital spines of same size or inner spine larger than outer; paramere with one slender seta on outer apical corner, inner apical corner of paramere drawn out to a long and narrow structure that looks just like a seta (Hansson (1996b) regarded this structure as a seta but there is no joint between structure and paramere, therefore it is no seta); aedeagus (Fig. ) with penis valves narrow at base and wide at apex. Flagellomeres with sensilla ampullacea short and asymmetric (type II sensu Hansson 1996b). Females with surface between antennal toruli and frontal cross-ridge pale, males also with frons below cross-ridge completely or predominantly pale.

*Apomorphies.*—Head with frontal cross-ridge; clypeus with rounded sides; male flagellomeres with verticillate setae. Male genitalia: inner apical corner of paramere drawn out; volsellar setae placed at different levels.

### 29. Omphale angusticornis n.sp.
### (Figs 54, 60, 65)

*Type material.*—Holotype female labelled "Chiapas, 12.1km S Palenque,

13.viii.1990, 1200', J.B. Woolley, 90/063" (USNM). Paratypes: 5 females with same label data as holotype (2 females LUZM, 3 females TAMU); 1 female "Chiapas, 8mi N Berriozabal, 9.viii.1990, 3600', J.B. Woolley, 90/057B" (TAMU); 4 females "Jalisco, 16mi S Autlan, 8.vii.1984, J.B. Woolley, 84/025" (2 females LUZM, 2 females TAMU); 9 females "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (5 females LUZM, 4 females TAMU); 1 female "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038" (TAMU); 12 females "Oaxaca, 4.7mi S San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/066" (6 females LUZM, 6 females TAMU); 2 females "Oaxaca, 2mi N Candelaria Loxicha, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/068" (LUZM, TAMU); 5 females "Oaxaca, 3.9mi NE San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley, 85/067" (2 females LUZM, 3 females TAMU); 1 female "Quintana Roo, 68km SW Chetumal, Kohunlich, 14–17.1983, 160m, M. Kaulbars" (CNC); 1 female "Tamaulipas, Reserva El Cielo Alta Cimas, 30.vii.1993, 3100', J.B. Woolley and K. Wikse, 93/035" (TAMU).

*Etymology.*—"Angusticornis" latin for "narrow antenna".

*Diagnosis.*—Body predominantly pale yellow to predominantly dark with weak metallic tinge; clypeus yellow to pale brown with weak metallic tinge, never dark and metallic; flagellum long and slender (Fig. 60); setae on vertex and thoracic dorsum black and long (Fig. 65).

*Description (female).*—Length of body = 1.0–1.4 mm.

Colour: Scape and pedicel pale yellow to infuscate; flagellum pale brown to dark. Frons pale yellow with golden-green stripe from eye to eye in level with antennal toruli, to golden-green with pale spots below toruli; clypeus pale brown with weak metallic tinge. Vertex pale yellow to dark with golden tinge, setae black. Thorax pale yellow, or mesoscutum dark with
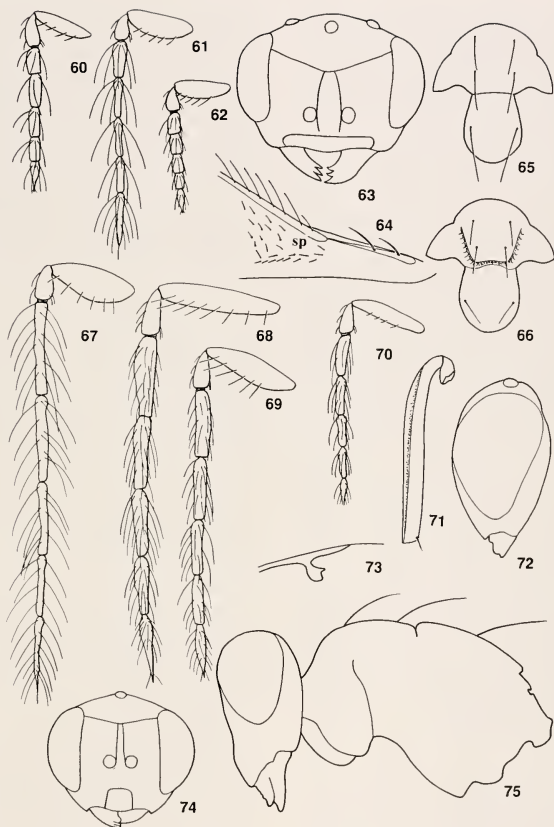
Figs. 60–75. 60–62. Antennae. 60, *angusticornis*, female. 61, *zolnerowichi*, male. 62, *oriampla*, female. 63, Head, frontal, *oriampla*, female. 64, Base of forewing, *zolnerowichi* (sp = speculum). 65–66. Mesoscutum+scutellum, dorsal. 65, *angusticornis*. 66, *fossata*. 67–70. Antennae. 67, *uruapana*, male. 68, *valida*, female. 69, *uruapana*, female. 70, *fossata*, female. 71, Foretibia, lateral, *valida*. 72, Head, lateral, *uruapana*, female. 73, Stigmal vein, *tempora*. 74, Head, frontal, *fossata*, female. 75, Head+mesosoma, lateral, *erginnus*.

golden tinge and scutellum yellowish-brown with median metallic stripe. Legs pale yellow, femora infuscate in dark specimens. Wings hyaline. Petiole pale. Gaster pale yellow with sides dark brown to entire gaster dark brown, apical part of ovipositor sheaths dark.

Head: Antenna as in Fig. 60. Frons with weak smallmeshed reticulation. Vertex with strong smallmeshed reticulation, hence dull. Clypeus 3.3× as wide as long. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with fine and weak reticulation; setae long, distance between a pair shorter than length of one seta. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline and with radial cell hairy.

Metasoma: Female gaster elongate.

### 30. Omphale cumbrensis n.sp.
#### (Fig. 55)

*Type material.*—Holotype male labelled "Oaxaca, 3.2mi SW La Cumbre, 8.vii.1985, J.B. Woolley, 85/071", gaster on slide (no. 283) (USNM). Paratype: 1 male with same label data as holotype (TAMU).

*Etymology.*—"From La Cumbre".

*Diagnosis.*—Frons close to mouth opening pale nonmetallic, but with clypeus dark and metallic; forewing speculum large (compared to *zolnerowichi*), open or closed below; male scape as in *zolnerowichi*, i.e. widest in median part (as opposed to *scutellata* and *vulgaris* in which scape is widest below middle).

*Description (male).*—Length of body = 1.0–1.2 mm.

Colour: Scape pale with apical ¼ dark; pedicel and flagellum dark. Frons, including clypeus, metallic bluish-green, below level of antennal toruli pale nonmetallic. Vertex golden. Mesoscutum golden-green to golden-purple. Scutellum golden-purple. Dorsellum golden-purple. Propodeum metallic bluish-green. Coxae dark and metallic, hind femur dark, remaining

parts of legs pale to infuscate. Wings hyaline. Petiole dark. Gaster golden-purple with anteromedian pale spot.

Head: Antenna as in *zolnerowichi* (Fig. 61). Frons and vertex smooth and shiny. Clypeus 2.3× as wide as long. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation. Dorsellum small, convex and smooth. Forewing speculum open or closed below; without stigmal hairline but with radial cell more or less bare.

### 31. Omphale oriampla n.sp.
#### (Figs 62, 63)

*Type material.*—Holotype female labelled "Guerrero, 32mi SE Petatlan, 10.vii.1985, J.B. Woolley, 85/047" (USNM). Paratypes: 1 female with same label data as holotype (TAMU); 1 female "Colima, 7mi SSW Colima, 9.vii.1984, J.B. Woolley, 84/026a" (LUZM); 1 female "Jalisco, 5.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/022" (LUZM); 1 female "Michoacan, 49mi SE Aquila, 13.vii.1984, J.B. Woolley, 84/031" (TAMU).

*Etymology.*—"Oriampla" latin for "large mouth".

*Diagnosis.*—Mouth opening and clypeus very wide (Fig. 63), mouth opening 1.3× as wide as height of eye and clypeus 8.5× as wide as long; mesoscutum and scutellum yellow nonmetallic with very weak superficial reticulation.

*Description (female).*—Length of body = 0.9–1.0 mm.

Colour: Scape pale with apex infuscate; pedicel and flagellum dark. Frons and vertex with golden-green tinges, frons below level of toruli pale nonmetallic. Mesoscutum, scutellum and dorsellum yellow nonmetallic, one specimen with anterior ⅓ of mesoscutum and a median stripe on scutellum golden-green; propodeum with golden-green tinges. Legs pale. Wings hyaline. Petiole pale. Gaster with golden-purple tinges.

Head: Antenna as in Fig. 62. Frons and vertex smooth and shiny. Clypeus 8.5× as wide as long. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with very weak superficial reticulation, almost smooth. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline and with radial cell hairy.

Metasoma: Gaster ovate.

## 32. Omphale scutellata (Girault)

Rhicnopeltomyia scutellata Girault, 1916b:40.
Rhicnopeltomyia belisarii Girault, 1917a:4, syn. Hansson (1996b:23).
Omphale scutellata (Girault), Schauff 1991:75.

Diagnosis.—Female mouth opening wide, 1.2–1.4× the height of an eye.

Distribution.—Colima, Guanajuato, Guerrero, Jalisco, Michoacan, Morelos, Oaxaca, Puebla. 118 females. New record for Mexico.

## 33. Omphale vulgaris Hansson

Omphale vulgaris Hansson, 1996b:24.

Diagnosis.—Female mouth opening narrow, 1.0× the height of an eye.

Distribution.—Chiapas, Guerrero, Jalisco, Michoacan, Oaxaca, Puebla. 74 females. New record for Mexico.

## Omphale scutellata/vulgaris

Distribution.—Colima, Guerrero, Jalisco, Michoacan, Oaxaca, Puebla. 55 males.

## 34. Omphale zolnerowichi n.sp.
### (Figs 56, 61, 64, 105, 122)

Type material.—Holotype male labelled "Chiapas, 12.1km S Palenque, 13.viii.1990, 1200', J.B. Woolley, 90/063'' (USNM). Paratypes: 1 male with same label data as holotype (TAMU); 2 males "Chiapas, 8mi N Berriozabal, 9.viii.1990, 3600', J.B. Woolley, 90/057B'' (LUZM, TAMU); 2 males "Chiapas, Ocozacoautla, 8.viii.1990, 1800–2200', J.B. Woolley, 90/055B'', 1 gaster on slide (no. 292) (LUZM, TAMU); 4 males

"Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032'' (2 males LUZM, 2 males TAMU); 1 male "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038'' (LUZM); 3 males "COSTA RICA: Heredia, La Selva, 50m, 22.i-2.ii.1991, J.S. Noyes'' (BMNH).

Etymology.—Name referring to collector of some of the type material of this species.

Diagnosis.—Clypeus large (Fig. 56), about 2× as wide as long; frons close to mouth opening dark and metallic; forewing speculum small and closed below (Fig. 64).

Description (male).—Length of body = 0.9–1.3 mm.

Colour: Scape pale with dorsal edge dark, to completely infuscate; pedicel and flagellum dark dorsally and pale ventrally, to completely dark. Frons, including clypeus, metallic bluish-green, bluish-purple or golden-green, with pale spots below toruli. Vertex golden-purple to golden-green. Mesoscutum with anterior ½ golden-green and posterior ½ yellow nonmetallic, to predominantly golden-green with only posterior border pale nonmetallic. Scutellum yellow nonmetallic, median ⅓ with longitudinal golden-green stripe, to predominantly golden-green with only sides pale nonmetallic. Dorsellum yellow nonmetallic. Propodeum metallic purple. Hind coxa dark and metallic, remaining parts of legs pale, tarsi infuscate. Forewing with infuscate spot below stigmal vein. Petiole dark. Gaster golden-purple with anteromedian pale spot.

Head: Antenna as in Fig. 61. Frons and vertex smooth and shiny. Clypeus large, 2× as wide as long. Frontal cross-groove V-shaped. Occipital margin rounded.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation. Dorsellum small, convex and smooth. Forewing speculum small and closed below; without stigmal hairline and with radial cell hairy.

## Species group semiglobosa

*Diagnosis.*—Clypeus semicircular to quadrangular with rounded corners (Fig. 74), dark and metallic. Head without frontal cross-ridge. Male flagellomeres with scattered setae (Fig. 67). Male genitalia (Fig. 106): volsellar setae long and strong and placed distinctly below parameres and volsellar ridges, and at same level; digitus elongate with inner digital spine enlarged and placed above outer spine; paramere with one long and slender seta at apex of paramere; aedeagus (Fig. 118) wide medially. Flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b). Forewing long and narrow, HW<LM.

*Apomorphies.*—Flagellomeres with elongate and asymmetric sensilla ampullacea. Forewing long and narrow. Male genitalia: digital spines placed at different levels; digitus elongate.

## 35. Omphale fossata n.sp.
### (Figs 66, 70, 74)

*Type material.*—Holotype female labelled "Oaxaca, 15.1mi N San Gabriel Mixtepec, 3850', 11.vii.1987, J.B. Woolley and G. Zolnerowich, 87/031" (USNM). Paratypes: 1 female with same label data as holotype (TAMU); 3 females "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (2 females LUZM, 1 female TAMU); 1 female "Michoacan, 10mi S Uruapan, 7.vii.1985, J.B. Woolley and G. Zolnerowich, 85/037" (TAMU).

*Etymology.*—"Fossata" meaning "with trench", referring to groove between mesoscutum and scutellum.

*Diagnosis.*—Midlobe of mesoscutum reticulate with elongate meshes, hence appearing striate; midlobe of mesoscutum delimited from scutellum by a distinct furrow (Fig. 66); clypeus quadratic, as wide as long (Fig. 74).

*Description (female).*—Length of body= 1.1–1.3 mm.

Colour: Antenna yellowish-brown, pedicel and flagellum slightly darker than scape. Head yellowish-brown with weak metallic tinges. Thorax yellowish-brown with weak metallic tinges. Mid and hind coxae pale, fore coxa and remaining parts of legs yellowish-brown. Forewing with a strong fuscous spot below median $\frac{1}{3}$ of marginal vein, spot reaching hind margin. Petiole pale. Gaster yellowish-brown, tergites 1–5 with darker hind margins, 7th tergite and apical ovipositor sheaths dark.

Head: Antenna as in Fig. 70. Frons below cross-groove with weak reticulation; frons above cross-groove and vertex smooth. Clypeus quadratic, as long as wide. Frontal cross-groove V-shaped. Occipital margin with sharp edge.

Mesosoma: Mesoscutum and scutellum with weak reticulation, midlobe of mesoscutum with elongate meshes and hence appearing striate; notauli deep and distinct in posterior $\frac{2}{3}$. Dorsellum small, convex and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Gaster elongate.

## 36. Omphale semiglobosa Hansson

*Omphale semiglobosa* Hansson, 1996b:39.

*Diagnosis.*—Mouth opening narrower than height of eye in both sexes; clypeus about as wide as long.

*Distribution.*—Campeche, Chiapas, Guerrero, Jalisco, Michoacan, Oaxaca, Puebla, Quintana Roo, Tamaulipas, Veracruz. 170 females 40 males. New record for Mexico.

## 37. Omphale uruapana n.sp.
### (Figs 67, 69, 72, 106, 118)

*Type material.*—Holotype female labelled "Michoacan, 10mi S Uruapan, 6.vii.1985, J.B. Woolley, 85/032" (USNM). Paratypes: 2 females 10 males with same label data as holotype, 1 male gaster on slide (no. 260) (1 female 5 males LUZM, 1 female 5 males TAMU); 1 male with same label data as holotype but collected

7.vii.1985 (LUZM); 1 female "Michoacan, 28.5mi S Nueva Italia, 9.vii.1985, J.B. Woolley and G. Zolnerowich, 85/045" (TAMU); 1 male "Guerrero, 2mi NE Cacahuamilpa, 4.vii.1987, 5300', R. Wharton" (TAMU); 1 female "Guerrero, 6.2mi SW Xochipala, 6.vii.1987, 5670', J.B. Woolley, 87/017" (LUZM, TAMU); 3 females 1 male "Jalisco, 17mi N Guadalajara, 6.vii.1984, J.B. Woolley, 84/019" (1 female 1 male LUZM, 2 females TAMU); 1 female "Jalisco, 6.7mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/021" (LUZM); 1 male "Jalisco, 8.3mi S Autlan on highway 80, 8.vii.1984, J.B. Woolley, 84/024" (TAMU); 1 female "Oaxaca, 8mi NE El Punto, 18.vii.1985, J.B. Woolley and G. Zolnerowich, 85/074" (TAMU); 1 female "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (LUZM).

*Etymology.*—"From Uruapan".

*Diagnosis.*—Mouth opening as wide as height of eye in female, slightly wider (1.1x) than eye in male; clypeus 2× as wide as long.

*Description.*—Length of body female= 1.6–2.0 mm, male= 0.8–1.4 mm.

Colour: Scape pale with dorsal edge dark; pedicel and flagellum dark, 5th flagellomere partly to completely pale in female. Frons golden-green. Vertex metallic bluish-green or golden-green. Mesoscutum metallic bluish-green, golden-green or golden-purple. Scutellum golden-green or golden-purple. Propodeum yellowish-brown with metallic tinge, completely yellow in a few specimens. Legs pale, fore coxa dark and metallic in one specimen, femora infuscate in a few specimens. Wings hyaline, weakly infuscate round stigmal vein. Petiole pale. Gaster dark brown with metallic bluish-green tinge, tergites 4 and 5 sometimes pale medially in female; apical part of ovipositor sheaths black.

Head: Antennae as in Figs 67, 69. Frons below frontal cross-groove with weak reticulation; above cross-groove and on ver-

tex smooth and shiny. Clypeus 2× as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove almost straight. Occipital margin with raised carina.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation; notauli distinct and clearly delimited in posterior ⅔. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Petiole in male transverse, 0.7× as long as wide. Female gaster ovate.

### 38. Omphale valida n.sp.
(Figs 68, 71)

*Type material.*—Holotype female labelled "Guerrero, 1mi NE La Laguna, 17.vii.1984, J.B. Woolley, 84/038" (USNM).

*Etymology.*—"Valida" is latin for large, referring to size of species.

*Diagnosis.*—Vertex, mesoscutum and scutellum with strong and raised reticulation; fore tibia with a raised carina along dorsal surface (Fig. 71).

*Description (female).*—Length of body= 2.1 mm.

Colour: Scape pale with dorsal edge dark; pedicel and flagellum dark. Head and mesosoma black and shiny with weak metallic tinge. Fore coxa dark and metallic, mid and hind coxae pale; femora infuscate; tibiae pale; tarsi pale with apical segment infuscate. Wings hyaline. Petiole pale. Gaster dark brown with metallic tinge.

Head: Antenna as in Fig. 68. Frons with weak reticulation. Vertex with raised and strong reticulation. Clypeus as wide as long. Antennal scrobes join on frontal cross-groove. Frontal cross-groove V-shaped. Occipital margin with raised carina.

Mesosoma: Mesoscutum and scutellum with raised and strong reticulation; notauli distinct and clearly delimited in posterior ⅔. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare. Propodeum with weak reticulation.

Metasoma: Gaster ovate.

UNPLACED SPECIES

### 39. Omphale dentata n.sp.
(Figs 78, 79, 87, 109, 121)

*Type material.*—Holotype female labelled "Chiapas, 12.1 km S Palenque, 13.viii.1990, 1200', J.B. Woolley, 90/063" (USNM). Paratypes: 1 male with same label data as holotype (TAMU); 1 female "Chiapas, 8mi N Berriozabal, 9.viii.1990, 3600', J.B. Woolley, 90/057B" (TAMU); 1 male "Oaxaca, 2mi N Candelaria Loxicha, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/068" gaster on slide (no. 236) (LUZM); 2 females "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (LUZM, TAMU); 2 females "Tamaulipas, Reserva El Cielo, Alta Cimas, 3100', 30.vii.1993, J.B. Woolley and K. Wikse, 93/035" (LUZM, TAMU).

*Etymology.*—"Dentata" meaning "with tooth", referring to medioventral dent on male scape.

*Diagnosis.* Head smooth and shiny without any reticulation; antennal scrobes join slightly below frontal cross-groove (Fig. 87); flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b); male scape with a dent medioventrally (Fig. 79); male petiole as long as wide.

*Description.*—Length of body female= 1.0–1.3 mm, male= 0.9–1.0 mm.

*Colour.* Antenna pale yellowish-brown, apical flagellomere sometimes pale in female. Clypeus dark and metallic. Frons golden-green. Vertex metallic bluish-green to golden-green. Mesoscutum and scutellum metallic bluish-green. Dorsellum and propodeum golden-purple, propodeum pale yellowish-brown in one specimen. Fore coxa infuscate to dark and metallic, remaining parts fore leg, mid and hind legs pale. Wings hyaline. Petiole pale. Gaster golden-purple.

*Head:* Without frontal cross-ridge. Antennae as in Figs 78, 79, i.e. male flagellomeres with verticillate setae (with a single basal whorl of setae on each flagellomere); flagellomeres with sensilla ampullacea long and asymmetric; male scape with a dent medioventrally. Frons and vertex smooth and shiny without reticulation; antennal scrobes join slightly below frontal cross-groove. Occipital margin with a sharp edge.

*Mesosoma:* Mesoscutum and scutellum with weak reticulation; notauli clearly to weakly delimited in posterior ⅔. Dorsellum small, flat and smooth. Forewing speculum closed below; radial cell hairy. Propodeum smooth, with complete median carina.

*Metasoma:* Petiole transverse in female, in male as long as wide, both sexes with a raised and sharp carina along anterior edge. Gaster elongate in female. Male genitalia (Fig. 109) with volsellar setae long and strong, placed at different levels, below parameres and base of volsellar ridges; digitus as long as wide, inner digital spine larger than outer; paramere with one seta at apex of paramere; aedeagus (Fig. 121) with aedeagal apodemes 1.2× as long as penis valves.

*Remarks.*—*Omphale dentata* is very close to *Holcopelte*, the only difference being the enlarged volsellar setae in male genitalia of *O. dentata* (as in all species of *Omphale*), volsellar setae are normal in *Holcopelte*.

### 40. Omphale erginnus (Walker)
(Figs A, 75, 88)

*Entedon erginnus* Walker, 1839:124.
*Omphale erginnus* (Walker), Graham 1959:202.

*Diagnosis.*—Setae on vertex and thoracic dorsum long and strong; scape with a small dent apicoventrally in male (this is the apical portion of the ventral sense area); flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b); vertex smooth and shiny; transepimeral sulcus straight.

*Distribution.*—Chiapas, Michoacan, Oa-
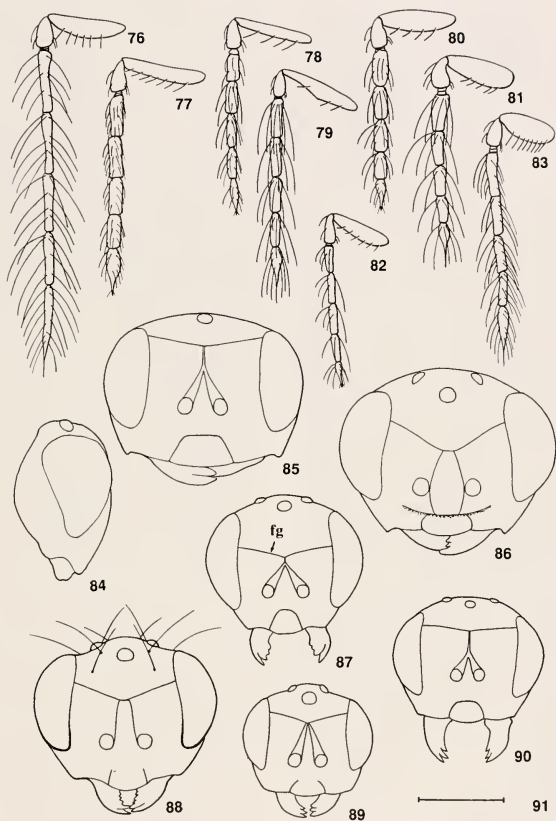
Figs. 76–91.  76–83. Antennae. 76, *tempora*, male. 77, Ditto, female. 78, *dentata*, female. 79, Ditto, male. 80, *sola*, female. 81, Ditto, male. 82, *indistincta*, female. 83, Ditto, male. 84. Head, lateral, *tempora*, female. 85–90. Head, frontal, female. 85, *tempora*. 86, *sola*. 87, *dentata* (fg= frontal cross-groove) 88, *erginnus*. 89, *indistincta*. 90, *nita*. 91, Scale = 0.2 mm (Figs. 1–90), except Figs. 13, 40, scale= 0.4 mm.
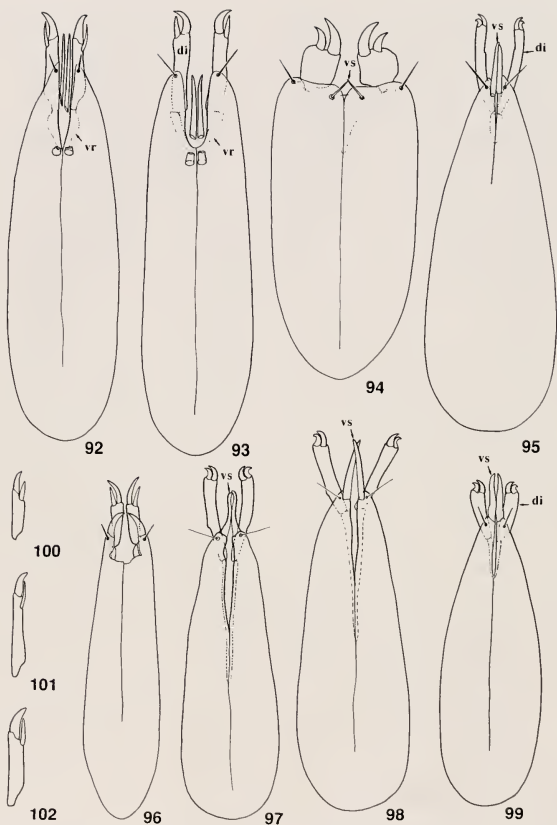
Figs. 92–102. 92–99. Phallobase, ventral. 92, *elevata*. 93, *woolleyi* (Figs. 92, 93 with part of volsellar setae omitted to show volsellar ridges). 94, *cherana*. 95, *tria*. 96, *petatlana*. 97, *divina*. 98, *australis*. 99, *carinata*. 100–102. Digitus, ventral. 100, *whartoni*. 101, *metallica*. 102, *petiolata*. di= digitus, vr= volsellar ridge, vs= volsellar seta.

xaca, Puebla. 9 females 2 males. New record for Mexico.

### 41. Omphale indistincta n.sp.
(Figs 82, 83, 89, 110, 123)

*Type material.*—Holotype female labelled "Jalisco, 4.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/023" (USNM). Paratypes: 2 females with same label data as holotype (LUZM, TAMU); 3 females "Jalisco, 16mi S Autlan, 8.vii.1984, J.B. Woolley, 84/025" (1 female, LUZM, 2 females TAMU); 2 females "Jalisco, 5.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/022" (LUZM, TAMU); 2 females "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038" (LUZM, TAMU); 2 females "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (LUZM, TAMU); 4 females 2 males "Oaxaca, 9mi W Tehuantepec, 13.vii.1987, G. Zolnerowich, 87/039", 1 male gaster on slide (no. 250) (2 females 1 male LUZM, 2 females 1 male TAMU).

*Etymology.*—Name referring to indistinct upper border of clypeus.

*Diagnosis.*—Clypeus not delimited dorsally (Fig. 89); flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b).

*Description.*—Length of body female= 1.0–1.4 mm, male= 1.0 mm.

Colour: Scape pale with dorsal edge dark; pedicel and flagellum darker. Frons golden-green to golden-purple in female, metallic bluish-green in male. Vertex golden-green. Mesoscutum and scutellum golden-purple to golden-green. Dorsellum and propodeum golden-green. Fore coxa dark and metallic to pale, mid and hind coxae pale; femora pale to infuscate; tibiae pale; tarsi pale with apical segment infuscate to completely pale. Wings hyaline. Petiole pale. Gaster golden-purple to golden-green.

Head: Without frontal cross-ridge. Antennae as in Figs 82, 83, i.e. male flagellum with scattered setae; flagellomeres with

sensilla ampullacea elongate and asymmetric. Frons and vertex smooth and shiny; male frons with weak reticulation. Clypeus 2× as wide as long, delimited laterally but not dorsally. Antennal scrobes join on frontal cross-groove. Frontal cross-groove V-shaped. Occipital margin with blunt carina.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation; notauli distinct and clearly delimited in posterior ⅔. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster ovate to elongate. Male genitalia (Fig. 110) with volsellar setae long and strong, placed at same level, below parameres and just below base of volsellar ridges; inner digital spine larger than outer; paramere with one seta close to apex of paramere; aedeagus (Fig. 123) with aedeagal apodemes 0.9× as long as penis valves.

### 42. Omphale nita n.sp.
(Fig. 90)

*Type material.*—Holotype female labelled "Puebla, 5mi SE Izucar de Matamoros, 20.vii.1984, J.B. Woolley, 84/044" (USNM).

*Etymology.*—No specific derivation.

*Diagnosis.*—Occipital margin smoothly rounded; mesoscutum and scutellum smooth and shiny with weak traces of reticulation in some places; antennal scrobes join below frontal cross-groove (Fig. 90); clypeus transverse, 2× as wide as long; flagellomeres with sensilla ampullacea long and asymmetric (type III sensu Hansson 1996b).

*Description (female).*—Length of body= 1.8 mm.

Colour: Antenna dark. Frons golden-purple; vertex metallic bluish-purple. Mesoscutum golden-green; scutellum golden-purple. Fore coxa dark and metallic, mid and hind coxae pale, hind coxa metallic at base; femora pale with dorsal surface infuscate; tibiae pale; tarsi pale with apical
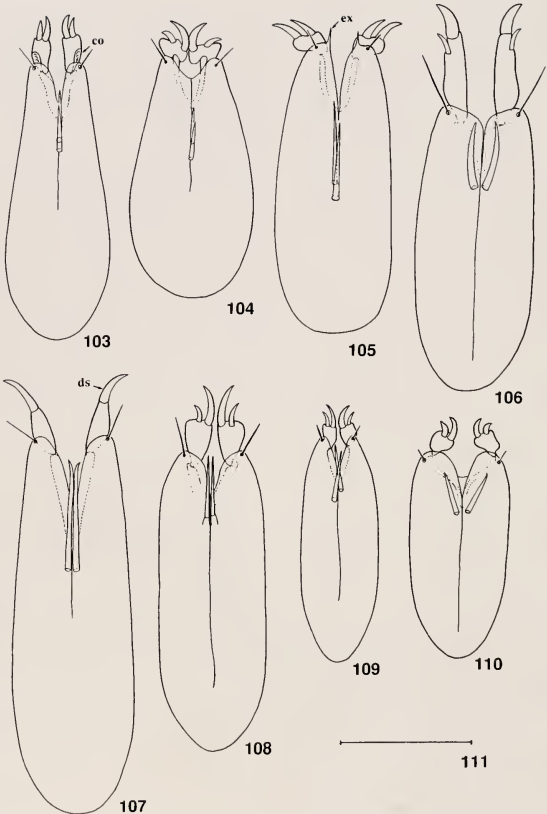
Figs. 103–111.   103–110. Phallobase, ventral. 103, *foveata* (co= concavity). 104, *pallida*. 105, *zolnerowichi* (ex= extension from phallobase). 106, *uruapana*. 107, *sola* (ds= digital spine). 108, *tempora*. 109, *dentata*. 110, *indistincta*. 111, Scale = 0.1 mm (Figs. 92–125).
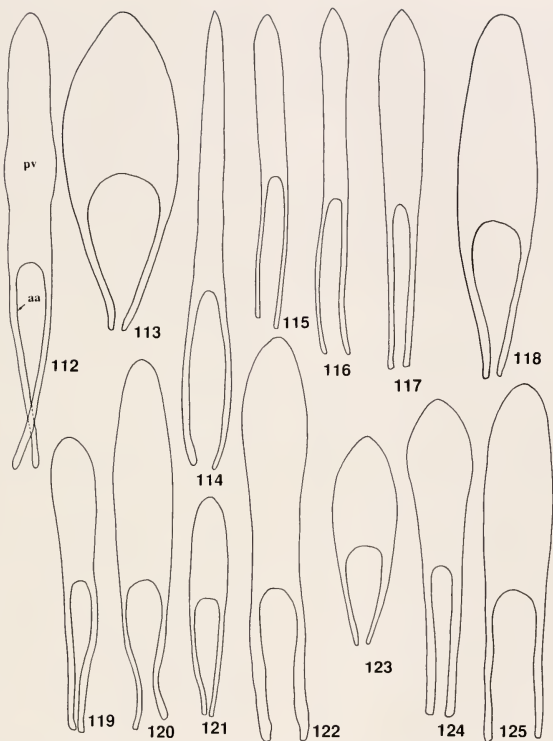
Figs. 112–125. Aedeagus, ventral. 112, *woolleyi* (aa= aedeagal apodemes, pv= penis valves). 113, *cherana*. 114, *tria*. 115, *petatlana*. 116, *carinata*. 117, *foveata*. 118, *uruapana*. 119, *fulgida*. 120, *tempora*. 121, *dentata*. 122, *zolnerowichi*. 123, *indistincta*. 124, *pallida*. 125, *sola*.

segment infuscate. Wings hyaline. Petiole pale. Gaster dark with metallic tinges, tergites 2–6 with paler median spot.

Head: Without frontal cross-ridge. Antenna as in *indistincta* (Fig. 82); flagellomeres with sensilla ampullacea elongate and asymmetric. Frons and vertex smooth and shiny. Clypeus 2× as wide as long. Antennal scrobes join below frontal crossgroove. Frontal cross-groove almost straight. Occipital margin smoothly rounded.

Mesosoma: Mesoscutum and scutellum smooth and shiny with weak traces of reticulation in some places; notauli distinct and clearly delimited in posterior 2/3. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Gaster elongate.

*Remarks.*—The placement of *nita* is difficult since the species groups are mainly based on appearances of structures in male genitalia, and *nita* is known only in the female sex. The female resembles females of *semiglobosa* group, but also females of *tempora* n.sp., another unplaced species.

### 43. **Omphale sola** n.sp.
(Figs 80, 81, 86, 107, 125)

*Type material.*—Holotype male labelled "Guerrero, 32mi SE Petatlan, 10.vii.1985, J.B. Woolley, 85/047" (USNM). Paratypes: 17 females 4 males with same label data as holotype (8 females 2 males LUZM, 9 females 2 males TAMU); 1 females 4 males "Guerrero, 6.2mi SW Xochipala, 13.vii. 1985, J.B. Woolley, 85/056" (2 males LUZM, 1 female 2 males TAMU); 1 female 1 male with same label data as previous but collected 5.vii (TAMU); 1 female 1 male "Guerrero, 18.2mi S Iguala, 5.vii.1987, 3000', J.B. Woolley, 87/013" (LUZM); 1 female 1 male "Guerrero, 2.1mi NE Cacahuamilpa, 4.vii.1987, 5250', J.B. Woolley, 87/011" (TAMU); 2 males "Guerrero, 2mi NE Cacahuamilpa, 4.vii.1987, 5300', R. Wharton", one gaster on slide (no. 265) (LUZM); 1 male "Guerrero, 15mi SW Chichihualco, 15.vii.1984, J.B. Woolley, 84/034" (TAMU); 1 male "Chiapas, 8.5km N Ishuatan, 2.viii.1990, 1000', J.B. Woolley, 90/050" (TAMU); 2 males "Colima, 7mi SSW Colima, 9.vii.1984, J.B. Woolley, 84/026A" (LUZM, TAMU); 2 females "Jalisco, 5.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/022" (LUZM, TAMU); 1 male "Jalisco, 4.2mi N Autlan Mine Road, 7.vii.1984, J.B. Woolley, 84/023" (TAMU); 1 female "Mi-

choacan, 3mi N Nueva Italia, 8.vii.1985, J.B. Woolley and G. Zolnerowich, 85/042" (TAMU); 1 female "Michoacan, 10mi S Uruapan, 7.vii.1985, J.B. Woolley and G. Zolnerowich, 85/037" (LUZM); 1 male "Michoacan, 49mi SE Aquila, 13.vii.1984, J.B. Woolley, 84/031" (TAMU); 1 female "Oaxaca, 15.1mi N San Gabriel Mixtepec, 3850', 11.vii.1987, J.B. Woolley and G. Zolnerowich, 87/031" (TAMU); 3 females 2 males "Oaxaca, 4.4mi S San Gabriel Mixtepec, 10–11.vii.1987, 2500', J.B. Woolley and G. Zolnerowich, 87/027A" (2 females 1 male LUZM, 1 female 1 male TAMU); 3 females 1 male "Oaxaca, 4.7mi S San Gabriel Mixtepec, 16.vii.1985, J.B. Woolley and G. Zolnerowich, 85/066" (1 female 1 male LUZM, 2 females TAMU); 3 females 1 male "Oaxaca, 29.1mi E Pochutla, 13.vii.1987, 80', J.B. Woolley and G. Zolnerowich, 87/038" (2 females LUZM, 1 female 1 male TAMU); 1 female 2 males "Oaxaca, 2mi N Candelaria Loxicha, 17.vii.1985, J.B. Woolley and G. Zolnerowich, 85/068" (1 male LUZM, 1 female 1 male TAMU).

*Etymology.*—"Sola" meaning "single", referring to single digital spine in male genitalia.

*Diagnosis.*—Notauli complete and deep throughout; radial cell hairy; frontal crossgroove placed low down on frons; mesoscutum and scutellum with strong engraved reticulation; digitus with one spine only (Fig. 107); flagellomeres with sensilla ampullacea short and asymmetric (type II sensu Hansson 1996b).

*Description.*—Length of body female and male = 1.0–1.6 mm.

Colour: Scape pale with dorsal edge infuscate, to completely infuscate; pedicel and flagellum dark. Frons below crossgroove golden-green, golden-red, golden-purple or golden in female, in male metallic greenish-blue or bluish-purple; above cross-groove and vertex golden-green or golden-purple in female, in male metallic greenish-blue or bluish-purple. Mesoscutum weak metallic greenish-blue,
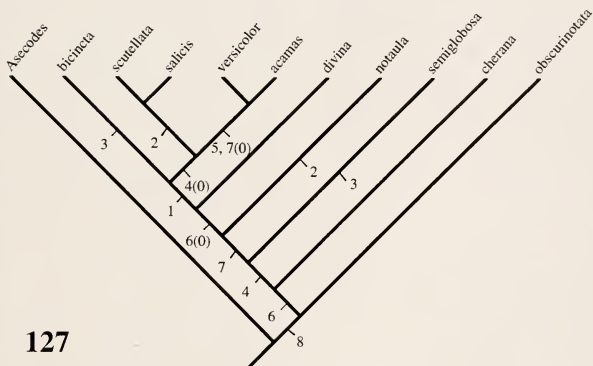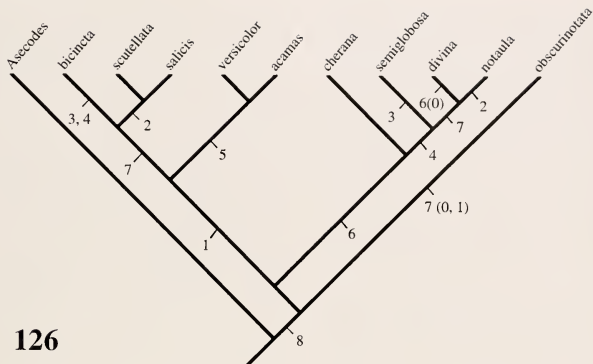
Figs. 126–127. Hypothesized relationships between North American species groups of *Omphale* (15 steps, CI=0.67, RI=0.76). Zero (0) indicates a reversal.

golden-red or golden-purple. Scutellum weak metallic greenish-blue or golden-green. Propodeum golden-green. Forecoxa dark and metallic, mid and hind coxae pale to all coxae dark and metallic; femora dark; tibiae and tarsi pale to infuscate, tibiae dark in a few specimens. Wings hyaline. Petiole dark. Gaster with 1st tergite

metallic greenish-blue (female) or golden-green (male), remaining tergites golden-green (female) or golden-purple (male).

Head: With frontal cross-ridge. Antennae as in Figs 80, 81, i.e. male flagellomeres with verticillate setae (with a single basal whorl of setae on each flagellomere); sensilla ampullacea short and asymmetric. Frons and vertex smooth and shiny; inside ocellar triangle with weak superficial reticulation. Clypeus semicircular and semicircularly protruding. Antennal scrobes join on frontal cross-groove. Frontal cross-groove V-shaped. Occipital margin with an edge.

Mesosoma: Mesoscutum and scutellum with strong engraved reticulation; notauli distinct and clearly delimited in posterior ⅔. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline and with radial cell hairy. Propodeum with weak reticulation.

Metasoma: Female gaster ovate. Male genitalia (Fig. 107) with volsellar setae long and strong, placed at same level, below parameres and just below base of volsellar ridges; with only one strong digital spine; paramere with one seta at apex of paramere; aedeagus (Fig. 125) with aedeagal apodemes 0.7× as long as penis valves.

### 44. **Omphale tempora** n.sp.
(Figs 73, 76, 77, 84, 85, 108, 120)

*Type material.*—Holotype female labelled "Michoacan, 13.1mi S Nueva Italia, 9.vii.1985, J.B. Woolley and G. Zolnerowich, 85/044" (USNM). Paratypes: 16 males with same label data as holotype, one male gaster on slide (no. 262) (8 males LUZM, 8 males TAMU); 1 male "Jalisco, 17mi N Guadalajara, 6.vii.1984, J.B. Woolley, 84/019" (TAMU).

*Etymology.*—"Tempora" meaning "temples", referring to large temples in this species.

*Diagnosis.*—Mouth opening very wide, 1.7× the height of eye in female, 1.5× in male; temples large (Fig. 84); stigmal vein

enlarged (Fig. 73); occipital margin smoothly rounded; clypeus transverse, 2× as wide as long; flagellomeres with sensilla ampullacea short and asymmetric (type II sensu Hansson 1996b).

*Description.*—Length of body female= 1.5 mm, male=1.0–1.6 mm.

Colour: Scape and pedicel yellowish-brown; flagellum dark. Frons dark with weak golden tinges; vertex dark with golden-green tinges. Mesoscutum and scutellum dark with weak golden tinge. Propodeum paler than scutellum, more or less brownish. Fore coxa infuscate, mid and hind coxae pale, hind coxa metallic at base; femora and tibiae pale, fore tibia pale to infuscate in male; tarsi pale with apical segment infuscate, all tarsal segments infuscate in some males. Wings hyaline. Petiole pale. Gaster dark with golden-green tinges.

Head: Without frontal cross-ridge. Antennae as in Figs 76, 77, i.e. male flagellomeres with scattered setae; sensilla ampullacea short and asymmetric. Frons and vertex smooth and shiny. Clypeus 2× as wide as long. Antennal scrobes join below frontal cross-groove. Frontal cross-groove almost straight. Occipital margin smoothly rounded.

Mesosoma: Mesoscutum and scutellum with fine engraved reticulation in some places; notauli distinct and clearly delimited in posterior ⅔. Dorsellum small, flat and smooth. Forewing speculum closed below; without stigmal hairline but with radial cell bare.

Metasoma: Female gaster ovate. Male genitalia (Fig. 108) with volsellar setae long and strong, placed at same level, below parameres and base of volsellar ridges; inner digital spine about twice as large as outer spine; paramere with one seta at apex of paramere; aedeagus (Fig. 120) with aedeagal apodemes 0.7× as long as penis valves.

### ACKNOWLEDGMENTS

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# Sting Autotomy, Sting Morphology and Sociality in Neotropical Vespids (Hymenoptera: Vespidae)

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*Abstract.*—Autotomy of the sting apparatus was investigated in twenty eight species of neotropical social wasps belonging to the Polistinae. Sting autotomy was found to be positively correlated with the number of acuminate barbs and with the degree of sociality.

## INTRODUCTION

The high degree of kinship among the cohabitants of social Hymenoptera colonies, their subsequent altruistic behavior and differential reproductive investment suggest that defense may have become progressively more important with increasing sociability (Hermann & Blum 1981). According to Starr (1985, 1988), sting development occurred due to the pressure exerted by predators that were attracted by the increase in colony size, especially in tropical regions.

Some species of social Hymenoptera display autotomy of the sting apparatus. Although this process has been known since 1933, according to Rau (apud Hermann 1971), no comparative studies are available to support a discussion about its contribution to the evolution of socia-
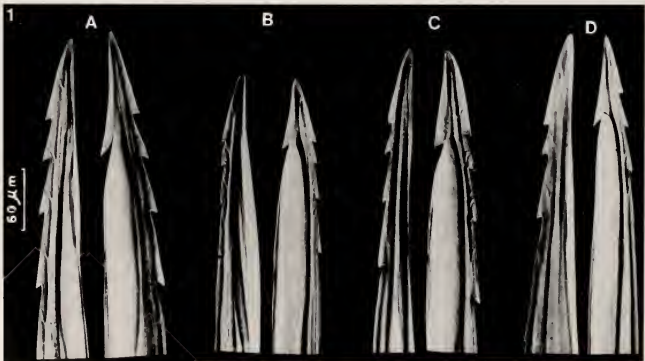


Fig. 1. Lancets of the stinging apparatus of the social wasps from genus *Mischocyttarus*. A. *M. drewseni*. B. *M. cassununga*. C. *M. latior*. D. *M. cerberus*.
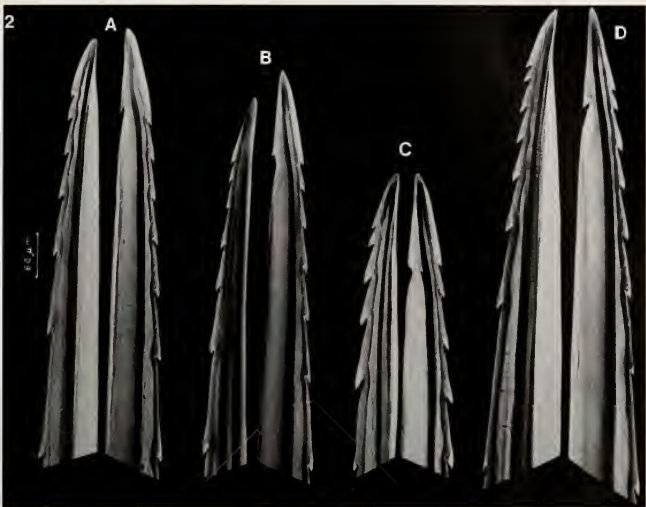
Fig. 2. Lancets of the stinging apparatus of the social wasps from genus *Polistes*. A. *P. versicolor*. B. *P. simillimus*. C. *P. subsericeus*. D. *P. lanio lanio*.

bility among wasps. Hermann (1971), Poore (1974a, 1974b) and Hermann & Blum (1981) demonstrated the existence of barbs in the lancets of the stings of both solitary and social Hymenoptera and speculated that the shape and size of these barbs, in addition to other variables, must contribute in some way to the autotomy process.

In the present study we have investigated the sting autotomy in various species of social wasps of the subfamily Polistinae and report here correlation both with the degree of sociality as defined by Evans (1958), and with the morphology of sting in agreement with the predictions of Hermann (1971).

## MATERIALS AND METHODS

The social wasps species studied were from the towns of Rio Claro, Ribeirão Preto and Pirassununga (State of São Paulo, southeastern Brazil) and from Belém (State of Pará, northern Brazil), as follow:

*Agelaia pallipes pallipes* (Olivier, 1791)
*Agelaia vicina* (de Saussure, 1854)
*Agelaia multipicta* (Halliday, 1836)
*Polybia (Myrapetra) paulista* H.von Ihering, 1896
*Polybia (Apopoiybia) jurinei* de Saussure, 1854
*Polybia (Myrapetra) occidentalis* (Olivier, 1791)
*Polybia (Trichothorax) sericea* (Olivier, 1791)

Fig. 3. Lancets of the stinging apparatus of the social wasps from genus *Apoica*. A. *A. pallens*. B. *A. flavissima*.
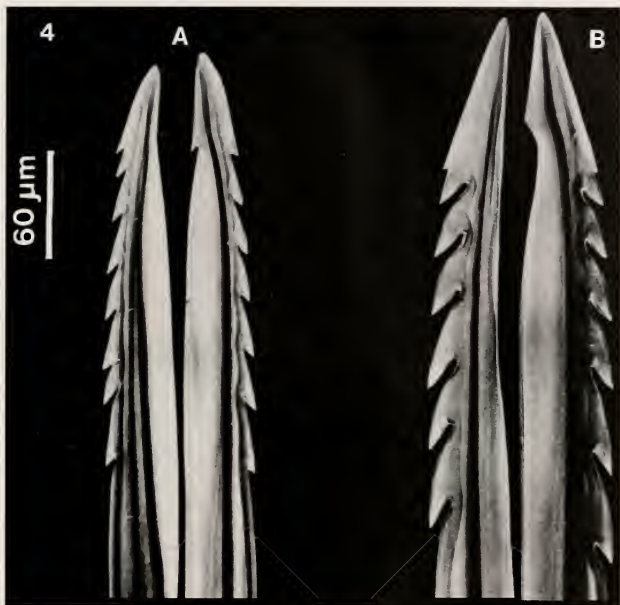
Fig. 4. Lancets of the stinging apparatus of the social wasps from genera *Metapolybia* and *Pseudopolybia*. A. *M. cingulata*. B. *P. vespiceps*.

*Polybia (Myrapetra) platicephala slyvestris* Richards, 1951

*Polybia (Formicicola) rejecta* (Fabricius, 1798)

*Polybia (Myrapetra) scutellaris* (White, 1841)

*Polybia (Myrapetra) fastidiosuscula* de Saussure, 1854

*Protonectarina sylveirae* (de Saussure), 1854

*Brachygastra lecheguana* (Latreille, 1824)

*Metapolybia cingulata* (Fabricius, 1804)

*Pseudopolybia vespiceps* (de Saussure, 1864)

*Protopolybia sedula* (de Saussure,1854)

*Protopolybia exigua exigua* (de Saussure, 1854)

*Synoeca cyanea* (Fabricius, 1775)

*Apoica (Apoica) pallens* (Fabricius, 1804)

*Apoica (Apoica) flavissima* Van der Vecht, 1973

*Mischocyttarus (Haplometrobius) cerberus* Ducke,1918

*Mischocyttarus (Mischocyttarus) drewseni* de Saussure, 1857

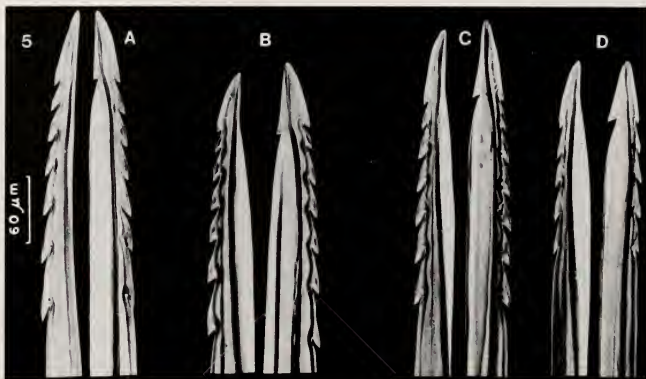*Mischocyttarus (Monocyttarus) cassununga* (R. von. Ihering, 1903)

Fig. 5. Lancets of the stinging apparatus of the social wasps from genera *Brachygastra*, *Protonectarina* and *Protopolybia*. A. *B. lecheguana*. B. *P. sylveirae*. C. *P. sedula*. D. *P. exigua exigua*.

*Mischocyttarus (Kappa) latior* (Fox, 1898)

*Polistes (Epicnemius) subsericeus* de Saussure, 1854

*Polistes (Aphanilopterus) versicolor* (Olivier, 1791)

*Polistes (Aphanilopterus) simillimus* Zikan, 1951

*Polistes (Aphanilopterus) lanio lanio* (Fabricius, 1775).

Sting autotomy was investigated in twenty-eight species of Polistinae using the methodology of Stort (1974) and Overal *et al* (1981). Targets consisting of black suede balls 5 cm in diameter attached with a string to a 2.00 m long pole were dangled and shaken 15 cm from the entrance to the nest and allowed to be attacked. Thus, the species endowed with the autotomy process lose their stings which remain fixed to the target. The sting apparati of these species were dissected and the right and left lancets separated, dehydrated in 90 and 100% ethyl alcohol (I, II and III) and cleared in xylene (I, II and III). The

lancets were cut in the middle for mounting and for better barb visualization, since the barbs are positioned laterally in the lancets. The lancet pieces containing the barbs were mounted on slides with Canada Balsam (Cruz-Landim & Beig 1966).

RESULTS AND DISCUSSION

In those social wasps that exhibit "sting autotomy", the venom reservoir and associated gland, various muscles and associated cuticular plates, as well as the sting proper are left attached to the victim's sting. As a consequence of this considerable damage, the individual wasp invariably dies soon, and afterwards so that the behavior might be thought in terms of "defensive altruism".

In all the wasps studied the left and right lancets we found to have several barbs (Figs. 1 to 9). There was some intraspecific variation and also some variation between left and right lancets. Anatomically, the left and right lancets differ both

Fig. 6. Lancets of the stinging apparatus of the social wasps *Synoeca cyanea*.

in thickness and in shape; the right lancet is wider from the median portion to the apex, which is shaped like an arrow positioned perpendicularly in relation to the barbs. The barbs are located on the external sides of the lancets and are distributed on the upper portion of the latter and may be either longer and of the acuminate type or shorter and of the serrate type.

The tables 1 and 2 are showing the recorded variation in the number of barbs/lancet for autotomisers and no autotomisers social wasps, respectively.

Even considering that are some species both with a reduced number of barbs among the autotomisers (Table 1) and species with large number of barbs among the non-autotomisers (Table 2), the direct comparison betweem these groups based on t-tests of means revealed that, overall, the number of bars/lancet were significatively higher (P< 0,01) in autotomisers. These results suggest that the morphology of sting is important character to the occurrence of the process of autotomy.

During the aggressivity tests no queen was identified among the aggressors. Some queens collected both in a specie which they are not morphologically distinct from workers, like *Polybia paulista,* and in species whose they are morphologically distinct from workers, like *Agelaia pallipes* and *Protonectarina sylveirae;* the morphology of theirs stings and the numbers of barbs were identical to those described for the workers. In spite to this similarity the queens do not attend the defense of their colonies. Overal *et al* (1981) also related the absence of queens during actions of colony defense in *Polybia rejecta.*

Among the autotomisers species the number of aggressors and stings left over the targets in each trial of the aggressivity tests, was very different from specie to specie. This aspect of the defensive answer must consider the level of sociability of each specie, which in turn seems to be influencing differentially the aggressive behavior of these species. As exemple of this influence, Manzoli—Palma (1993), observed that in spite of *Metapolybia cingulata and Polybia occidentalis,* present sting autotomy, during the tests of aggressivity the most individual of these colonies scaped away to a far place or hidden themself
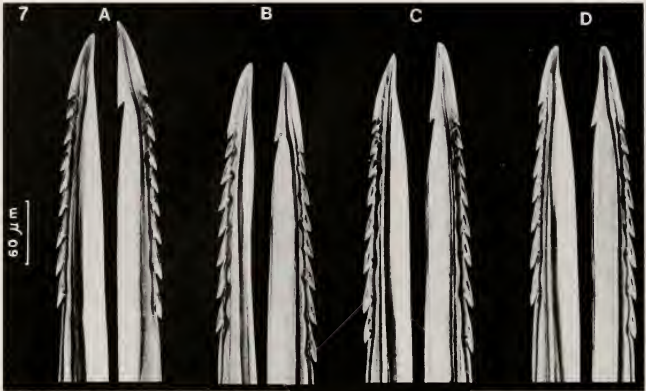
Fig. 7. Lancets of the stinging apparatus of the social wasps from genus *Polybia*. A. *P. paulista*. B. *P. platicephala sylvestris*. C. *P. scutellaris*. D. *P. occidentalis*.

inside the nest, rarely stinging the target or the experimenter. Thus, in this situation the number of aggressors and stings left over the targets were very small even after intense provocation.

According to West-Eberhard (1973) and Jeanne (1991) these species belong to the group that alternate between monogyny and polygyny. These species seems to opt preferentially for flight since they present small populations in which the loss of a single individual may be important. Thus, it would be of high adaptive value to maintain the malleability of the colony; in other words, in an emergency situation the population may abandon the nest as a whole, so that the occurrence of temporary polygyny will permit a rapid establishement of a new brood.

In addition to this, there are other aspects that may influence the level of aggressivity even from nest to nest of the same specie. The population structure of each colony at the moment of the tests,

such as: the total number of adults (number of workers, queens and males), larvae and pupae are important factors that also must be considered. Thus, as exemple of the influence of these factors, Manzoli-Palma & Gobbi (1994) demonstrated in *Polybia paulista* that the number of aggressors and stings left over the targets, increases as function the increasing in the number of workers and is amazingly potentiated by an increasing in the number of pupae.

In general, the species that do not present autotomy of the sting apparatus belong to the tribes **Polistini** and **Polybiini**, whereas those that present such a process belong to a group from the tribe **Polybiini** which presents a higher degree of sociability (Evans 1958). Thus, it was observed that, the increase in the number and development of barbs only occurred after the establishment of greater social complexity, although independent of morphological female differentiation. Thus, the study of sting apparatus mor-
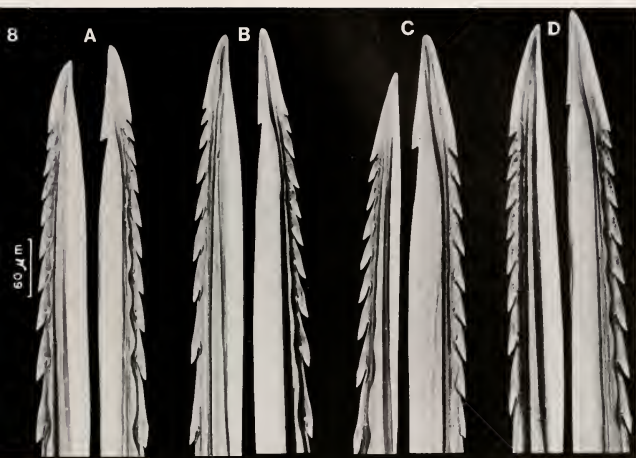
Fig. 8. Lancets of the stinging of the social wasps from genus *Polybia*. A. *P. fastidiosuscula*. B. *P. rejecta*. C. *P. sericea*. D. *P. jurinei*.

phology contributes to a better understanding of the probable extent of specialization of each genus.

When analyzing the relation between the level of sociability, autotomy process, nest architecture and number of barbs, the genus *Mischocyttarus* presents the smaller number of barbs that are less acuminate (Fig. 1) (barbs = 4), whereas the barbs of *Agelaia* are more pronounced and present in larger numbers (Fig. 9) (barbs = 9 to 14). These genera are located on the 11th and 13th steps of the evolutionary scale of Evans (1958), respectively, with well differentiated aggressive behaviors. Individuals of the *Mischocyttarus*, species observed by us adopted a posture of indifference in situations of danger, never stung the experimenter and at times abandoned the nest. This species present, social regulation via individual dominance, are

monogynous, build opened nests, with small populations where a situation in which the loss of some individuals might be highly harmful to colony maintenance and/or continuity.

However, wasps of the genus *Agelaia* attack in groups, are extremely aggressive pursue the experimenter and easily lose their stings in the target. This species build nest inside a preexisting structure to shelter it, are polygynous, present large populations, swarm-founding and sometimes worker caste morphologically distinct from queen. For these neotropical wasp species, sting autotomy is a process that favors colony defense when the loss of some individuals is not significant for the colony as a whole. Thus, in danger situations such as attack by a predator, the sacrifice of some altruistic individuals for colony defense is preferable to the flight
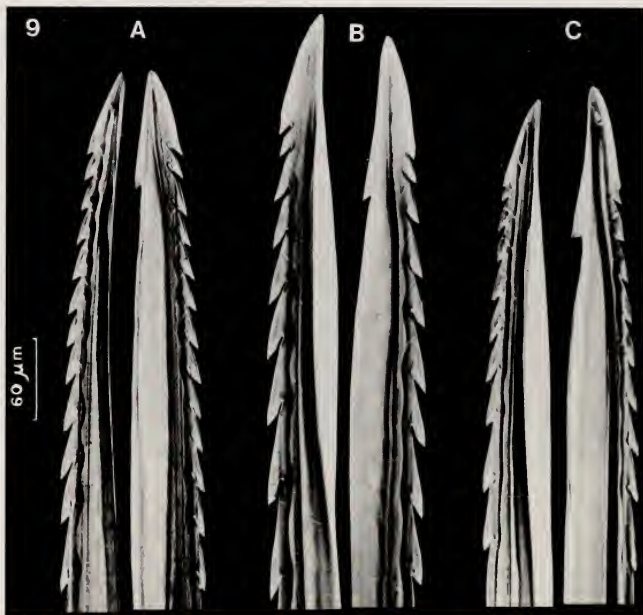
Fig. 9. Lancets of the stinging of the social wasps from genus *Agelaia*. A. *A. vicina*. B. *A. pallipes pallipes*. C. *A. multipicta*.

of the entire population in order to found a new nest.

Species that alternate between monogyny and polygyny still may produce more complex interactions between those factors that are influencing the occurrence of sting autotomy creating some exceptions in relation to the established patterns of autotomy. Thus, for exemple individuals of the genus *Apoica* that alternate between monogyny and polygyny (Gobbi, 1987; Shima, 1991), have some characteristics of

autotomisers such as: large number of well developed barbs, large population and nests founding by swarm but have also a characteristics of non-autotomisers such as: nest with a single comb without envelop (Richards & Richards, 1951), but *Apoica pallens* did not show the autotomy process. After stinging a target, this species remains attached to it and fights intensely to try to escape, twisting its abdomen in circles and applying pressure to it with its legs. This causes some barbs to

Table 1. Variation in the number of barbs/lancet observed in social wasps that present sting autotomy.

| Species | Autotomisers | | |
|---|---|---|---|
| | N | No. barbs/ lancet (Mean ± SD) | Range |
| *Agelaia pallipes* | 80 | 9.8 ± 0.6 | 9–11 |
| *Agelaia multipicta* | 166 | 9.4 ± 1.1 | 8–10 |
| *Agelaia vicina* | 78 | 12.3 ± 0.9 | 11–14 |
| *Synoeca cyanea* | 32 | 11.5 ± 0.6 | 10–13 |
| *Polybia rejecta* | 52 | 9.2 ± 0.3 | 9–10 |
| *Polybia scutellaris* | 42 | 9.0 ± 0.4 | 8–10 |
| *Polybia fastidiosuscula* | 30 | 9.5 ± 0.6 | 8–11 |
| *Polybia jurinei* | 72 | 9.0 ± 0.1 | 8–10 |
| *Polybia paulista* | 264 | 8.9 ± 0.3 | 8–10 |
| *Polybia sericea* | 72 | 8.0 ± 0.1 | 7–9 |
| *Polybia occidentalis* | 62 | 8.0 ± 0.1 | 7–9 |
| *Polybia platicephala sylvestris* | 10 | 8.2 ± 0.3 | 8–9 |
| *Protonectarina sylveirae* | 50 | 6.8 ± 0.3 | 6–7 |
| *Brachygastra lecheguana* | 58 | 6.9 ± 0.3 | 6–7 |
| *Protopolybia sedula* | 124 | 7.0 ± 0.0 | 7 |
| *Protopolybia exigua* | 72 | 5.0 ± 0.2 | 4–6 |
| *Metapolybia cingulata* | 18 | 7.0 ± 0.1 | 6–8 |
| *Pseudopolybia vespiceps* | 52 | 6.9 ± 0.3 | 6–7 |

N = Number of lancets observed for each species.

break, permitting sting withdrawal and the aggressor escaping this is a different type of behavioral strategy. That adapts the insect to escape after stinging and would reduce the loss of individuals.

Thus, the results of the present work

Table 2. Variation in the number of barbs/lancet observed in social wasps that not present sting autotomy.

| Species | Non-autotomisers | | |
|---|---|---|---|
| | N | No. Barbs/ lancet Mean ± SD | Range |
| *Apoica pallens* | 76 | 9.1 ± 0.2 | 9–10 |
| *Apoica flavissima* | 36 | 9.2 ± 0.4 | 9–10 |
| *Polistes versicolor* | 28 | 7.5 ± 0.9 | 7–8 |
| *Polistes lanio lanio* | 18 | 8.0 ± 0.0 | 8 |
| *Polistes subsericeus* | 18 | 5.1 ± 0.5 | 4–6 |
| *Polistes simillimus* | 20 | 7.1 ± 0.4 | 6–8 |
| *Mischocyttarus drewseni* | 16 | 4.0 ± 0.0 | 4 |
| *Mischocyttarus cassununga* | 20 | 4.0 ± 0.0 | 4 |
| *Mischocyttarus cerberus* | 18 | 4.0 ± 0.0 | 4 |
| *Mischocyttarus latior* | 22 | 4.0 ± 0.0 | 4 |

N = Number of lancets observed for each species.

clearly show that sting autotomy in social wasps is correlated with morphological aspects which in combination with social and behavioral aspects form an altruistic defense system.

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# Notes on *Bembecinus* of southern Africa, Madagascar, and Australia with descriptions of new species (Hymenoptera, Sphecidae, Nyssoninae, Stizini)

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*Abstract.*—Twelve new species of *Bembecinus* are described and figured: *B. chilwae,* Mozambique; *B. gilvus,* Namibia; *B. pakhuisae,* South Africa; *B. ruficaudus,* South Africa; *B. zebratus,* South Africa; *B. admedius,* Ivory Coast; *B. brooksi,* Madagascar; *B. irwini,* Namibia; *B. namibicus,* Namibia; *B. rozenorum,* Namibia; *B. tinkeri,* Western Australia; *B. wenzeli,* Madagascar. A rearrangement of species groups and subgroups of *Bembecinus* is presented. New synonymy of *Bembecinus caffer* (Saussure) and *B. argentifrons* (F. Smith) is given: *bredoi* (Arnold) 1940 = *caffer* (Saussure) 1854; *braunsii* (Handlirsch) 1894 and *barkeri* (Arnold) 1940 = *argentifrons* (F. Smith) 1856.

Wasps of the genus *Bembecinus* A. Costa occur worldwide. Bohart and Menke (1976) listed 150 species. Bohart (1996), working with North and Central American fauna, raised two subspecies to species status, and described two additional forms as new. With about 175 species, barring unknown synonymy, *Bembecinus* has the second most species of any genus in the Nyssoninae (after *Bembix*). Bohart and Menke (1976) discussed the relationships of the Stizini, separating from Bembicini by the exserted but short labrum of the former. In its tribe *Bembecinus* is most easily identified by having only a single distal vein issuing from the hindwing median cell.

Principal authors who dealt with *Bembecinus* from southern Africa were Frederick Smith, Anton Handlirsch, and George Arnold. The detailed descriptions and accompanying figures, as well as the key to species of southern African *Bembecinus* by Arnold (1929) have been particularly useful. The principal worker on the Australian fauna was Handlirsch. A summary of the species known from that continent was given by Cardale (1985).

The following possibly unfamiliar symbols are used in descriptions: F-I etc., flagellomere; ID, interocular distance; PD, puncture diameter; S-I etc., sternum; T-I etc., tergum; UA, upper profile of propodeal flange; tarsomere V, fifth segment of tarsus.

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  ry, A. S. Menke                    WASHINGTON

### The group and subgroup concept in *Bembecinus*

Handlirsch (1892) in his landmark treat-
ment of Nyssoninae was the first to intro-
duce the group concept in *Bembecinus*. He
mentioned and partly diagnosed the fol-
lowing groups, placing them in the genus
*Stizus*: *tridens*, *meridionalis*, *loriculatus*, *per-
egrinus*, *caffer*, *discolor*, *inermis*. Arnold in
his most comprehensive paper on *Bembe-
cinus* (1929) discussed and keyed the
South African species, using the group
names of Handlirsch and adding the *oxy-
dorcus*, *cinguliger*, and *rhopalocerus* groups.
All of these were still placed in the genus
*Stizus*.

Bohart and Menke (1976) revised and
condensed the group system, listing *iner-
mis* (including *caffer*) and *cinguliger* (in-
cluding *oxydorcus* and *rhopalocerus* groups
as one major group. The other major
grouping included the *discolor*, *tridens*, and
*peregrinus* (including *meridionalis*, *crassipes*,
and *gynandromorphus*) groups. All were
placed in *Bembecinus*.

The twelve new species described here
belong to various groups that have been
used for separation by former authors.
The following summary of groups elabo-
rates that of Bohart and Menke. It is orig-
inal mainly in the outlining of subgroups.

In one of the more revisional publica-
tions on *Bembecinus* Jacques de Beaumont
(1954) stressed the importance of the pres-
ence of spines on the inner surface of the
hindfemur on males of some species. In
dealing with the palearctic fauna Beau-
mont listed 19 species with such spines.
He placed all of these in his "*peregrinus*
group". I have added some Ethiopian Re-
gion species, and have divided this assem-
blage into 3 subgroups: first, those with a
median projection on male S-II (*peregrinus*
subgroup); second, those with a median
projection on male S-III (*meridionalis* sub-
group); and third, those without a projec-
tion on male S-II or III (*spinicornis* sub-
group). Females in the 3 subgroups above
have little to distinguish them from those
in the *tridens* subgroup except the sternal
punctation, which is more spaced in the
latter. The presence of a spine or spines on
the inside of the male hindfemur occurs in
all of the Madagascan species in the *tridens*
group. However, this character has not
been found in any of the New World spe-
cies, or in those of Australia. An addition-
al subgroup of the *tridens* group I have la-
beled the *irwini* subgroup. It is character-
ized by the short and subequal F-I-II-III in
both sexes (of *irwini*). Also, the sternal
punctation is fine and close. The female of
the other included species, *distinctus*, is
unknown.

### Groups and subgroups of *Bembecinus*

I. *Bembecinus caffer* group—Male anten-
  na simple, slender (Fig. 8a), female
  foretarsal V and arolium not unusu-
  ally large, no spines on inner side of
  male hindfemur.
   A. *B. caffer* subgroup—Medium large
     (11–20 mm long) stout species
     with lateral tergal markings, ID at
     midocellus less than 2× that of
     clypeal base. Representative spe-
     cies: *caffer* (Handlirsch), *laterima-
     cula* (Handlirsch), *haplocerus* (Han-
     dlirsch), *chilwae* R. Bohart, new
     species.
   B. *B. inermis* subgroup—Small spe-
     cies (5–10 mm long), more slen-
     der, tergal markings various but
     not predominantly lateral, LID at
     midocellus more than 2× that at
     clypeal base. Representative spe-
     cies: *inermis* (Handlirsch), *mirus*
     (Arnold), *assentator* (Arnold).
II. *Bembecinus rhopalocerus* group—Male
  and female antennae simple but
  clubbed (Fig. 6), ID at midocellus

more than 2× that at clypeal base, female foretarsal V and arolium larger than those of the midtarsus or hindtarsus. No spines on inner side of male hindfemur.

A. *B. rhopalocerus* subgroup—Propodeal flange with UA evenly curved in profile (Fig. 7f) no sternal projections in male. Representative species: *gilvus* R. Bohart, new species, *hyperocrus* (Arnold), *lomii* (Guiglia), *mutabilis* (Arnold), *pakhuisae* R. Bohart, new species, *rhopaloceroides* (Arnold), *rhopalocerus* (Handlirsch), *ruficaudus* Bohart, new species, *somalicus* (Arnold), *zebratus* Bohart, new species.

B. *B. oxydorcus* subgroup—Propodeal flange with UA incurved or notched below, S-II of male with median projection (*cinguliger*) or without (*oxydorcus*). Representative species: *oxydorcus* (Handlirsch), *cinguliger* (F. Smith).

III. *Bembecinus tridens* group—Male F-IX with a lateral, spinelike projection (Fig. 1d).

A. *B. tridens* subgroup—Medium small (6–10 mm long), ID at midocellus more than 2× that at clypeal base (Fig. 1a), F-I much longer than broad, propodeal flange with UA usually notched or sharply incurved below (Fig. 2f) male hindfemur without spines on inner side, male S-II or S-III without projections, female sterna (especially S-III) with spaced punctation. Representative species: *abmedius* R. Bohart, new species, *argentifrons* (F. Smith), *barbarus* Beaumont, *bytinskii* Beaumont, *cyanescens* (Radozkowsky), *egens* (Handlirsch), *haemorrhoidalis* (Handlirsch), *hirtulus* (F. Smith), *hungaricus* (Frivaldsky), *tenellus* (Klug), *tinkeri* R. Bohart, new species, *tridens* (Fabricius).

B. *B. irwini* subgroup—Small to medium (5–10 mm long), ID at midocellus about 2× that at clypeal base (Fig. 4a), F-I-II-III subequal, broader than long (Fig. 4c), propodeal flange with UA evenly curved in profile (Fig. 4f), male hindfemur without spines on inner side, male sterna without projections, sternal punctation fine and close. Representative species: *distinctus* (Arnold), *irwini* R. Bohart, new species.

C. *B. spinicornis* subgroup—Medium small to medium (7–11 mm long), ID at midocellus at least 2× that at clypeal base, propodeal flange incurved below but not usually sharply incurved, male hindfemur with spine or spines on inner side, or deformed, male sterna without projections, female sterna (especially S-III) with punctation fine and close. Representative species: *acanthomerus* (Morice), *bernardi* Beaumont, *brooksi* R. Bohart, new species, *buyssoni* (Arnold), *carpetanus* (Mercet), *crassipes* (Handlirsch), *cyprius* Beaumont, *fertoni* (Handlirsch), *fraterculus* (Arnold), *hirtiusculus* (Arnold), *kobrowi* (Arnold), *mattheyi* (Beaumont), *naefi* (Beaumont), *namibicus* R. Bohart, new species, *podager* (Beaumont), *polychromus* (Handlirsch), *rozenorum* R. Bohart, new species, *spinicornis* (Saussure), *spinifemur* (Beaumont).

D. *B. meridionalis* subgroup—ID at midocellus about 2× that at clypeal base, F-I much longer than broad, propodeal flange various, male hindfemur usually with one or more spines on inner side, male S-III with a median projection, sternal punctation usually fine and close. Representative species: *gynandromorphus* (Handlirsch), *la-*
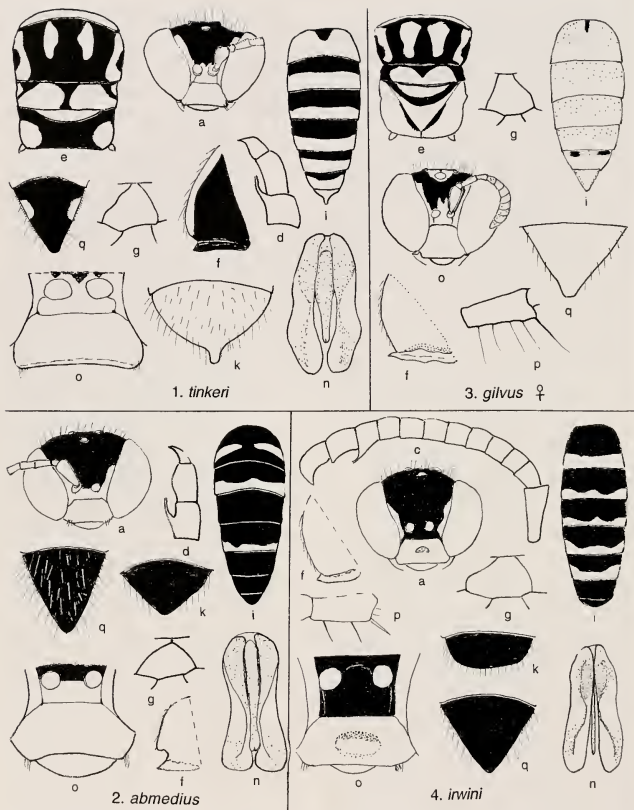
Figs. 1–4. Morphological characters of *Bembecinus* spp.: 1, *tinkeri*; 2, *abmedius*; 3, *gilvus* female; 4, *irwini*. Arabic letters a–n indicate male characters (except *gilvus*), o–r indicate female characters (a, face; b, lower face enlarged; c, antenna, front view; d, flagellomeres IX–XI, lateral; e, thoracic pattern; f, outline of left propodeal flange in lateral view; g, second submarginal cell of forewing; h, hindfemur, outer view; i, abdomen with tergal banding, dorsal; k, outline of T-VII; m, terminal terga VI–VII, shape and pattern; n, genitalia, dorsal; n', enlargement of genitalia toward apex; o, lower face except eyes; p, forebasitarsus, lateral outline; q, shape and markings of T-VI; r, markings of female T-III-VI).

ticinctus (Arnold), *meridionalis* A. Costa, *zibanensis* (Morice).

E. *B. peregrinus* subgroup—About as in subgroup D , but male S-II with a median projection. Representative species: *dentiventris* (Handlirsch), *gazagnairei* (Handlirsch), *hoplites* (Handlirsch), *mayri* (Handlirsch), *monodon* (Handlirsch), *peregrinus* (F. Smith), *proteus* (Arnold), *revindicatus* (Schulz).

F. *B. loricatulus* subgroup—ID at midocellus less than 2× that at clypeal base, propodeal flange UA with 2 indentations and 3 teeth, male hindfemur without spines on inner side, male sterna without projections, sternal punctation of female fine and close, female foretarsal V and arolium not enlarged. Representative species: *loricatulus* (F. Smith).

G. *B. discolor* subgroup—ID at midocellus less than 2× that at clypeal base, propodeal flange UA at most broadly incurved below, male S-II and S-III without projections but S-VI with a mediobasal groove or tooth, female foretarsal V and arolium enlarged. Representative species: *discolor* (Handlirsch), *nyasae* (Turner), *wenzeli* R. Bohart, new species.

*Bembecinus caffer* group, *caffer* subgroup
**Bembecinus chilwae** R. Bohart,
new species
(Fig. 8)

Male holotype. Length 13.0 mm. Body black, yellow, and red. Yellow are: facial marks including scape (Fig. 8a), narrow posterior band across pronotum, summit of propodeal flange (Fig. 8f); foreleg partly, including basal three tarsomeres, lateral tergal markings (Fig. 8i); brownish red are: antennal flagellum, occipital band, pronotum behind yellow margin, scutum laterally, scutellum, metanotum posteriorly, large upper mesopleural spot, legs

mostly, T-VII, S-VI and following; wings basally and veins reddish, membrane clear. Pubescence pale and short on vertex, quite short and reddish on notum, abundant and erect as well as red on S-VII to VIII, lateral fringe on genitalia (Fig. 8n). Punctation close, mostly fine, a little more coarse on mesopleuron. Facial proportions including antenna as in Figs. 8a, 8b, lateral view of propodeal flange as in Fig. 8f; hindfemur concave toward base, excavated within (Fig. 8h); second submarginal cell not petiolate (Fig. 8g), genitalia slender (Fig. 8n).

Female. Length 14 mm. About as in male, but facial proportions as in Fig. 8o, labrum red, markings of propodeal flange reddish, clypeus with scattered punctures (Fig. 8o), forebasitarsus with 3 preapical rake setae, more apical ones stouter (Fig. 8p); T-VI long, red, smooth (Fig. 8q), propodeal flange UA with a very small notch.

Holotype male (LONDON), southwest of Lake Chilwa, Mozambique, I-9–14 (S. A. Neave). Paratype female (LONDON), Mlange, Mozambique, I-20–14 (S. A. Neave).

This species belongs in the *caffer* group with male antenna slender and apically simple. The lateral tergal spots (Fig. 8i) place it in the *caffer* subgroup. The weakly defined margin of the propodeal flange UA (Fig. 8f) is small and irregular which distinguishes both sexes of *chilwae* from *caffer* Handlirsch, *laterimacula* Handlirsch, and *haplocerus* Handlirsch. Also, the male of *chilwae* differs from *caffer* by its simple S-V, from *laterimacula* by its more slender genitalia (Fig. 8n) and from *haplocerus* by its deformed male hindfemur (Fig. 8h). The specific name refers to the locality of the holotype, Lake Chilwa.

**Bembecinus caffer** (Saussure)

*Stizus caffer* Saussure 1855:28, Fig. 9. Holotype female, Natal Province, South Africa (GENEVA).

*Stizus bredoi* Arnold 1946:88. Syntype males, fe-

males, "Albercorn," Gambia ("N. Rhodesia"), (PRETORIA ?). New synonymy.

This has been essentially an unknown species since the original description because the holotype has the second submarginal cell of the forewing briefly petiolate above, unusual in the group. However, I collected a series of specimens on sand dunes at St. Lucia, Natal Province, South Africa in 1972. One of the males has the second submarginal cell petiolate just as in the holotype female of *caffer*. Otherwise, the females all agree closely with that holotype, which I have studied. I have not seen the syntypes of *bredoi*, but Arnold's detailed description and figures leave little doubt that it is synonymous with *caffer*. Males have a patch of fine, close setae basomedially on S-V, a unique feature.

*Bembecinus rhopalocerus* group,
*rhopalocerus* subgroup
**Bembecinus gilvus** R. Bohart,
new species
(Fig. 3)

Female holotype. Length 9.0 mm. Body black with extensive light orange and yellow to yellowish white. Light orange are: flagellum beyond F-II, broad basal tergal bands (stippled on Fig. 3i); yellowish white are: facial marks including antennal base (Fig. 3o), posterior bands on terga and sterna (unstippled areas on Fig. 3i); yellow are: thoracic notal (Fig. 3e) and pleural areas, legs (a little lighter beyond femora); wings transparent. Pubescence pale, inconspicuous. Punctation fine, close. Facial proportions including antenna as in Fig, 3o, thoracic pattern as in Fig. 3e, propodeal flange UA evenly curved (Fig. 3f), second submarginal cell as in Fig. 3g, forebasitarsus as in Fig. 3p, T-VI nearly triangular (Fig. 3q).

Male. Unknown.

Holotype female (WASHINGTON), Gobabeb, Namibia, I-6-80 (Wharton, Coll.) Paratype female (DAVIS), same data as holotype. Paratype female (GAINESVILLE), 20 km w. Usakos, Namibia, II-4-83 (L. Stange, R. B. Miller).

This species is remarkable for its extensive yellow and yellowish orange coloration. In the only comprehensive key to South African *Bembecinus* (Arnold, 1929) it runs between numbers 40 and 41. On the basis of the clavate antennae and rounded UA it falls in the *rhopalocerus* subgroup. The strong submedian yellow marks of the scutum (Fig. 3a) relate it to *quadristrigatus* Arnold. *B. gilvus* differs from *quadristrigatus* and from other *Bembecinus* by the greatly reduced black areas, particulary on the abdomen. It is a small species, 9–10 mm long, in contrast to *quadristrigatus*, whose length is 11–14 mm, according to the original description. The specific name refers to the extensively yellow and light orange coloration.

**Bembecinus pakhuisae** R. Bohart,
new species
(Fig. 5)

Male holotype. Length 13.0 mm. Body black marked with sulfur yellow on antenna toward base, face below middle (Fig. 5a), posterior margin of pronotum including lobes, scutal spot over wing base, tegula, post-tegula, lateral streaks on scutellum and metanotum, legs mostly but black toward base, apical bands on all terga (Fig. 5i), narrow apical bands on S-II to IV; flagellum mostly pale tan in front; wings clear, veins reddish brown. Pubescence whitish, moderate, erect on vertex and T-I toward base. Punctation moderate, extensive, punctures mostly 1.0 PD apart, clypeus with punctures 1–3 PD apart. Flagellum clubbed, F-I $5.3\times$ as long as broad (Fig. 5c), F-XI slightly incurved within (Fig. 5d), facial proportions as in Fig. 5a, propodeal flange UA evenly rounded (Fig. 5f), second submarginal cell as in Fig. 5g, terga moderately slender (Fig. 5i), T-VII broadly truncate at apex (Fig. 5m), genitalia slender (Fig. 5n).

Females. Length 10–12 mm. About as in
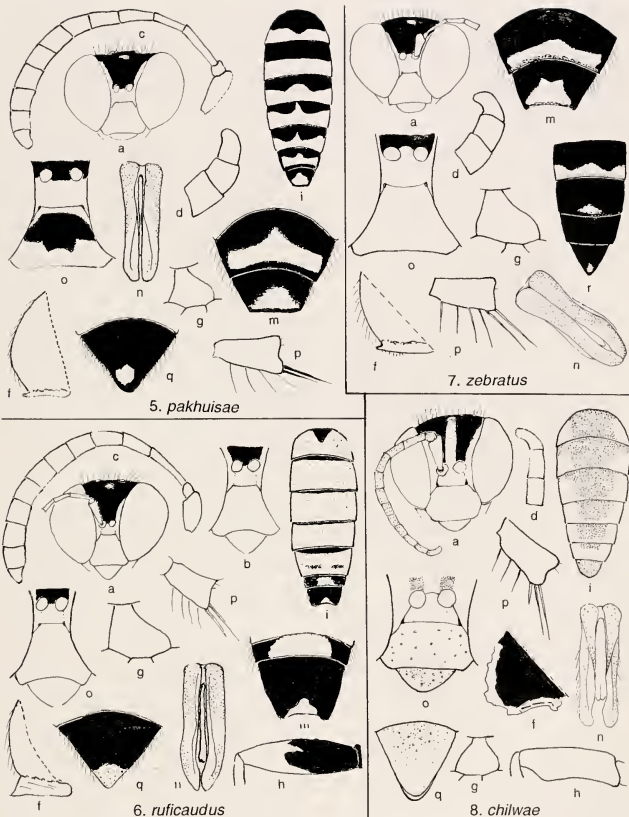
Figs. 5–8. Morphological characters of *Bembecinus* spp.: 5, *parkhuisae*; 6, *ruficaudus*; 7, *zebratus*; 8, *chilwae*. Arabic letters a–n indicate male characters, o–r indicate female characters (a, face; b, lower face enlarged; c, antenna, front view; d, flagellomeres IX–XI, lateral; e, thoracic pattern; f, outline of left propodeal flange in lateral view; g, second submarginal cell of forewing; h, hindfemur, outer view; i, abdomen with tergal banding, dorsal; k, outline of T-VII; m, terminal terga VI–VII, shape and pattern; n, genitalia, dorsal; n', enlargement of genitalia toward apex; o, lower face except eyes; p, forebasitarsus, lateral outline; q, shape and markings of T-VI; r, markings of female T-III–VI).

male except: clypeus broader and with a broad median or basal transverse black mark (Fig. 5o); legs extensively orange; tergal bands on I to IV narrower, whitish, edged with red; T-V and VI often with whitish apical spot (Fig. 5q); T-VI laterally spiculate, weakly setose (Fig. 5q); forebasitarsus with 4 pale, preapical rake setae, 2 stout apical setae (Fig. 5p), foretarsal V and arolium much larger than others.

Holotype male (DAVIS), Pakhuis Pass, Cape Province, South Africa, X-7-75 (R. M. Bohart). Paratypes (DAVIS and other cooperating museums), 47 males, 32 females, same data as holotype.

In Arnold's (1929) key both sexes of *pakhuisae* run to the *rhopalocerus* subgroup and close to *mutabilis* Arnold. The latter has deep yellow to orange tergal bands, a broad and incised male T-VII, an incurved male F-XI, extensively yellowish female mesopleuron, and abundant orange markings in the female. In *pakhuisae* the markings of both sexes are mostly lemon yellow to whitish yellow. Reddish is confined to narrow edging of markings in the female, and some females have the legs partly orange. However, the female mesopleuron is all black. Male T-VII has a broad but truncate or slightly convex posterior edge (Fig. 5m). Also, F-XI is only weakly incurved. The type series was collected as the wasps flew rapidly between bushes at Pakhuis Pass, east of Clanwilliam. The name is dedicated to the Pass.

## Bembecinus ruficaudus R. Bohart, new species
### (Fig. 6)

Male holotype. Length 12.0 mm. Black, yellow, orange yellow, and reddish orange. Yellow are: lower face, antenna in front to F-II (Fig. 6a, c) posteriorly, pronotal lobe; orange yellow are: lateral scutal spot, wing base, scutellum laterally, lateral streak on metanotum, legs mostly, distal one-third of hindfemur (Fig. 6h); reddish orange are: abdominal terga mostly (Fig. 6i, stippled areas), S-I posteromedial spot,

S-II to S-IV posterolateral spots (slightly joined on S-II-III); wings clear, veins dark. Pubescence silvery, erect on vertex and T-I toward base, scattered elsewhere, appressed and abundant on face. Punctation moderate, extensive, mostly close but punctures about 1 PD apart on scutum. Flagellum clubbed, F-I 5.3× as long as broad (Fig. 6c), facial proportions (Figs. 6a, 6b), propodeal flange UA broadly rounded (Fig. 6f), second submarginal cell as in Fig. 6g, terga moderately slender (Fig. 6i), T-VII broad apically where it is slightly concave (Fig. 6m), genitalia slender (Fig. 6n).

Female paratypes. Length 10.5–11.0 mm. About as in male except: larger triangular yellow spot on mesopleuron, spots larger on scutellum, metanotum, spot along crest of propodeal flange, T-VI to VII mostly black or mostly reddish orange. T-VI laterally spiculate. Proportions of face (Fig. 6o), forebasitarsis (Fig. 6p), T-VI (Fig. 6q). Foretarsal V and arolium enlarged.

Holotype male (DAVIS), Doorn R., Moedverloor, Cape Prov., South Africa, X-8-75 (R. M. Bohart). Paratypes, 2 females (DAVIS), Pakhuis Pass, Cape Prov., South Africa, X-7-75 (R. M. Bohart); female (GAINESVILLE), 10 km w. Steinkopf, Cape Prov., South Africa, XI-10-90 (L. Stange, R. Miller).

In Arnold's (1929) key the female runs to *hyperocrus* Arnold mainly because of the extensively red T-I-V. At that time the male was not known to Arnold. Subsequently it was found to be similar to the female but with orange-red on T-I-IV only. The male of *hyperocrus* has the clypeus and pronotum all black, incised apex of T-VII one-half as broad as F-I length. The male of *ruficaudus* has the clypeus light yellow, pronotum with a yellow posterior band, weakly emarginate apex of T-VII that is as broad as F-I length (Fig. 6m). Females of *hyperocrus* have a large basal black clypeal spot contiguous with a black supraclypeal area. In *ruficaudus* these areas

are all whitish yellow (Fig. 6o). Also, *hyperocrus* females have T-VI slightly expanded apically, whereas T-VI of *ruficaudus* females tapers evenly to a narrow apex (Fig. 6q). The specific name refers to the red abdomen.

### Bembecinus zebratus, R. Bohart, new species
#### (Fig. 7)

Male holotype. Length 11.0 mm. Body black marked with sulfur yellow as follows: antenna toward base, face below middle (Fig. 7a); posterior margin of pronotum including lobes, scutal spot over wing base, tegula, post-tegula, lateral traces on scutellum and metanotum, spot on mesopleuron, legs mostly but black toward base, apical tergal bands (Fig. 7i), apicolateral traces on S-II-IV; flagellum mostly pale tan in front; wings clear, veins dark brown. Pubescence whitish, moderate, erect on vertex and T-I basally. Punctation moderate, extensive, 1–3 PD apart on clypeus. Flagellum clubbed, F-I 5.3× as long as broad, F-XI distinctly incurved within (Fig. 7d), facial proportions as in Fig. 7a, propodeal flange UA evenly rounded (Fig. 7f), second submarginal cell as in Fig. 7g, terga moderately slender and T-VII slightly but distinctly emarginate apically (Fig. 7m), genitalia slender (Fig. 7n).

Females. Length 9–12 mm. About as in male except: clypeus broader (Fig. 7o); tergal bands whitish, narrower on T-I-III, with only a trace on IV, absent on V-VI (Fig. 7r), legs sometimes partly deep yellow to light orange, sterna nearly always entirely black; T-VI laterally spiculate, weakly setose (Fig. 7q); forebasitarsus with 4 pale, preapical rake setae, 2 stout apical setae (Fig. 7p); foretarsal V and arolium are enlarged.

Holotype male (DAVIS), Worcester, Cape Prov., South Africa, X-?-75 (R. M. Bohart). Paratypes (DAVIS) and other cooperating museums), 10 males, 9 females, same data as holotype.

This species is very close to *pakhuisae* R. Bohart. However, *zebratus* males differ by the more strongly curved F-XI (compare Figs. 7d, 5d), the distinctly concave apex of T-VII (Fig. 7m), and the usual occurrence of a mesopleural yellow spot. In the female of *zebratus* the unmarked clypeus (Fig. 7o), large mesopleural yellow spot, absence of markings on T-V and reduction of those on T-IV (Fig. 7r) are differentiating. The name refers to the striping of the abdomen.

### *Bembecinus tridens* group, *tridens* subgroup
### Bembecinus abmedius R. Bohart, new species
#### (Fig. 2)

Male holotype. Length 8.0 mm. Body black, marked with whitish as follows: lower face except black mandible (Fig. 2a), pronotal margin including lobe, fore- and midcoxae partly, fore- and midfemora distally, tibiae and tarsi mostly, restricted tergal marks (Fig. 2i), lateral traces on S-II-IV; yellowish white are: antenna in front, lateral spot on scutum posteriorly, lateral spot on scutellum, trace on metanotum; wings clear. Pubescence silvery, clypeus with a small and sublateral apical tuft (Fig. 2a). Punctation fine. Antenna slender; facial proportions as in Fig. 2a, propodeal flange roundly notched below (Fig. 2f), second submarginal cell with a short petiole above (Fig. 2g), T-VII narrowly rounded at apex (Fig. 2k), genitalia expanded toward apex (Fig. 2n).

Female paratypes. Length 9.0 mm. About as in male. Facial proportions as in Fig. 2o; T-VI slender, all black, with long pale hair (Fig. 2q).

Holotype male (DAVIS), Foro-Foro, Bouake, Ivory Coast, Africa, I-31-72, savannah (D. Duviard). Paratypes (DAVIS, PARIS), PRETORIA), 1 male, 4 females, Foro-Foro, Bouake, Ivory Coast, II-28-72 to IV-10-72 (D. Duviard).

This species is in the *tridens* subgroup. It is similar in size to the widespread *ar-*

*gentifrons* F. Smith. The second submarginal cell (Fig. 2g), is also similar. However, *argentifrons* has T-III banded, mandible and hindfemur partly yellow, and UA incision sharply pointed in contrast to *abmedius* (Fig. 2f). *B. corpulentus* (Arnold) has the same tergal pattern as *abmedius* but it belongs in the *spinicornis* subgroup. The common North African *bitinskii* has a similar tergal pattern but its mandible is yellow and the propodeal flange has at most a tiny notch. The specific name *abmedius* refers to the all-black T-III of the tergal pattern.

*Bembecinus tridens* group,
*spinicornis* subgroup
**Bembecinus brooksi** R. Bohart,
new species
(Fig. 12)

Male holotype. Length 9.0 mm. Body black with extensive yellow and orange-yellow markings. Yellow to light orange-yellow are: antenna in front; lower frons, clypeus, labrum (Fig. 12a); scutum except median and lateral black stripes, remaining thorax except small black at middle of propodeum, legs almost entirely, terga except weak brownish transverse subapical stripes on T-IV-V, median darkened area on T-VII (Fig. 12k). Wings transparent. Pubescence pale, inconspicuous. Punctation fine, close, appearing granular on T-VII. Facial proportions including antenna (Figs. 12a, d), propodeal flange UA obtusely emerginate below (Fig. 12f), second submarginal cell not petiolate (Fig. 12g), terga moderately stout as in paratype (Fig, 12i), T-VII laterally incurved toward rounded apex (Fig. 12k), genitalia rounded laterally and apically (Fig. 12n).

Females. Length 8.0–9.0 mm. Body black and yellow to orange-yellow. Yellow are: lower frons, clypeus, labrum (Fig. 12o), antenna in front; pronotum all across, lateral spots on scutum, scutellum, propodeum; strip across metanotum, legs mostly but femora black above, apical bands on T-I-V, slightly enlarged medially

and laterally, S-II large lateral spot, apical bands on S-II-V. Orange-yellow are: T-VI but darkened basally and a little apically (Fig. 12q), S-VI elongate medial spot. Wings slightly stained. Sternal punctation fine and close.

Holotype male (LAWRENCE), Beza Mahafaly Res., Tulear Prov. Madagascar XI-21-84 (R. W. Brooks). Paratypes (LAWRENCE, DAVIS, etc.), 182 males, 72 females, same data as holotype, both sexes from nesting aggregations.

The other *Bembecinus* known from Madagascar (Arnold, 1945) are: *mirus* (Arnold), *assentator* (Arnold), *spinicornis* (Saussure), *hirtiusculus* (Arnold), *wenzeli* R Bohart, new species, and *rectilateralis* Arnold. I have identified specimens of all of these, and *brooksi* is quite different. The lectotype female (seen) of *rectilateralis* in the PARIS Museum agrees closely with Arnold's original description. Among other points there is a black spot on the supraclypeal area of the type (and of an associated male), the forebasitarsus is black-edged posteriorly, T-VI is all black, and the thoracic sides are practically straight as seen from above. The lectotype female of *rectilateralis* here designated was from Bekily. Other syntypes were from Antanimora, and Ranomafana.

In any case, *brooksi* is quite different, distinguished from all previously described Madagascan species by the untoothed male S-VIII, extensively yellow T-VI in both sexes and a broad notch on the propodeal flange.

Of the total 277 males of *brooksi* 271 are the yellow phase and the scutum always has at least a pair of submedian yellow stripes. However, the extent of yellow varies considerably, particularly on the abdomen. Females are of the dark phase, with medially black scutum and more regularly banded terga, on a black background. Six males (less than 2.2%) resemble the females in markings. The name is dedicated to the collector, my friend, Robert Brooks.
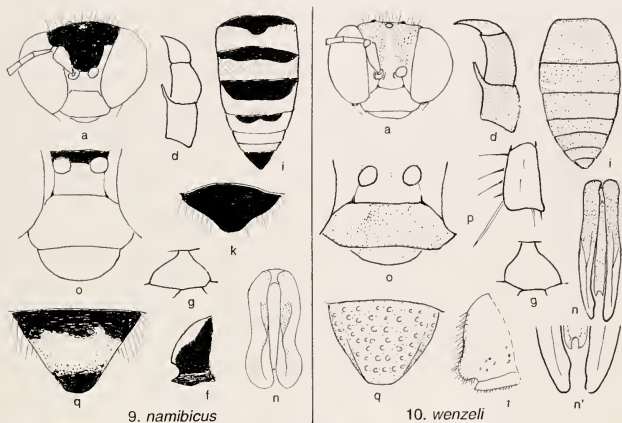
Figs. 9–12. Morphological characters of *Bembecinus* spp.: 9, *nambicius*; 10, *wenzeli*; 11, *rozenorum*; 12, *brooksi*. Arabic letters a–n indicate male characters, o–r indicate female characters (a, face; b, lower face enlarged; c, antenna, front view; d, flagellomeres IX–XI, lateral; e, thoracic pattern; f, outline of left propodeal flange in lateral view; g, second submarginal cell of forewing; h, hindfemur, outer view; i, abdomen with tergal banding, dorsal; k, outline of T-VII; m, terminal terga VI–VII, shape and pattern; n, genitalia, dorsal; n', enlargement of genitalia toward apex; o, lower face except eyes; p, forebasitarsus, lateral outline; q, shape and markings of T-VI; r, markings of female T-III-VI).

*Bembecinus tridens* group, *irwini* subgroup
**Bembecinus irwini** R. Bohart,
new species
(Fig. 4)

Male holotype. Length 5.0 mm. Black and light yellow to whitish. Light yellow are: facial marks (Fig. 4a), antenna in front, scutal spot over wing base, lateral scutellar spot, femoral apex and beyond; whitish are: posterior band on pronotum including lobes, posterior bands on T-I-V (Fig. 4i), lateral traces on S-II to III; wings transparent. Antenna (Fig. 4c) with basal segments unusually short, "spine" of F-VIII short, second submarginal cell (Fig. 4g), propodeal flange UA evenly curved (Fig. 4f), abdomen slender (Fig. 4i), apex broadly rounded (Fig. 4k), genitalia moderately slender (Fig. 4n).

Females. Length 5.0 mm. About as in male. Scutellum with or without lateral spot, sternum all dark, lower facial proportions as in Fig. 4o, T-I-V apically banded, forebasitarsus (Fig. 4p) with one developed rake seta on apex, T-VI black (Fig. 4q); pedicel, F-I-II about as in male, each about as broad as long; clypeus with small but distinct apicolateral setal tuft (Fig. 4o).

Holotype male (DAVIS), Maltahohe, Namibia, II-17-74 (M. E. Irwin). Paratypes, 9 males, 1 female (DAVIS, WASHINGTON, PRETORIA), same data as holotype; female (GAINESVILLE) 10 km w. Steinkopf, Cape Prov., South Africa, XI-10-90 (L. Stange, R. Miller).

The size of *irwini* (about 5 mm long), the smallest of any *Bembecinus* which I have studied, is a remarkable feature. However, there are a number of characters which contrast *irwini* and *B. tridens* (Fabricius), which taken together distinguish *irwini* from all other known members of the genus. These are: the short F-I-II-III (about as long as broad) (Fig. 4c), evenly curved UA (Fig. 4f), all black supraclypeal area, oval spot in clypeal middle in both sexes (Figs. 4a, 4o), and very broadly rounded apical margin of male T-VII (Fig. 4k). I

have placed it a separate subgroup along with the much larger *distinctus*. The species is dedicated to the collector of most of the type series, my friend Mike Irwin.

*Bembecinus tridens* group,
*spinicornis* subgroup
**Bembecinus namibicus** R. Bohart,
new species
(Fig. 9)

Male holotype. Length 7.0 mm. Body black, yellow, whitish yellow, and orange-red. Yellow are: facial markings and antenna in front (Fig. 9a), pronotum all across, scutum laterally, mark on scutellum posteriorly but narrowed medially, metanotum, large spot on propodeal flange (Fig. 9f), large mesopleural spot, legs mostly, posterior bands on T-I-IV, all of T-V to VI (Fig. 9i); (bands become whitish posteriorly) orange to orange red are: femora partly (especially hindfemur), T-I-III (stippled area, Fig. 9i). Pubescence pale. Punctation moderate on upper face, T-VII, fine elsewhere. Antenna slender, "spine" on F-VIII one-half as long as F-IX (Fig. 9d), facial proportions (Fig. 9a), second submarginal cell not petiolate (Fig. 9g), UA broadly incurved below (Fig. 9f), hindfemur on lower part of inner surface with small spine at middle, abdomen rather stout (Fig. 9i), T-VII rounded at apex (Fig. 9k), genitalia expanded toward apex, gonostyles broadly rounded there (Fig. 9n).

Females. Length 7 mm. About as in male. Posterior yellow bands on T-I-III, irregular bands on IV-V, and most of T-VI (bands partly or mostly whitish). Orange-red are: legs partly, edging on T-I-V medial bands, T-VI medially (Fig. 9q stippled area). Facial proportions (Fig. 9o).

Holotype male (DAVIS), 45 km w. Seeheim, Bethanien Dist., Namibia, sandy river bank, II-19-74 (M. E. Irwin). Paratypes (DAVIS), female, same data as holotype, 2 males (DAVIS), Namib Desert, II-15-74 (M. E. Irwin), female (GAINESVILLE), 26 km n. Gochas, Namibia, II-6-83 (L. Stange, R. Miller).

*B. namibicus* is one of the many *Bembecinus* in the *spinicornis* subgroup with body length falling between 7 and 10 mm. Many of these, like *namibicus*, have UA obtusely angled in below (Fig. 9f). A distinguishing feature of *namibicus* is the leg coloration in which orange-red and yellow are almost evenly divided. Also, submarginal cell II is not petiolate (Fig. 9g), and F-XI of the male is unusually short (Fig. 9d). *B. namibicus* vaguely resembles *buyssoni* (Arnold) and *mitulus* (Arnold) (holotypes seen) which have more extensively red legs and red on terminal terga. Another red-legged form is *witzenbergensis* (Arnold) (holotype seen), which has inner eye margins much less divergent above. Differences from *rozenorum* are discussed under that species. The name is an adjective indicating "from Namibia."

### Bembecinus rozenorum R. Bohart, new species

Male holotype. Length 10 mm. Body black, deep yellow, and orange-red. Yellow are: facial markings and antenna in front as far as F-I (Fig. 11a), pronotum all across, scutum and scutellum laterally, metanotum, large spot on propodeal flange (Fig. 11f), large mesopleural spot, legs mostly, posterior bands on T-I-VI, enlarged laterally, that on T-I composed of large lateral spots narrowly connected medially (Fig. 11i), S-I band, lateral spots on S-II-V. Orange-red are: antenna in front (lightly) beyond F-I, slight mark on forefemur, midfemur and hindfemur above basally, trochanters partly, T-VII lightly except for basolateral dark areas (Fig. 11k). Pubescence pale. Punctation fine, close, a little more coarse on T-VII. Antenna slender, "spine" on F-VIII reaching middle of F-IX (Fig. 11d) facial proportions (Fig. 11a), second submarginal cell not petiolate (Fig. 11g), UA broadly incurved below (Fig. 11f), hindfemur on lower part of inner surface with small spine at basal one-third, abdomen rather stout (Fig. 11i), T-VII narrowed to slightly

indented apex (Fig. 11k), genitalia expanded toward apex, gonostyles rather narrowly rounded there (Fig. 11n).

Females. Length 10 mm. About as in male. Hindfemur more extensively orange-red. Facial proportions (Fig. 11o), T-VI shape and markings (Fig. 11q).

Holotype male (NEW YORK), 38 km n. Usakos, Namibia, III-26-76 (J. G. and B. L. Rozen). Paratypes (NEW YORK, DAVIS), 3 females, 38 km n. and 19 km e. Usakos, Namibia, III-18-26-76 (J. G. and B. L. Rozen).

This species is close to *namibicus* and may occur with it. However, *rozenorum* is considerably larger (7 vs 10 mm long), the female tergal bands more deeply yellow, and male gonostyle less blunt (compare Fig 9n, 11n). The name is dedicated to the collectors.

### *Bembecinus tridens* group, *tridens* subgroup
### Bembecinus tinkeri R. Bohart, new species
### (Fig. 1)

Male holotype. Length 9.0 mm. Black with extensive yellow markings. Yellow are: lower face (Fig. 1a), antenna in front (F-II-XI orange-tinted), pronotum all across, notum marked as in Fig. 1e, legs almost entirely, bands on abdominal terga (Fig. 1i), S-I-V, VI partly, wings slightly stained, veins dark brown. Pubescence pale, abundant and erect on vertex, laterally on terga. Punctures fine, moderately close, about 1.0 PD apart on notum, mesopleuron, terga. Antenna slender, F-I about 2.0× as long as broad, slightly longer than F-II (Fig. 1a), "spine" of F-IX reaching middle of F-X (Fig. 1d); facial proportions (Fig. 1a); propodeal flange UA evenly rounded in profile (Fig. 1f); second submarginal cell not petiolate (Fig. 1g); T-VII drawn out apically (Fig. 1k); genitalia with gonostyles expanded toward apex (Fig. 1n).

Female paratypes: Length 8.0–10.0 mm. About as in male; facial proportions as in

Fig. 1o, T-VI as in Fig. 1q (lateral spots sometimes larger).

Holotype male (PERTH), 22 km n. Eneabba, Western Australia, dry bed of Arrowsmith River, I-2-13-95 (A. Tinker). Paratypes (DAVIS and other cooperating museums listed in Acknowledgments), 15 males, 54 females, same data as holotype.

The only other Australian *Bembecinus* with markings similar to those of *tinkeri* is *signatus* Handlirsch (1892:53). The holotype male of *signatus* was from Sydney, South Australia. It was deposited in the Hamburg Museum, and was subsequently destroyed. According to the description by Handlirsch the male of *signatus* differs from *tinkeri* in several characters: body length 11 mm, clypeus with a median black mark, UA with an excision, legs partly black, wings strongly "citrinae" in part, T-VII with a median yellow strip. The type series of *tinkeri* was taken in a Malaise trap by Alan Tinker, and the name is dedicated to him.

*Bembecinus tridens* group,
*discolor* subgroup
**Bembecinus wenzeli** R. Bohart,
new species
(Fig. 10)

Male holotype. Length 11.5 mm. Body dark reddish brown to black (background color), markings light brownish and yellow. Yellow are: posterior rim of pronotum, lateral spot on scutellum, submedian dash across metanotum, legs in front beyond femur, forefemur in front, short subapical mark on T-I, narrow subapical bands on T-II-III (that on III somewhat translucent) (Fig. 10i), lateral spots on S-II-III, traces on S-IV-V; light brownish are: facial markings (Fig. 10a), F-XI, most wing veins; wing membrane faintly reddish. Pubescence pale, partly erect, partly appressed; erect but not thick on upper face and mesopleuron; long and thick on S-VII-VIII. Punctures mostly moderate, sparse on clypeus, larger in front of ocellar triangle and on mesopleuron, 2–3 PD apart

on scutellum, 1 PD apart or closer on propodeal enclosure and more terminal terga. Proportions of face including antenna (Figs. 10a, 10d); second submarginal cell not petiolate (Fig. 10g); propodeal flange UA obtusely rounded before posterior notch (Fig. 10f); abdomen stout (Fig. 10i), T-VII broad; obtusely truncate (Fig. 10i); S-VI with small basomedial tooth; S-VII lateral lobes fully exposed; genitalia slender (Fig. 10n) aedeagus strongly notched at apex (Fig. 10n').

Female paratype. Length 11.0 mm. About as in male, but facial proportions as in Fig. 10o, scutellum all brown, legs all brown, yellow band only on T-II, lateral spots only on S-II, foretarsal V and arolium much larger than others, forebasitarsus about 1.7× as long as broad (Fig. 10p), T-VI with a definitive pygidial plate and large punctures (Fig. 10q).

Holotype male (LAWRENCE), 38 km n. Toliara, Madagascar, XII-2-86 (J. W. Wenzel). Paratypes (LAWRENCE, DAVIS), 9 males, same data as holotype; female (LAWRENCE), 10 km e. Sakaraha, Madagascar, XII-4-86 (J. W. Wenzel).

This species belongs to the *tridens* group according to the projection on male F-IX, and to the *discolor* subgroup by the basomedian tooth on S-VI of the male, and short forebasitarsus of the female, (Fig. 10p). The extensive dark reddish brown coloration (Fig. 10i, stippled area), broadly subtruncate T-VII of the male (Fig. 10i), and coarse punctation of the partial pygidial plate of the female (Fig. 10q), distinguish the species. No other species of *Bembecinus* known to me is like it on Madagascar or on continental Africa. The specific name is dedicated to the collector, John W. Wenzel.

NOTES ON PREVIOUSLY DESCRIBED
SPECIES
*Bembecinus tridens* group,
*tridens* subgroup
**Bembecinus argentifrons** (F. Smith)

*Larra argentifrons* F. Smith 1856:339. Syntype males "Port Natal", Natal Prov., South Africa, (LONDON).

*Stizus braunsii* Handlirsch 1894:287. Lectotype female (here designated), "Transvaal", Transvaal Prov., South Africa, (GENEVA). New synonym.

*Stizus barkeri* Arnold 1940:114. Holotype female, Durban, Natal Prov., South Africa (PRETORIA ?). New synonym.

I have studied the lectotype of *braunsii* and a paratype male of *barkeri* from PRETORIA. They agree nicely with specimens in a long series (32 males, 5 females) that I collected on a sandy bank at the mouth of Umgazi River, Natal Prov., South Africa, October 28, 1972. Characteristics of this species are: Both sexes with length usually 7–9 mm; a quite sharp notch below on UA; second submarginal cell briefly petiolate; black and yellow markings, including those of legs, but tending toward whitish on female terga; males with yellow bands or spots on T-I-VII, females with bands or spots on T-I-IV or sometimes a lateral spot on V, females with a median black clypeal spot, and with foretarsal V and arolium not enlarged.

A presumed male syntype of *argentifrons* was sent to me from the British Museum. It bears the label "Port Natal" but the clypeus is mostly black contrary to Smith's original description. Therefore, I have not designated it as lectotype. Nevertheless, I feel quite certain that *argentifrons* is the senior synonym for *braunsii* and *barkeri*.

### *Bembecinus tridens* group,
### *spinicornis* subgroup
### Bembecinus spinicornis (Saussure)

*Stizolarra spinicornis* Saussure 1887:9. Holotype male, Madagascar. (type seen, PARIS).

*Stizus varians* Arnold 1945:73. Holotype male, Bekily, Madagascar (type seen, PARIS). Synonymy by Leclercq 1940.

Arnold (1945) suggested the possibility of the above synonymy although he had not seen the holotype of *spinicornis*. A comparison of this type, a flavid male, and

the type of *varians*, both furnished by Dr. J. Casevitz-Weulersse, verifies the relationship of the two names. Arnold's description and figures of *varians* based on 7 males, particularly the bladelike tooth of S-VIII, are unmistakable. The flavid holotype of *spinicornis* has 3 small spines scattered along the lower edge of the inner surface of the hindfemur. Also, the forebasitarsus is all yellow.

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# Description and biology of a new species of *Meteorus* Haliday (Hymenoptera: Braconidae, Meteorinae) from Costa Rica, parasitizing larvae of *Papilio* and *Parides* (Lepidoptera: Papilionidae)

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*Abstract.*—*Meteorus papiliovorus* Zitani, a new species from Costa Rica, is described and illustrated. This species is a gregarious koinobiont endoparasitoid of papilionid larvae including *Papilio anchisiades idaeus* Fabricius on *Citrus* and *Parides sesostris zestos* (Gray) on *Aristolochia tonduzii*. Notes on its biology, distribution, and cocoon-forming behavior are given. This is the first record of any New World *Meteorus* attacking Papilionidae, and the first record of *Meteorus* utilizing "nasty" hosts that are believed to contain toxic secondary chemicals.

## INTRODUCTION

During March of 1993 one of us (SRS) visited the La Selva Research Station in Costa Rica, where Ronald Vargas (a parataxonomist working on the ALAS project—Arthropods of La Selva) called to my attention a parasitoid wasp that he had recently reared from *Papilio anchisiades idaeus* Fabricius on *Citrus* (Rutaceae). This was immediately recognized to be a new species of *Meteorus* Haliday, of particular interest for several reasons: it provides the first New World record of *Meteorus* attacking Papilionidae, it is a gregarious species with remarkably short cocoon-suspending threads (Figs. 1–2, 4), and it is potentially of interest as a biocontrol agent for *Citrus*-feeding papilionids. We returned to the collecting site and made an even more remarkable observation—the *Citrus* tree had been virtually defoliated by leaf cutter ants, except for one leaf with another cluster of *Meteorus* cocoons (Figs. 1–2). This observation, combined with the short cocoon threads, raises the exciting possibility that either this new species, or its host, has evolved some defense mechanism to deter leaf cutter or other ants—a discovery that

might be of considerable economic benefit to INBio or other bioprospecting ventures. Subsequent studies of the INBio collection indicated that this species is widely distributed in Costa Rica. In 1995 one of us (DHJ) discovered that *Parides* on *Aristolochia* (Aristolochiaceae) is another host of this parasitoid. DHJ had also reared this wasp from *P. anchisiades* in the dry forest of the Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica. During June of 1996 NMZ reared this species from *Parides sesostris zestos* (Gray) on *Aristolochia tonduzii* (Fig. 6) at the Pitilla Biological Station, ACG. The purpose of this paper is to provide a scientific name for this new *Meteorus* species, to facilitate ongoing studies of its biology, and as a contribution to the ALAS project and the biodiversity inventory of the ACG.

*Meteorus* Haliday is the most prominent genus of the braconid subfamily Meteorinae (sensu S. Shaw 1985, 1994; Maetô 1990; M. Shaw and Huddleston 1991), sister-group of the Euphorinae (*sensu stricto*), which is a moderately large subfamily comprising at least 174 species worldwide (S. Shaw 1988). Meteorines are sometimes

Figs. 1–5.  1. Cocoons of *Meteorus papiliovorus* on leaf of *Citrus* tree at La Selva. Note extensive defoliation of adjacent foliage. 2. Close-up of gregarious cocoons of *Meteorus papiliovorus* on leaf of *Citrus* tree at La Selva. 3. Ultimate instar of *Parides sesostris zestos*, larval form A, on *Aristolochia tonduzii* at Pitilla. 4. Close-up of single cocoon of *Meteorus papiliovorus*. 5. Cocoons of *Meteorus papiliovorus* at Pitilla. Note one exceptionally long cocoon thread.
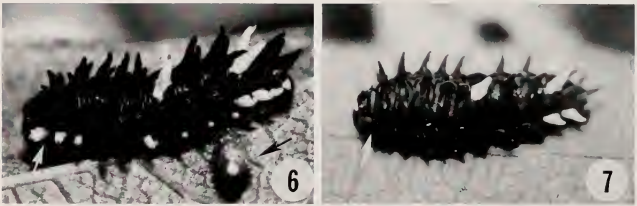
Figs. 6–7.  6. Penultimate instar of *Parides sesostris zestos*, larval form A, with *Meteorus papiliovorus* cocoon. 7. Penultimate instar of *Parides sesostris zestos* (?), larval form B.

classified as a tribe within the Euphorinae (e.g. Marsh 1979; Gauld and Bolton 1988; Quicke and van Achterberg 1990). *Meteorus* has been seldom studied in the New World tropics, and only a few works are directly applicable to the Costa Rican fauna (Muesebeck 1923, 1956; S. Shaw 1995). One of us (NMZ) is currently working on a revision of Costa Rican *Meteorus*.

Meteorines are solitary or gregarious koinobiont endoparasitoids of larval Coleoptera or Lepidoptera, and many *Meteorus* species have broad host ranges (Achterberg 1979; West and Miller 1989; Maetô 1990). The vast majority of meteorines are solitary parasitoids attacking exophytic (exposed-feeding) lepidopteran larvae, and many are nocturnally active. Others utilize hosts that are only weakly concealed (e.g. in leaf rolls or under webbing). The most frequently utilized hosts are Noctuidae, Geometridae, and Tortricidae, but many other lepidopterans including Hepialidae, Zygaenidae, Tineidae, Gelechiidae, Pyralidae, Papilionidae, Lycaenidae, Nymphalidae, Lasiocampidae, Thaumetopoeidae, and Arctiidae have been recorded as hosts (Muesebeck 1923; Huddleston 1980; Maetô 1989, 1990). The solitary parasitoids of arboreal Lepidoptera typically emerge from the host larva and pupate away from the host remains in a pendant cocoon that is often suspended by a long slender thread (Gauld and Bolton 1988), and it is from this character-

istic cocoon that the genus *Meteorus* gained its name. Cocoon threads are usually about 1–8 cm long, with some as long as 20 cm (M. Shaw and Huddleston 1991). It has been postulated that this suspended cocoon is an anti-predator defensive adapatation. The cocoons are also commonly subject to hyperparasitism. The gregarious *Meteorus* species usually form their cocoons together in a loose, irregular heap (Huddleston 1980), although the terminal threads may still be present, but intertwined (S. Shaw 1985). A few highly specialized gregarious species from Africa and Sri Lanka form a very organized spherical cocoon mass, with all the exit holes facing outwards (Nixon 1943; Huddleston 1983). Those species attacking Coleoptera larvae typically utilize hosts concealed in wood, bark or fungus, especially Cerambycidae, Tenebrionidae, Scolytidae, Biphyllidae, Melandryidae, and Cisidae (Huddleston 1980). As far as known, the *Meteorus* species attacking coleopterous larvae form stalkless cocoons within the beetle gallery (DeLeon 1933; Mason 1973), and these are regarded as relatively primitive (Mason 1973; Maetô 1990).

The only previous record of *Meteorus* attacking Papilionidae is a record of the Old World species *Meteorus pulchricornis* (Wesmael) using a papilionid (Maetô 1990), and this may be only an opportunistic association, since records indicate that *pulchricornis* is a generalist species that oth-

erwise attacks a variety of hosts including noctuids, arctiids, geometrids, lymantriids, lasiocampids, nymphalids, and lycaenids. This paper provides the first record of any New World *Meteorus* attacking Papilionidae, and the first record of *Meteorus* utilizing "nasty" hosts that are assumed to contain toxic secondary chemicals.

## METHODS

Species covered in this paper can be identified as members of the subfamily Meteorinae using the keys of S. Shaw (1995) or M. Shaw and Huddleston (1991). Our definition of *Meteorus* follows that of Huddleston (1980, 1983), S. Shaw (1985), and Maetô (1989, 1990). Specimens can be determined as *Meteorus* using the key of Marsh *et al.* (1987).

Terminology mostly follows that used for *Meteorus* by Huddleston (1980, 1983) and Maetô (1989, 1990). Microsculpture terminology follows that of Harris (1979). Wing venation terminology agrees with the system being adopted for the *Identification Manual for New World Genera of the Family Braconidae* (in preparation), and agrees closely with that of Goulet and Huber (1993). To avoid confusion, a labelled diagram is provided here (Fig. 10). Because of varied body metasomal positions in many specimens, body length was taken as the combined measure of the length from head to end of propodeum, added to the length from base of the first tergite to end of metasoma (not including ovipositor). Abbreviations for museums can be found in the Acknowledgments section. Authorship of this new species is attributed to the senior author (NMZ).

**Meteorus papiliovorus** Zitani,
new species
(Figs. 8–10)

*Holotype female.*—**Body color**: (Fig. 8) body yellow except head orange dorsally, antenna black; mesonotum brown anteriorly and laterally, orange dorso-medially;

prothoracic leg with femur brown apically, tibia brown basally and apically, apical tarsomere and pretarsus dark brown; mesothoracic leg with femur brown apically, tibia brown apically, apical tarsomere and pretarsus dark brown; metathoracic leg with coxa brown apically, trochantellus brown, femur dark brown apically, tibia dark brown basally and apically, tarsus dark brown; metasoma dark brownish black dorsally except first tergite yellow basally, third tergite with lateral orange spots; laterotergites orange; wings deeply infused with dark blackish pigment. **Body length**: 4.6 mm. **Head**: (Fig. 9) 1.2× wider than high in anterior view, head height 1.7× eye height in anterior view; antenna filiform with 26 flagellomeres; flagellar length/width ratios as follows: F1 = 3.2, F2 = 3.0, F3 = 3.0, F22 = 2.5, F23 = 2.8, F24 = 2.6, F25 = 2.2, F26 2.8× longer than wide basally, pointed apically; eye not large but protuberant; eyes not strongly convergent, nearly parallel in anterior view; maximum face width 1.2× minimum face width; minimum face width 1.2× clypeus width; ocelli not conspicuously large, ocellar-ocular distance 1.9× diameter of lateral ocellus; malar space length 2.4× mandible width basally; face protuberant medially, laterally depressed above anterior tentorial pits, polished, punctate; clypeus polished, punctate; mandible strongly twisted. **Mesosoma**: notauli areolate; mesonotum polished, punctate dorsally; scutellar furrow 2-foveate; mesopleuron polished, punctate; sternaulus rugose; propodeum areolate-rugose, median depression present. **Legs**: hind coxa polished, punctate; tarsal claws simple. **Wings**: (Fig. 10) forewing length 3.9 mm; vein m-cu antefurcal; vein r 2× length of 3RSa; second submarginal cell strongly narrowed anteriorly. **Metasoma**: polished, smooth and shining; first tergite dorsally longitudinally costate, dorsopes absent, ventral borders joined along basal ½ of segment; ovipositor 1.6× longer than first tergite.
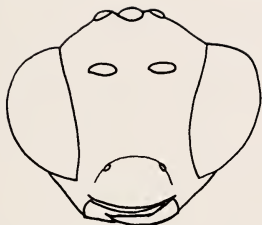
Fig. 8. Lateral habitus of *Meteorus papiliovorus*.

Fig. 9. Anterior view of head of *Meteorus papiliovorus* showing eye shape.

*Variation, paratype females.*—26 to 28 flagellomeres; fore wing length 3.4 to 3.9 mm; vein m-cu interstitial; fore wing veins r and 3RSa about equal in length; ovipositor 1.6 to 1.9× longer than tergite 1; brown areas vary from light brown to dark brownish-black except metasoma; mesonotum yellow; propodeum with brown spots dorsally; hind coxa almost completely dark brown; tergite 1 completely yellow; tergite 3 without lateral orange spots; body length 4.1 to 4.6 mm.

*Variation, paratype males.*—As in females except 26–32 flagellomeres; body length 3.6 to 4.3 mm; mesonotum orange; fore and mid legs orange except apical tarsomere and pretarsus brown; hind coxa, trochantellus, and femur yellow.

*Description of cocoon.*—(Figs. 1–2, 4–5)

length 4.6 to 5.7mm, 1.9 to 2.2mm wide medially; suspended dorsally from a short thread usually 1.0 to 1.7mm long, exceptionally 4.5–10cm long (Fig. 5); terminating ventrally with a rounded nipple-like projection (Figs. 4–5); silk color mostly glossy brown, lighter at ventral apex; emergence hole neatly cut as a ⅞th semicircle, apex remaining attached as a cap.

*Material Examined.*—Holotype female with cocoon: **COSTA RICA: Heredia Province:** Est. Biol. La Selva, 50–150m, 10° 26'N, 84° 01'W, March 1993, R. Vargas, INBio-OET, INBIOCR1001219752, reared from *Papilio anchisiades idaeus* larva on *Citrus.* Deposited in INBio. Paratypes: **COSTA RICA: Alajuela Province:** 4 females, 5 males, M-12, Naranjo, October 17, 1990, col. Marvia R., INBIOCR1001008313–321. **Guanacaste Province:** 1 female, 1 male, ACG, Santa Rosa, Bosque Humedo, each reared from *Papilio anchisiades* on *Xanthoxylum setulosum*, D.H. Janzen voucher specimen #90-SRNP-2177; 2 females, ACG, Est. Pitilla, reared from *Parides sesostris zestos* larva, wasps eclosed 28 June 1995, D.H. Janzen voucher specimen #95-SRNP-4760; 2 females with cocoons, ACG, Est. Pitilla, 600m, reared from *Parides sesostris zestos* larva on *Aristolochia tonduzii*, larvae coll. 14 June 1996, wasps em. 8–9 July 1996, #96-NZ-25, N. Zitani; 4 females with cocoons, ACG, Est. Pitilla, 600m, reared from *Parides sp.* larva on *Aristolochia ton-*
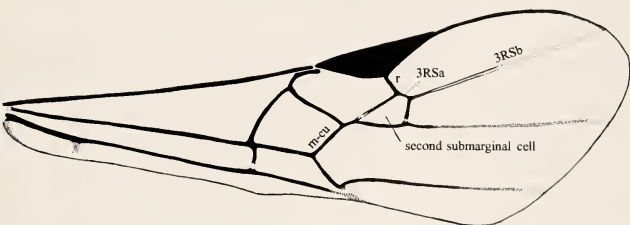


Fig. 10. Forewing venation of *Meteorus papiliovorus.*

*duzii*, larva coll. 23 June 1996, wasps em. 4–6 July 1996, #96-NZ-42, N. Zitani; 4 females with cocoons, ACG, Est. Pitilla, 600m, reared from *Parides* sp. larva on unidentified host plant, larva coll. 26 June 1996, wasps em. 5–7 July 1996, #96-NZ-44, N. Zitani. **Heredia Province:** 4 females with cocoons, same data as holotype except INBIOCR1001219750-751, 753–754. **Limon Province:** 1 male, Sector Cerro Cocori, Fca. de E. Rojas, 150m, March 1993, E. Rojas, L-N-286000, 567500, INBIOCR-1001406312; 1 female, P.N. Tortuguero, Est. Cuatro Esquinas, 0m, September 1992, R. Delgado L-N 280000, 590500, IN-BIOCR1000840248. **Puntarenas Province:** 20 females, 8 males with cocoons, Peninsula de Osa, Rancho Quemado, 200m, August 1991, F. Quesada, L-S-292500, 511000, INBIOCR1001329113-140. Paratypes deposited in INBio, UCR, RMSEL.

*Distribution.*—Known only from the type localities in Costa Rica.

*Biology.*—*Meteorus papiliovorus* is a gregarious koinobiont endoparasitoid of papilionid larvae including *Papilio anchisiades idaeus* Fabricius on *Citrus* and *Parides sesostris zestos* (Gray) on *Aristolochia tonduzii*. A second *Parides* species may also be utilized. At the Pitilla research site NMZ found two distinct larval forms, A and B, of the host caterpillars (Figs. 3, 6–7) feeding on *Aristolochia tonduzii* (one individual of larval form B was found on an unidentified host plant). These two larval forms are distinguished by the presence of lateral white tubercles immediately posterior to the head (Fig. 6), or their absence (Fig. 7), on the penultimate instar. The presence of these white tubercles on the ultimate instar of larval form A, along with distinct maroon-colored circular markings on the dorsal surface (Fig. 3) further serves to separate the two larval forms. Form A was reared to the adult, and identified as *Parides sesostris zestos* using DeVries (1987). Form B was not reared to adult because all the larvae collected were parasitized.

When utilizing *Parides sesostris zestos*, M.

*papiliovorus* emerged from both the penultimate and ultimate instars. The adult wasps emerged from their cocoons 10–12 days later.

DeVries (1987) indicated that larvae of *Papilio anchisiades idaeus* are parasitized by braconid wasps, but gave no more detail. Also, there are unconfirmed reports of this parasitoid emerging commonly from *Papilio* larvae collected in *Citrus* groves near San Jose.

*Comments.*—The distinctive color pattern of this species (Fig. 8), with bright yellow body, black dorsally, and black tinted wings, and the strongly narrowed second submarginal cell (Fig. 10) are fully diagnostic. In specimens where forewing veins r and 3RSa are about equal in length, the second submarginal cell remains strongly narrowed. Another species that has been examined, but is still undescribed, shares with *M. papiliovorus* dark tinted wings and a strongly narrowed second submarginal cell. However, it has a shorter, curved ovipositor (ovipositor about equal to length of first tergite), moderately twisted mandibles, and was reared from *Manduca sexta* (D.H. Janzen voucher specimen #95-SRNP-7538, and #95-SRNP-7539). *M. papiliovorus* keys to couplet 20 in Muesebeck's (1923) key.

*Etymology.*—Derived from the Latin *papilio* for butterfly, and *voratus* for devourer, in reference to the feeding habits of this species.

## ACKNOWLEDGMENTS

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## In Memoriam
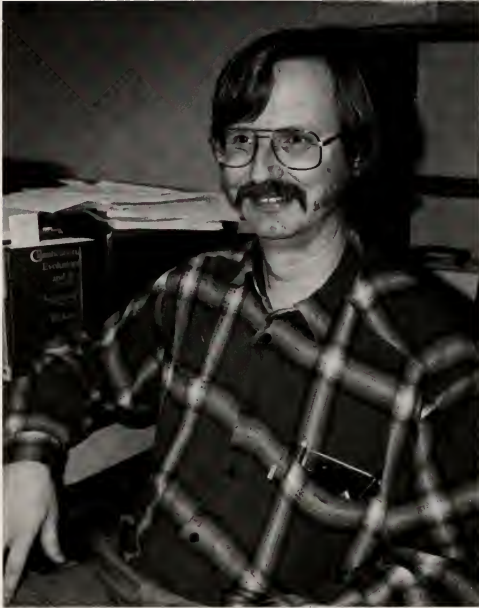


BYRON ALLEN ALEXANDER
1952–1996

Research on the systematics, behavior and morphology of bees and sphecid wasps suffered a tragic loss with the sudden and unanticipated death of a promising young investigator, Byron Alexander, on November 30, 1996. His brief professional career of only seven years was one of impressive scholarly productivity in addition to his teaching and curatorial duties. Byron was an associate professor in the Department of Entomology and the Department of Systematics and Ecology at the University of Kansas, as well as a half-time curator in the Snow Entomological Collection of the Natural History Museum. He had contributed two important

papers to the Journal of Hymenoptera Research.

Byron was most importantly an enthusiastic and capable teacher. On a regular cycle, he taught insect classification, external morphology of insects, social insects and introductory systematics. In addition, he had taught two undergraduate biology courses and a summer field course in entomology. In the summer of 1990, he co-taught a field course on bee behavior and ecology at the Centro de Ecología, Hermosillo, Mexico; and in 1994 he taught in a course on identification of Hymenoptera, sponsored by the University of Hawaii and the Bernice P. Bishop Museum, in Honolulu, Hawaii. Students regarded his courses highly, and he had received an award for outstanding teaching while at Cornell University.

He was both a student of the natural history of insects and a practitioner of the most up-to-date computer methods in the cladistic analysis of various groups of Hymenoptera. Another of his interests was morphology of bees and wasps, particularly of the female reproductive system. His research was supported, at one time or another, by the National Science Foundation, a Smithsonian Postdoctoral Research Fellowship, and the General Research Fund of the University of Kansas.

Byron was an artist of unusual talent. Examples of his artistic work may be seen in his last publication, "Comparative Morphology of the Female Reproductive System of Nomadine Bees" (Mem. Entomol. Soc. Washington, no. 17, pp. 14–35, 1996). Earlier, he had exhibited drawings at a national meeting of the Guild of Natural Science Illustrators (in 1984) and at the Eastern Branch meeting of the Entomological Society of America, in Syracuse, New York (1988). He made the illustrations for "The Natural History and Behavior of the North American Beewolves," a book by Howard Evans and Kevin O'Neill (1988). While working for the National Park Ser-

vice, he illustrated brochures on wildlife of the parks.

Byron Allen Alexander was born in El Paso, Texas, on April 14, 1952, the son of Harold and Betty Alexander. He attended the University of Texas at El Paso and graduated with highest honors in 1974. Fascinated by the work of Jane Goodall in Tanzania, he enrolled in a graduate program in primatology at Stanford University. The program was discontinued after a year; however, Byron had an opportunity to study chimpanzees in Senegal with a group of Scottish primatologists. After only six months in Africa, he contracted hepatitis and had to return to the United States. In 1976 and in 1978–1981, he was employed as a seasonal park naturalist, at Capitol Reef National Park, Utah, Great Sand Dunes National Monument, Colorado, and Tuzigoot National Monument, Arizona. During this period, Byron's interest in entomology and particularly in wasp behavior, was stimulated by his contacts with students of Prof. Howard Evans of Colorado State University. Thus influenced indirectly by hymenopterist-behaviorist Evans, he went to Colorado State University and there earned the M.S. degree in 1983. He continued graduate studies with George Eickwort at Cornell University. At Cornell, Byron was awarded the John Henry Comstock Scholarship, a National Science Foundation Graduate Fellowship and three other fellowships. He received the Ph.D. degree from Cornell in 1989, and in the summer of that year joined the Entomology faculty at the University of Kansas, as an assistant professor. He was promoted to associate professor, with tenure, in 1995.

In addition to his membership in the International Society of Hymenopterists, Byron was active in the Entomological Society of America (associate editor of the Thomas Say Publications in Entomology, since 1994), the Central States Entomological Society (president in 1995, member of the editorial board since 1994), the Animal

Behavior Society, the International Union for the Study of Social Insects, the Society of Systematic Biology, the American Association for the Advancement of Science, and the Sigma Xi Scientific Research Society.

Byron is survived by his parents, Prof. and Mrs. Harold Alexander of El Paso, Texas and two brothers, Harold, of Las Cruces, New Mexico and David, of Portland, Oregon. A memorial service was held in the Natural History Museum, University of Kansas, on December 5, 1996. At this service, it was evident that Byron had many friends, some of whom (former students and others) had come from distant parts of the country to pay their final respects to this unusual man.

A memorial fund in Byron's name has been established with the Kansas University Endowment Association, to keep his memory alive and to benefit entomology students, to whom he had devoted most of his professional career.

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GEORGE W. BYERS, Department of Entomology, University of Kansas, Lawrence, KS 66045, USA.

# MEMORIAL PUBLICATION HONORING BYRON ALEXANDER
## CALL FOR PAPERS

The Natural History Museum, University of Kansas, including the Snow Entomological Division, plans to publish a memorial volume honoring Dr. Byron A. Alexander in the series "Scientific Papers, Natural History Museum, The University of Kansas (a continuation of the University of Kansas Science Bulletin). This book will be part of a numbered series that is distributed to libraries and sent to abstracting services. The general theme of the volume, "The Friends of Byron Alexander," is broad enough that contributions can be in systematics, evolutionary biology, ecology, behavior, phylogeny or other fields of biology that were of interest to our friend, Byron.

Contributed papers will follow the format of what was formerly the University of Kansas Science Bulletin and should be no more than 30 double-spaced manuscript pages. The format will be double column; a printed page without illustrations will contain about 1400 words. Papers initially must be submitted as three "hard" copies. After the paper has been accepted and the editor's and reviewers' comments have been considered, the final version must be submitted on a 3.5 inch floppy disk in Microsoft Word, preferably for the Macintosh; however, Microsoft Word for Windows (3.1 or later), DOS version will also be accepted. All figures must be no larger than 8 1/2" × 11" (218 mm ×

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Page charges will be assessed at $32/printed page (containing 1400 words). *This is 1/3 the cost of an equivalent page in a journal such as the Journal of the Kansas Entomological Society.* Note: Illustration space will be charged at the same rate as printed space and only papers which have paid their page charge bills prior to printing will be accepted for the final volume. Reprints will not be provided, but authors are authorized to make xerox or offset copies as desired. Each author will receive two copies of the entire volume so one can be separated for making reprints.

Deadline for submission of manuscripts is Oct. 1, 1997.

Send manuscripts, figures and final disks to the editors:

Robert W. Brooks or George W. Byers, Snow Entomological Division, Natural History Museum, University of Kansas, Lawrence, Kansas 66045, USA.

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**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, such as 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.

**The deadline for receipt of manuscripts is 1 October (for the April issue) and 1 April (for the October issue).**

**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 one copy 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, Mac-Write, or MacWrite II. 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.

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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 if the subject is complex. Cladograms must be hung with characters and these should include descriptors (not numbers alone) when feasible. The number of parsimonious cladograms generated should be stated and reasons given for the one adopted. Lengths and consistency indices should be provided. Adequate discussions should be given for characters, plesiomorphic conditions, and distributions of characters among outgroups when problematical.

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 multiple authors, use the word "and," not the symbol "&" (Smith and Jones 1999). 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 and in italics.

**Charges.** Publication charges are $10.00 per printed page. At least one author of the paper must be a member of the International Society of Hymenopterists. 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.

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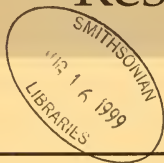Phone: (202) 382-1782  Fax: (202) 786-9422  E-mail: egrissel@sel.barc.usda.gov

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Organized 1982; Incorporated 1991

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

# A Revision of the Genus *Hambletonia* Compere
# (Hymenoptera: Encyrtidae)

Andrey Sharkov and James B. Woolley

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*Abstract.*—The encyrtid genus *Hambletonia* is redescribed. Eight new species, *H. calvifrons*, n. sp. (Costa Rica), *H. marticephala*, n. sp. (USA: Florida, Georgia), *H. pilosifrons*, n. sp., *H. punctifrons*, n. sp. (Costa Rica), *H. roseni*, n. sp. (Panama, Costa Rica), *H. setosifrons*, n. sp., *H. squalicephala*, n. sp., and *H. undulitibiae*, n. sp. (Costa Rica) are described. A key to species is provided.

The genus *Hambletonia* was originally described by Compere (1936) for a single species, *H. pseudococcina* Compere. It remained monotypic until the present study, inspired by the discovery in Florida and Georgia (USA) of a very peculiar encyrtid bearing a large protrusion on the frontovertex between the compound eyes, a feature not found in any other representative of the family. After analyzing its characters and consulting with Dr. J.S. Noyes (The Natural History Museum, London), we came to the conclusion that this encyrtid constitutes an aberrant new species of *Hambletonia*. Study of specimens received on loan from various institutions revealed seven more undescribed species, bringing a total number of species currently included in the genus to nine. The present article reviews the concept of *Hambletonia* based on the new material, and includes descriptions of eight new species and a key to species.

## MATERIALS AND METHODS

Specimens originally collected in alcohol were critical-point-dried (CPD), or prepared using hexamethyldisilazane (HMDS), a technique used as a chemical alternative to CPD (Brown, 1993; Heraty, personal communication and Internet posting). Balsam mounted microscope slides were prepared following the method described by Noyes (1982), with slight modifications. Measurements were made from dry mounted specimens and from microslides using a stereomicroscope equipped with a filar ocular micrometer. All measurements (except body length) are given in units of the micrometer (1 unit = 0.01 mm). They are all comparable to each other, and can be translated into millimeters by multiplying the number of units by 0.01. Terminology follows Sharkov (1996), except "pygostyli" are called "cerci." All illustrations are original line drawings prepared by Sharkov from card mounted and pointed specimens, and microslides using a camera lucida on a compound microscope. Abbreviations for depositories of type materials and institutions that provided loans of specimens are as follows: AMNH (American Museum of Natural History, New York, NY, USA), BMNH (The Natural History Museum, London, UK), INBio (Instituto Nacional de Biodiversidad, San José, Costa Rica), OSUC (Ohio State University, Columbus, OH, USA), TAMU (Texas A & M University, College Station, TX, USA), UCDC (University of California, Davis, CA, USA), UCRC (University of California,

Riverside, CA, USA), USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA).

## HAMBLETONIA Compere

Hambletonia Compere, 1936:172–173. Type species: H. pseudococcina Compere, by original designation.

The original description of Hambletonia (Compere 1936) was based on a single species, H. pseudococcina Compere. Therefore, many of the characters Compere had thought to be of generic value (such as the shape of the head and the relative size of the head structures, the ability to retract the antennae in the facial depression, the shape of the scape, the number of funicular segments, the presence of "coarse, flattened setae on the dorsal margin at apex" of the pedicel, and the "very narrowly separated at inner tips" axillae), following discovery and study of new species, turned out to be of only specific value. We redescribe the genus based on all material available to us. Unique features of H. marticephala n. sp. are stated separately in the Comments section.

*Female.*—General body color from yellow to orange yellow or orange brown, sometimes brown or dark brown. Frontovertex sometimes with very slight purple, greenish or bluish metallic luster that can be seen only at certain illumination. Forewing slightly to moderately infuscate, especially in basal part. Body length 1.0–2.5 mm. **Head** (Figs. 1–18) hypognathous, length 0.5–0.63× width, 0.65–0.8× height, in lateral view more or less triangular, line outlining frontovertex straight to moderately convex, at angle of about 30° to 60° to longitudinal axis of body (when posterior margin of gena is vertical) (Figs. 3, 12, 15, 18). Frontovertex convex to almost flat, smooth, often with scattered (sometimes, numerous) non-piliferous punctures, naked or with scattered hairs, and one row of hairs along each inner eye orbit, length

1.1–1.6× width, width 0.4–0.6× width of head, anterior margin (dorsal view) convex to straight or concave (Figs. 2, 8, 11, 14, 17). Ocelli in obtuse triangle, with anterior angle of 96°–154°. Eyes oval, naked to setose, maximum diameter from less than ½ to more than ¾ head length (dorsal view), posterior orbit reaching, or almost reaching occipital margin, anterior orbit separated from margin of facial depression by 0.2–0.3× maximum diameter of eye (Figs. 1–18). Facial depression deep, sharply separated from frontovertex and genae (in H. undulitibiae n. sp. border of facial depression and genae slightly rounded laterally, as in Fig. 10), with two concavities (one on each side) to accomodate apex of scape when antennae are enclosed in facial depression. Antennal toruli 1.7–2.6× closer to mouth margin than to each other. Interantennal prominence extending upwards as thin low carina, almost reaching margin of frontovertex. Antennae (Figs. 21–32) compact, can be retracted into facial depression. Scape moderately to strongly broadened and flattened, length 1.6–2.9× maximum width; pedicel with more or less expressed tuft of elongated thickened setae at apex dorsally; funicle 4- to 6-segmented, segments transverse to strongly transverse; clava solid, heart-shaped, broader than funicle. Mandibles bidentate, with sharp teeth, upper tooth conspicuously larger than lower tooth. Maxillary palpi 4-segmented; labial palpi 3-segmented. **Mesosoma** compact, at most 1.23× longer than wide. Pronotum transverse, sometimes concealed by occiput. Mesoscutum transverse, width about twice length, anterior part sometimes concealed by occiput. Sculpture of mesoscutum smooth to shallowly reticulate or reticulate-punctate. Axillae with inner corners meeting to relatively widely separated. Scutellum slightly wider than long, smooth to shallowly reticulate, with distinct longitudinal median groove in anterior one- or two-thirds. Dorsum of metasoma with appressed to suberect hairs,
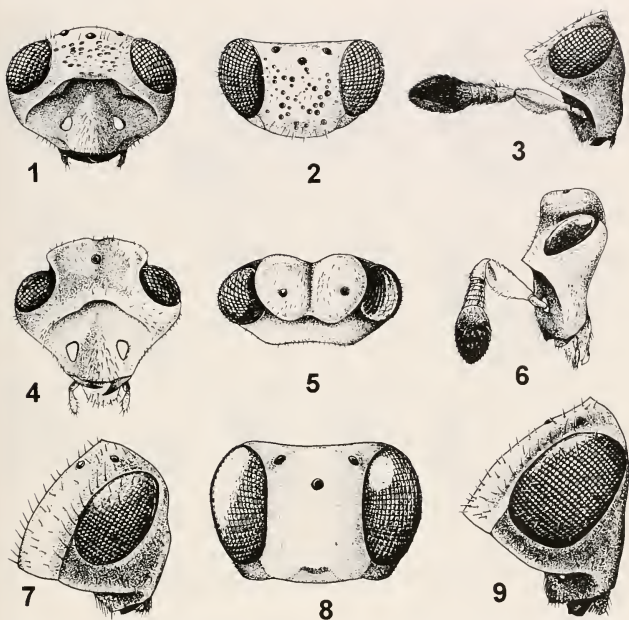
Figs. 1–9. Heads of *Hambletonia* species. 1–3. *H. punctifrons*. 1, frontal view; 2, dorsal view; 3, lateral view, with antenna. 4–6. *H. marticephala*. 4, frontal view; 5, dorsal view; 6, lateral view, with antenna. 7. *H. pilosifrons*, semiprofile view. 8. *H. calvifrons*, dorsal view. 9. *H. setosifrons*, semiprofile view.

and often with scattered non-piliferous punctures. Metanotum and propodeum short, dorsally more or less carinate. Forewing (Figs. 34, 36, 38–41) 2.0–2.4× longer than broad. Costal cell usually bent ventrally (wing plane positionned horizontally). Basal part of forewing (proximad of linea calva) from almost hairless, with only few long hairs (Figs. 39, 40), to more or less densely ciliated, with hairs longer than on wing disk (Figs. 36, 38, 41). Linea

calva entire and open (Figs. 39, 40), or almost closed by one or two lines of hairs along posterior wing margin (Figs. 34, 36, 41). Marginal vein punctiform to about twice as long as broad. Stigmal vein 1.1–1.5× postmarginal vein, almost straight to slightly curved toward anterior wing margin; stigma sometimes weakly expressed. Legs relatively short, slightly to moderately thickened. **Metasoma** very slightly longer than wide. Cerci situated slightly clos-
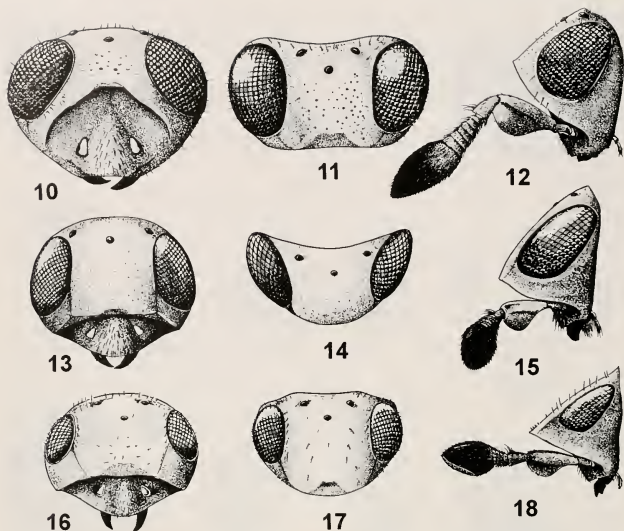
Figs. 10–18. Heads of *Hambletonia* species. 10–12. *H. undulitibiae*. 10, frontal view; 11, dorsal view; 12, lateral view, with antenna. 13–15. *H. pseudococcina*. 13, frontal view; 14, dorsal view; 15, lateral view, with antenna. 16–18. *H. squalicephala*. 16, frontal view; 17, dorsal view; 18, lateral view, with antenna.

er to base, or closer to apex of metasoma[1]. Ovipositor short, not protruding, directed slightly upwards.

*Male.*—General body color black or very dark brown, lateral and ventral surface of mesosoma and metasoma usually slightly lighter than dorsal surface, brown. Antennae light to dark brown. Forewings hyaline, or very slightly infuscate in basal part. Body length 1.0–1.7 mm. **Head** hypognathous, length approximately 0.5×

width, and approximately 0.5× height. Frontovertex convex to almost flat, coarsely reticulate-punctate to superficially transversely reticulate or coriaceous, slightly longer to slightly shorter than broad. Ocelli in slightly to strongly obtuse triangle. Eyes with posterior margin reaching, or almost reaching occipital margin, and with anterior orbit reaching, or almost reaching margin of facial depression. Frontovertex and eyes with sparse to rather dense hairs. Facial depression separated from frontovertex by sharp carina, and with rounded margin separating it from gena, smooth to superficially reticulate. Interantennal prominence rounded dorsally, or extending into

[1] The position of cerci in preserved specimens is affected by the method of preparation: they appear to be closer to base of the metasoma in air-dried specimens, and closer to the apex of the metasoma in critical-point-dried and HMDS-treated specimens.

thin, low, rounded carina, sometimes reaching margin of frontovertex. Antenna subcompact to compact; scape slightly broadened and flattened; funicle 5-segmented, segments strongly to moderately transverse, sometimes some of them subquadrate, round in transection, slightly increasing in width toward clava; clava solid, same width as last funicular segment. Mandibles and palpi as in female. **Mesosoma** compact. Relative dimensions approximately same as in female. Mesoscutum from coarsely deeply reticulate to smooth (in *H. squalicephala* n. sp.); scutellum and axillae from reticulate to smooth. Axillae meeting at inner corners, usually slightly rising above scutellum (in *H. squalicephala* n. sp., axillae fused with scutellum). Metanotum laterally of dorsellum, and propodeum dorsally irregularly carinate. Forewing (Fig. 37) hyaline to extremely slightly infuscate in basal part. Marginal vein punctiform to about 1.5× longer than broad; postmarginal vein up to 1.5× longer than stigmal vein; stigmal vein straight to slightly curved toward anterior wing margin. Legs normal. **Metasoma** about as long as broad. Cerci situated slightly closer to base, or closer to apex of metasoma. Terga II to IV with shallow, transverse, reticulate or coriaceous sculpture.

*Comments.*—*H. marticephala* n. sp. differs from all other *Hambletonia* species in several aspects. Its head has a more complex shape because the frontovertex is produced dorsally between the eyes into a large prominence, slightly subdivided medially in two parts by frontal and occipital depressions and by a weak dorsal depression (Figs. 4–6, 19); head length is only 0.41–0.47× its height, and 0.36–0.38× its width. The anterior ocellus is located on the frontal surface of the frontovertexal prominence, inside the frontal depression, and is positioned vertically; the posterior ocelli are positioned horizontally on the dorsal surface of the prominence (Figs. 4, 5). The anterior margin of the frontovertex

is slightly concave (Figs. 5). The facial depression is shallow, the carina separating it from the frontovertex is sharp only medially and has rounded margins laterally (Fig. 4). Antennae (Figs. 25, 26) lack the elongated, thickened setae on the pedicel, and cannot be retracted into the facial depression. The forewings are very narrow, 3.6–4.9× as loang as broad (Fig. 35).

*Biology.*—The host is known only for *H. pseudococcina*, which is a parasitoid of the pineapple mealybug, *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae).

*Distribution.*—Brazil, Argentina, Peru, Ecuador, Colombia, Venezuela, Trinidad, Panama, Costa Rica, Guatemala, Mexico, USA (Florida, native and introduced, Georgia), Hawaii (introduced), Puerto Rico (introduced), Jamaica (introduced), and Taiwan (probably, introduced). All the introductions refer to *H. pseudococcina* (see below).

*Systematic position.*—Since phylogenetic relationships within the family Encyrtidae are poorly understood (Noyes & Hayat, 1994) and are beyond the scope of the present work, we provide here only a brief synopsis of recent placement of the genus *Hambletonia* within the subfamily Tetracneminae by different authors. Trjapitzin and Gordh (1978) and Gordh and Trjapitzin (1979) included *Hambletonia* in the tribe Chrysoplatycerini, subtribe Chrysoplatycerina, according to Trjapitzin's (1973) classification of the Encyrtidae. Later, Noyes and Hayat (1984) suggested that the genus might be more closely related to *Taftia* Ashmead, and transferred *Hambletonia* to the subtribe Taftiina (tribe Chrysoplatycerini), indicating that "in all probability Taftiina should be considered synonymous with Chrysoplatycerina." Trjapitzin (1989) accepted the placement of *Hambletonia* in Taftiina, but retained the subtribe name as valid. Most recently, Noyes and Hayat (1994) modified Trjapitzin's classification, and included all the genera previously placed in Chrysoplatycerini into the tribe Aenasiini, although

they did not formally synonymize the two tribes. Therefore, the placement of the genus *Hambletonia* within the subfamily Tetracneminae remains subjective and unstable. Further study is required to determine phylogenetic relationships between the genera and tribes of Tetracneminae.

In the original description Compere (1936) wrote: "[*Hambletonia*] is most closely related to *Tropidophryne* Compere. It is distinguished from the latter by having the funicle six-jointed instead of four to five jointed; the scape without a dorsal fold; the pedicel is circular in cross section instead of triangular; the marginal vein is almost as long as the postmarginal vein instead of absent; the anterior margin of the head, in dorsal view, is slightly convex instead of concave, etc." In fact, this diagnosis was based on differences between two species, *H. pseudococcina* and *T. africana* Compere, at that time the only known representatives of the respective genera. Analysis of these structures in other species of *Hambletonia* and *Tropidophryne* has shown that some of them are subject of intraspecific and individual variation. Thus, the number of funicular segments can be different in different species of both genera, and also can vary within a single species of either genus (e. g., *H. marticephala* n. sp., Figs. 25, 26). This phenomenon was originally observed by Kerrich (1978) in *T. natalensis* Compere. In *H. marticephala* n. sp., even left and right antennae of the same specimen can have different number of funicular segments. The anterior margin of the head (frontovertex) can be convex, straight, or concave in different species of *Hambletonia* (Figs. 2, 5, 8, 11, 14, 17). The marginal vein, although always present in *Hambletonia*, can be very short and inconspicuous. The only character from among those listed by Compere (1936) that appears to be reliable for separating *Hambletonia* from *Tropidophryne* is the shape of the antennal scape and pedicel. We stud-

ied the holotype and two paratypes of *T. africana*, the type species of *Tropidophryne*, and found additional characters that can be used to differentiate the two genera. The costal cell in *Hambletonia* is gradually narrowed toward its distal end, which is pointed, while in *Tropidophryne* the costal cell is about equally broad along its entire length, and its distal end is truncate, forming an incision on the anterior margin of the wing, as shown in Compere's (1931) drawing. The stigmal vein in *Tropidophryne* is without stigma, narrowed at the apex, strongly curved toward the anterior wing margin, and at least as long as ¼ the submarginal vein. In *Hambletonia* the stigma is present (although sometimes can be weakly expressed), stigmal vein is straight or only slightly curved toward the wing margin, and less than ⅙ as long as the submarginal vein. The reticulate sculpture of the head, mesosoma and metasoma is much deeper in *Tropidophryne* than in *Hambletonia*, and is also present on the mesopleuron (at least anteriorly) and all metasomal terga. The pubescence of the mesoscutum, axillae and scutellum in *Tropidophryne* is very inconspicuous, and consists of very short appressed translucent hairs, compared to longer, semiappressed to semierect, often brown hairs in *Hambletonia*.

At present it appears that *Hambletonia* is most closely related to an undescribed genus from Brazil, a single specimen of which we found among *Hambletonia* material from the UCRC. The specimen bears a label "ex *Pseudococcus* sp. # 15, Saõ Paolo, Brasil, Aug. 1935, Hambleton," and an identification label "*Hambletonia* n. sp." in Compere's handwriting. Analysis of its features has shown that it does not belong to *Hambletonia*, and apparently represents a new genus. It displays mixed characters of *Hambletonia* (sculpture and pubescence) and *Tropidophryne* (shape of the antennal scape and pedicel, wing venation, and shape of the costal cell of the forewing), differing from both genera by the lateral

position of the propodeal spiracles, which are situated dorsally in both *Hambletonia* and *Tropidophryne*. Insufficient material and the poor condition of the specimen do not allow for a description of a new genus at this time.

## KEY TO SPECIES OF *HAMBLETONIA* BASED ON FEMALES

1.  Frontovertex between eyes forming characteristic bilobed vertical prominence, slightly overhanging interior eye orbits (Figs. 4–6, 19); anterior ocellus situated vertically on frontal side of prominence in its median depression, posterior ocelli situated horizontally on dorsal side of prominence (Figs. 4, 5); pedicel without tuft of elongated hairs on dorsal side (Figs. 25, 26); forewing very narrow, length 3.6–4.9× maximum width (Fig. 35) .......................................................................... *H. marticephala* n. sp.
–   Frontovertex without prominence; anterior and posterior ocelli situated in same plane (Figs. 2, 8, 11, 14, 17); pedicel with tuft of elongated hairs on dorsal side (Figs. 21, 24, 27–32); forewing length 2–2.5× maximum width ................................................. 2

2 (1).  Frontovertex with distinct, conspicuous, rather dense punctures, which can be relatively large (Figs. 1, 2) or small (Figs. 10, 11) ........................................................ 3
–   Frontovertex without punctures, or at most with scattered small inconspicuous punctures (Figs. 7–9, 13, 14, 16, 17) ........................................................................ 4

3 (2).  Mid tibia flattened laterally, undulate dorsally; hind tibia carinate dorsally (Fig. 43); punctures on frontovertex relatively small and deep (Fig. 10, 11); anterior edge of frontovertex (occipital plane oriented vertically) slightly concave (Fig. 11); basal cell of forewing almost hairless, with only few long setae (Fig. 39); funicle 6-segmented (Fig. 31) ...................................................................................... *H. undulitibiae* n. sp.
–   Mid and hind tibiae rounded dorsally, without undulation or carina (Fig.33); punctures on frontovertex large and shallow (although small punctures also present) (Fig. 1, 2); anterior edge of frontovertex (occipital plane oriented vertically) convex (Fig. 2); basal cell of forewing with numerous setae (as in Fig. 34, 36); funicle 4-segmented (Fig. 27) ...................................................................................... *H. punctifrons* n. sp.

4 (2).  Frontovertex and eyes completely hairless, or with extremely minute hairs visible only at higher magnification when viewed and illuminated at certain angle (Figs. 8, 13, 14) ..................................................................................................... 5
–   Frontovertex and eyes with distinct, conspicuous setae (Figs. 7, 9, 16–18) ............ 7

5 (4).  Basal part of forewing naked or with single seta (Fig. 40) ............. *H. roseni* n. sp.
–   Basal part of forewing with numerous setae (Fig. 38) .......................................... 6

6 (5).  Anterior edge of frontovertex in dorsal view (occipital plane oriented vertically) distinctly convex (Fig. 14); frontovertex and eyes completely naked (at most few very short hairs are present behind posterior ocelli); costal cell of forewing with several rows of setae dorsally (Fig. 38) .................................... *H. pseudococcina* Compere
–   Anterior edge of frontovertex in dorsal view (occipital plane oriented vertically) straight (Figs. 8); frontovertex and eyes with extremely minute translucent hairs that can be observed only at higher magnification, when viewed and illuminated at certain angle; costal cell of forewing with only one row of setae dorsally (Fig. 34) .. *H. calvifrons* n. sp.

7 (4).  Eyes relatively small, maximum diameter less than ½ head length (dorsal view) (Fig. 17); funicle 5-segmented (Fig. 24) ........................................ *H. squalicephala* n. sp.
–   Eyes relatively large, maximum diameter more than ¾ head length (dorsal view) (as in Fig. 14); funicle 6-segmented (Figs. 21, 30) ........................................................ 8

8 (7).  Antennal club basally brownish yellow, same color as funicle, remainder of club dark brown to black; length 1.0–1.2× maximum width; scape yellow to brownish yellow, with dark brown flange (Fig. 21); anterior edge of frontovertex (frontovertex oriented horizontally) slightly convex, maximally protruding forward in middle, between sub-

ocular sulci; posterior ocelli situated closer to occipital margin that to eyes . . . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **H. pilosifrons** n. sp.

－ Antennal club completely black; length 1.4–1.5× maximum width; scape dark brown
to black (Fig. 30); anterior edge of frontovertex (frontovertex oriented horizontally)
almost straight, slightly protruding forward laterally of subocular sulci; posterior ocelli
situated closer to eyes than to occipital margin . . . . . . . . . . . . . . . . . **H. setosifrons** n. sp.

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### *Hambletonia calvifrons* Sharkov & Woolley, new species
### (Figs. 8, 28, 34)

*Female* (holotype).—Body length 1.75 mm.

*Relative measurements.*—**Head** width 1.9× length and 1.23× height (66.5:35.5: 54); frontovertex width at level of anterior ocellus 0.71× its length, 0.44× width of head (29.5:41.5:66.5); ocelli in obtuse triangle, with angle at anterior ocellus of 113°; POL:OOL:LOL:OCL = 19:3:10.5:2.5; OOL 0.67× diameter of posterior ocellus (3:4.5); distance between antennal toruli twice distance between torulus and mouth margin, 0.66× mouth width (15:7.5:23); eye maximum diameter 1.36× minimum diameter (36:26.5); posterior orbit of eye reaching occipital margin (dorsal view); antenna as in Fig. 28; scape strongly broadened and flattened, length 1.96× maximum width (23.5:12); funicle 6-segmented. **Mesosoma** length 1.35× width (77:57); mesoscutum length 0.52× width (29.5:57); scutellum length 1.03× width (32.5:31.5); mid tibial spur 0.88× as long as mid basitarsus, 0.3× as long as mid tibia (15:17:50); forewing length 2.31× maximum width (120:52); venation and setation as in Fig. 34. **Metasoma** length 1.06× width (72:68); distance from cerci to base of metasoma 0.8× corresponding distance to apex of metasoma (32:40).

*Color.*—**Head** orange yellow; frontovertex at certain illumination with very slight pink, purple, and green metallic luster; antenna (Fig. 28) with radicle, scape, pedicel and funicle orange yellow, clava orange to brownish yellow in basal ⅓ or so, brown in apical ⅔ or so, with whitish-yellow truncation. **Mesosoma** orange yellow; tegulae translucent, slightly brownish yellow; forewing with very weak infuscation in basal ⅓ or so, very slightly stronger infuscation in area outlining distal margin of basal cell, and almost inconspicuous infuscation anteriorly in apical part of wing beyond postmarginal vein (Fig. 34); all legs yellow. **Metasoma** yellow to orange yellow.

*Sculpture and pubescence.*—**Head:** frontovertex (Fig. 8) very slightly convex, almost flat, smooth, matt, with extremely small translucent hairs, visible only at certain angle and illumination, and with a row of sparse, very short brownish hairs along edge of facial depression laterally, below lower orbit of eye; vertex between and behind posterior ocelli shallowly, minutely transversely coriaceous; anterior edge of frontovertex (dorsal view) almost straight (Fig. 8); face smooth, hairless, except for short translucent yellowish hairs on interantennal prominence and clypeus; eyes with extremely short translucent hairs; gena smooth, with very few scattered brownish hairs; posterior margin of gena carinate. **Mesosoma:** mesoscutum with extremely shallow, almost inconspicuous, minute isodiametric reticulation and scattered small punctures; axillae and scutellum smooth, with very few scattered small punctures; pronotum, mesoscutum, axillae and scutellum with semiappressed to semierect brown hairs; mesopleuron glabrous; metanotum laterally of dorsellum irregularly carinate; propodeum dorsally with short longitudinal carinae, laterally smooth, with irregular impressions in upper half, and few short, slightly

curved hairs dorsolaterally. **Metasoma** almost smooth, with extremely shallow, almost inconspicuous, transverse coriaceous sculpture on dorsal surface of tergum II; pubescence consisting of few brown hairs on lateral part of terga IV–VI and along posterior edge of terga V–VII, and more numerous, and slightly longer hairs on syntergum VIII.

*Male.*—Unknown.

*Hosts and Biology.*— Unknown.

*Material examined.*—Holotype ♀: COSTA RICA: Heredia, OTS—La Selva, 75 m, 10°26′N 84°01′W, xii.1993, (ALAS) (left antenna and left wings in microslide # OSU-0020) (BMNH).

*Distribution.*—Costa Rica.

*Etymology.*—The name reflects the bold appearance of the frontovertex (from the Latin words *calvus*, bold, and *frons*).

*Diagnosis.*—From *H. pseudococcina* differs by the presence of minute hairs on the frontovertex and eyes, almost straight anterior edge of the frontovertex (Fig. 8), and the slightly more elongated and light colored scape, which is maximally broadened in distal half (Fig. 28) (in *H. pseudococcina* the scape is dark colored and maximally broadened in the middle part (Fig. 32)).

### *Hambletonia marticephala* Sharkov & Woolley, new species
(Figs. 4–6, 19, 25, 26, 35)

*Female* (holotype measurements in parentheses).—Body length 1.49–1.72 (1.67) mm.

*Relative measurements.*—**Head** width 2.6–2.77× length, 1.14–1.22× height (66.5:24:54.5); frontovertex width at level of anterior ocellus 1.18–1.25× its minimum width, 0.53–0.61× width of head (39:33:66.5); ocelli in obtuse triangle, with angle at anterior ocellus of 95°–116° (102°); POL:LOL:OCL = 19:12:10 (in holotype); OOL cannot be measured, because of shape of frontovertexal prominence (Figs. 4, 5); diameter of posterior ocellus 3–3.5 (3.5); distance between antennal toruli 0.71–0.79× distance between torulus and eye orbit, 1.65–1.92× distance between torulus and mouth margin (13.5:19:8); malar space 1.12–1.25× mouth width, 1.76–2.12× height of eye (frontal view) (30:24:17); eye maximum diameter 1.38–1.41× minimum diameter (23.5:17); posterior orbit of eye reaching occipital margin (dorsal view) (Fig. 5); length of eye (dorsal view) 16–19 (19); antenna as in Figs. 25, 26; scape moderately broadened and flattened, length 2.4–2.88× maximum width (25.5:10); number of funicular segments varies from 4 to 6, and can be different in left and right antennae; sometimes funicular segments are only partly fused together on one side, and remain separated on other side (Fig. 26). **Mesosoma** length 1.13–1.23× width (64:52); mesoscutum length 0.48–0.52× width (25:52); scutellum length 0.79–0.87× width (29:33); mid tibial spur 0.63–0.86× as long as mid basitarsus, 0.15–0.19× as long as mid tibia (8.5:11.5:50); forewing length 3.58–4.86× maximum width (122:33); venation, setation and shape as in Fig. 35. **Metasoma** length 1.28–1.44× width (77:53.5); distance from cerci to base of metasoma 1.41–1.48× corresponding distance to apex of metasoma (45:32).

*Color.*—**Head:** frontovertex brownish yellow to yellowish light brown, slightly lighter on dorsal part of frontovertexal prominence; face brownish yellow, slightly darker in lower part; gena yellow in upper part (near eye orbit), yellowish light brown in lower part; occiput yellow above occipital foramen, yellowish brown below it; antenna (Figs. 25, 26) yellow, with dark brown clava, except for its basal ⅓ or so, which is same color as funicle. **Mesosoma:** pronotum with brownish yellow collar, and light brown collum; mesoscutum with yellow area anteriorly in middle, outlined by diffuse brown band, light brown posteriorly; scutellum and axillae yellowish light brown, with inner corner of axilla yellow; mesopleuron brown, lighter anteriorly and posteriorly; forewing with light diffuse brownish infuscation, slightly more expressed in basal part (Fig. 35); legs yellow to brownish yellow; metanotum
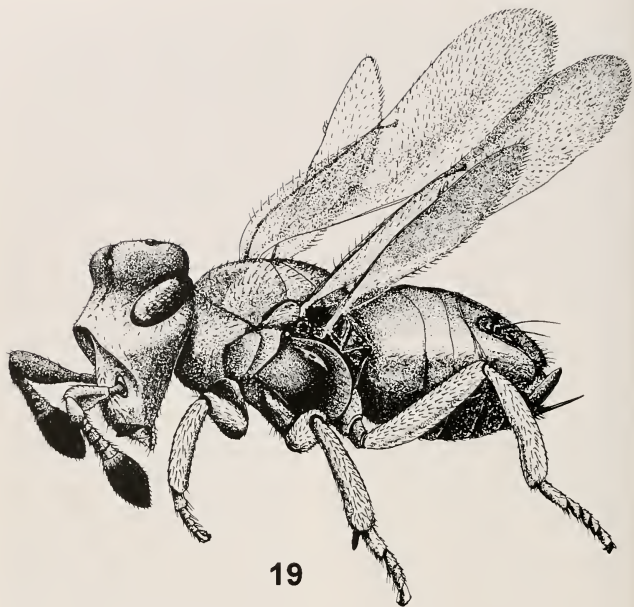
Fig. 19. *Hambletonia marticephala,* female habitus.

and propodeum yellowish light brown. **Metasoma** yellowish light brown dorsally, brownish yellow laterally and ventrally.

*Sculpture and pubescence.*—**Head** (Figs. 4–6): frontovertex forming characteristic prominence, arising vertically between eyes, subdivided in middle by frontal and occipital depressions, and weak dorsal depression (Figs. 4, 5), smooth, glossy, with scattered minute, erect, translucent hairs on its frontal part, and with very slightly longer and denser, translucent brownish hairs on dorsal part of frontovertexal prominence; anterior margin of frontov-

ertex concave (Fig. 5); occipital surface of frontovertexal prominence strongly concave; anterior ocellus positioned vertically in frontal depression on frontal surface of frontovertexal prominence; posterior ocelli positioned horizontally on dorsal surface of prominence (Figs. 4, 5); face smooth, facial depression with upper margin carinate only in middle, rounded laterally, with semierect minute hairs on rounded part of margin; interantennal prominence with vertical rows of semiappressed, minute, translucent brownish hairs; eyes with minute, inconspicuous translucent hairs;

gena smooth, with scattered minute trans-
lucent hairs; posterior margin of gena
rounded; antennal pedicel without tuft of
longer hairs on dorsal side (Fig. 25, 26).
**Mesosoma:** pronotum, mesoscutum, axil-
lae and scutellum smooth, with suberect,
thin, translucent hairs, hairs slightly lon-
ger and slightly curved in posterior part
of scutellum; mesoscutum with very few
scattered small punctures; mesopleuron
glabrous; legs with translucent hairs; tibi-
ae of all legs very slightly curved; meta-
notum laterally of dorsellum with low,
oblique carinae; propodeum with several
irregular carinae in callar and plical
regions. **Metasoma** with terga II–V ex-
tremely shallowly transversely reticulate,
almost smooth, shiny, terga VI–VIII
smooth; pubescence consisting of very few
minute hairs on lateral part of terga II–VI,
on posterior margin of terga VI and VII,
and slightly longer hairs on syntergum
VIII, especially in its posterior part.

*Male.*—Unknown.

*Hosts and Biology.*—Unknown.

*Material examined.*—*Holotype* ♀: USA:
31°40.9′N 81°08.8′W, Georgia, Liberty Co., St. Cath-
erines Isl., 6–10.iv.1995, yellow pan traps (A. Shar-
kov) (OSUC). *Paratypes:* same data, 7 ♀ (left antenna
and left wings of 2 ♀ in microslides # OSU-0017 and
# OSU-0018); same data, 30.iv–4.x.1995, white pan
traps, 1 ♀; same data, light-blue pan traps, 1 ♀; same
data, blue-green pan traps, 1 ♀; Florida, Gainesville,
24–30.iv.1986 (J. LaSalle), 1 ♀. (OSUC, BMNH,
TAMU).

*Distribution.*—USA (Georgia, Florida).

*Etymology.*—Dr. J. LaSalle, who collect-
ed the first specimen of this species, hu-
morously labelled it "Hammerheadencyr-
tus". We retain this name in the Latinized
form (from the Latin words *martus*, the
hammer, and *cephalon*, the head).

*Diagnosis.*—From all other species of
*Hambletonia* differs by the very peculiar
shape of the head, with a characteristic
frontovertexal prominence (Figs. 4–6), by
the absence of the tuft of hairs on the ped-
icel (Figs. 25, 26), and by the very narrow
forewings (Fig. 35).

## *Hambletonia pilosifrons* Sharkov & Woolley, new species
### (Figs. 7, 21, 22, 36, 37)

*Female* (holotype measurements in pa-
rentheses).—Body length 1.58–2.06 (1.92)
mm.

*Relative measurements.*—**Head** width
1.6–1.76× length, 1.17–1.21× height (75.5:
43:63); frontovertex width at level of an-
terior ocellus 0.62–0.67× its length, 0.5–
0.54× width of head (41:61:75.5); ocelli in
obtuse triangle, with angle at anterior
ocellus of 125°–134° (133°); POL:OOL:OCL:
OCL = 23.5:7:11.5:5 (in holotype); OOL
1.44–1.67× diameter of posterior ocellus
(7:4.5); distance between antennal toruli
2.58× distance between torulus and
mouth margin, 0.44× mouth width (15.5:
6:35—in paratype); eye maximum diame-
ter 1.56–1.63× minimum diameter (41:
25.5); posterior orbit of eye almost reach-
ing occipital margin (dorsal view); temple
very short (1.5); antenna as in Fig. 21;
scape strongly broadened and flattened,
length 1.42–1.72× maximum width (21.5:
12.5); funicle 6-segmented. **Mesosoma**
length 1.11–1.18× width (70:63); mesos-
cutum length 0.5–0.53× width (31.5:63);
scutellum length 0.83–0.88× width (31:
37.5); mid tibial spur 0.8–1.0× as long as
mid basitarsus, 0.26–0.29× as long as mid
tibia (14:14:50); forewing length 1.98–
2.18× maximum width (128:59); venation
and setation as in Fig. 36. **Metasoma**
length 1.15× width (85:74); distance from
cerci to base of metasoma 1.45–1.57× cor-
responding distance to apex of metasoma
(52.5:33.5).

*Color.*—**Head:** frontovertex yellowish to
brownish orange, slightly darker posteri-
orly at occipital margin, at certain illumi-
nation with pink, purple, and, sometimes,
blue and green metallic luster; face yellow;
gena and occiput yellowish to brownish
orange; antenna (Fig. 21) with radicle yel-
low, scape yellow to brownish yellow,
with dark brown flange, especially on its
inner surface and edge, pedicel and funi-

cle yellow to brownish yellow, clava very dark brown to black, except for its base, which is same color as funicle. **Mesosoma:** pronotum dorsally, mesoscutum, scutellum and axillae orange brown to dark brown, anterolateral corners of mesoscutum lighter; forewing with diffuse brownish infuscation, darker in basal part (Fig. 36); sides and ventrum brownish orange yellow; all legs yellow; metanotum and propodeum brownish orange yellow. **Metasoma** yellowish light brown dorsally, and brownish yellow laterally and ventrally.

*Sculpture and pubescence.*—**Head** (Fig. 7): frontovertex convex, smooth, matt, with scattered small setiferous punctures, and erect brownish hairs, with row of hairs along inner eye orbit; vertex between posterior ocelli with transverse coriaceous sculpture; anterior edge of frontovertex (dorsal view) convex; face smooth, its lower margin and clypeus with short brownish hairs; eyes with translucent hairs; gena smooth, with semierect brown hairs (scattered in middle part, and forming short rows along eye orbit and lower margin of gena); posterior margin of gena more or less rounded, with very low carina separating it from occiput. **Mesosoma:** lateral part of pronotum and prepectus slightly longitudinally reticulate; mesoscutum very shallowly, slightly transversely reticulate, with scattered small punctures; axillae and scutellum smooth, with very few scattered punctures; mesoscutum with semiappressed to semierect brown hairs; scutellum with semierect to erect brown hairs; mesopleuron glabrous; metanotum laterally of dorsellum with irregular longitudinal and oblique carinae; propodeum reticulate laterally in upper part, with carinate callar region, and longitudinally carinate plical region. **Metasoma** with tergum II (first visible) very shallowly, transversely coriaceous to reticulate, shiny, terga III–VIII almost smooth; pubescence consisting of brown hairs on lateral part of all terga, on posterior edge of terga VI

and VII, and longer brown hairs on syntergum VIII.

*Male.*—Body length 1.06–1.57 mm.

*Relative measurements.*—**Head** width about twice length, about 1.2× height; frontovertex width at level of anterior ocellus slightly less to equal to its length, 0.4–0.5× width of head; ocelli in almost right to slightly obtuse triangle, with angle at anterior ocellus of 92°–101°; POL:OOL: LOL:OCL = 12:2:7:2; OOL 0.3–0.4× diameter of posterior ocellus; distance between antennal toruli about 3.5× distance between torulus and mouth margin, 0.6× mouth width; eye maximum diameter 1.2× minimum diameter; posterior orbit of eye almost reaching occipital margin (dorsal view); antenna as in Fig. 22. **Mesosoma** length about equal width; mesoscutum length about 0.5× width; scutellum length about 0.7× width; mid tibial spur 0.9× as long as mid basitarsus, about 0.25× as long as mid tibia; forewing length twice maximum width; venation and setation as in Fig. 37. **Metasoma** length 1.1× width; distance from cerci to base of metasoma 1.2× corresponding distance to apex of metasoma.

*Color.*—**Head:** frontovertex black; face very dark brown, almost black; occiput black; antenna (Fig. 22) with radicle and scape yellow to brownish yellow, pedicel, funicle, and clava light brown to brown. **Mesosoma:** pronotum dorsally, mesoscutum, scutellum and axillae black; pronotum laterally, prepectus, and mesopleuron very dark brown; tegula very dark brown, almost black; forewing hyaline, or with very light diffuse brownish infuscation in basal part (Fig. 37); all legs with coxae very dark brown, femora, tibiae and tarsi yellowish light brown to yellowish brown, with slightly darker base of femora; metanotum and propodeum very dark brown. **Metasoma** brown to dark brown.

*Sculpture and pubescence.*—**Head:** frontovertex almost flat, with anterior edge slightly concave, minutely superficially reticulate, with numerous piliferous punc-

tures and translucent brownish semierect to erect hairs, some hairs directed anteriorly and some posteriorly; face with extremely shallow reticulation, appears smooth; interantennal prominence with light brown hairs; eyes with rather dense translucent hairs; gena finely reticulate, with scattered piliferous punctures and semierect brownish hairs. **Mesosoma:** pronotum dorsally, mesoscutum, axillae and scutellum coarsely minutely reticulate, with piliferous punctures and semiappressed to erect brown hairs; pronotum laterally and prepectus reticulate; mesopleuron smooth, with slightly coriaceous area in lower part in middle; metanotum laterally of dorsellum with few irregular oblique carinae; propodeum reticulate laterally in upper part, with few carinae in callar region behind spiracle, and longitudinally carinate plical region. **Metasoma** with terga II–IV very shallowly transversely reticulate, shiny, terga III–VIII almost smooth; pubescence consisting of one transversal row of appressed brown hairs on terga II–V, which is interrupted in middle ½ on terga II and III, in middle ⅓ on tergum IV, and in middle ¼ on tergum V, two rows of hairs on terga VI and VII, and several irregular rows of longer, light brown hairs on syntergum VIII.

*Hosts and Biology.*—Unknown.

*Material examined.*—*Holotype* ♀: COSTA RICA: Heredia, La Selva BS, 50 m, ii.1991, MT/YPT (J.S. Noyes) (INBio). *Paratypes:* same data, 4 ♀ (on 3 pins) (left antenna and left wings of 1 ♀ in microslide # OSU-0016), 1 ♂; same location, 22.i–3.ii.1991, MT/YPT (J.S. Noyes), 1 ♀, 1 ♂; 10°26'N 84°01'W, Prov. Heredia, F. La Selva, 3 km S Puerto Viejo, 29.iii.1987 (H.A. Hespenheide), 1 ♂; same location, 27.iii.1988 (H.A. Hespenheide), 1 ♂; same location, 5–8.iii.1984, malaise trap (S.A. Cameron), 1 ♀; same location, 100 m, ii–iii.1993 (P. Hanson), 3 ♀, 1 ♂; same location, viii.1992 (P. Hanson, C. Godoy), 1 ♂; Heredia, 10 km W Puerto Viejo, La Selva Verde, 3.iii.1991 (A.E.H. Howden), BM 1991–85, 1 ♀; 10°26'N 84°01'W, Heredia, OTS-La Selva, 75 m, xii.1993 (ALAS), 1 ♀; Alajuela, Cordiliera, Peñas Blancas, 700 m, rainforest, ix–x.1986 (E. Cruz), BM 1986-154, 3 ♀; Alajuela, San Ramon BS, 900 m, vii–viii.1995 (P. Hanson), 3 ♀; Limon, 16 km W Guapiles, 400 m, viii–ix.1988 (P. Hanson), 1 ♀; Guanacaste, Guanacaste NP, Cacao Est., xi–xii.1990 (P. Hanson), 1 ♀; Guanacaste, SW side Volcan Cacao, Estac. Cacao, 1100 m, 1988–1989, 1 ♀; Guanacaste Pv, Sta. Rosa NP, Hacienda-2-C, 14.ix–15.x.1985 (Janzen & Gauld), 1 ♂; same location, 14.vi–5.vii.1986, 1 ♂; same location, 22.vi–13.vii.1985 (Janzen & Gauld), 1 ♂ (in microslide); same location, Hacienda-1-O, 2–23.iii.1986 (Janzen & Gauld), 2 ♂ (1 in microslide); same location, 20.xii.1986–10.i.1987 (Janzen & Gauld), 1 ♂; same location, Hacienda-3-O, 10–31.i.1987 (Janzen & Gauld), 1 ♀ (in microslide); Guanacaste Pv, Sta. Rosa NP, Sn. Emilio-5-O, 17–24.iv.1985 (Janzen & Gauld), 1 ♂; Guanacaste, Cacao (ACG), 1100 m, 26.I–24.ii.1996, MT/YPT (J.S. Noyes), 5 ♀; Guanacaste, Pitilla (ACG), 700 m, 12–16.ii.1996, MT/YPT (J.S. Noyes), 1 ♀, 1 ♂; San José, San Antonio de Escazu, 1300 m, YPT (L. Masner), 2 ♀; same location, vi.1988 (W. Eberhard), 1 ♀; San José, Ciudad Colon, iv–v.1990 (P. Hanson), 1 ♂; Cartego, Turrialba CATIE, Reventazon, 550 m, 4.ix.1986 (L. Masner) CR-19, BM 1986-330, 2 ♀ [BMNH, University of Costa Rica (San José), OSUC]. *Additional material:* GUATEMALA, Nov. 1932 (W. Carter), 5 ♀, 4 ♂ (UCRC).

*Comments.*—Five females and four males from Guatemala were identified as *H. pilosifrons* n. sp. but were not included in the type series because of their poor condition.

*Distribution.*—Costa Rica, Guatemala.

*Etymology.*—The name reflects the presence of setae on the frontovertex.

*Diagnosis.*—Very close to *H. pseudococcina*, from which differs by the presence of setae on the frontovertex and eyes (Fig. 7).

### *Hambletonia pseudococcina* Compere
### (Figs. 13–15, 20, 32, 38)

*Hambletonia pseudococcina* Compere 1936: 173–174.

*Distribution.*—Brazil, Colombia, Venezuela. Introduced to Hawaii (from Brazil and Venezuela), Puerto Rico (from Brazil, via Hawaii), Jamaica (from Hawaii), and USA (Florida) (from Puerto Rico). The species was also reported from Argentina, Trinidad, Antilles (De Santis, 1979), Mexico (Trjapitzin & Ruiz-Cancino, 1995), and Taiwan (probably, intorduced) (Tachikawa, 1980).

*Hosts and biology.*—A parasitoid of the pineapple mealybug *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae).
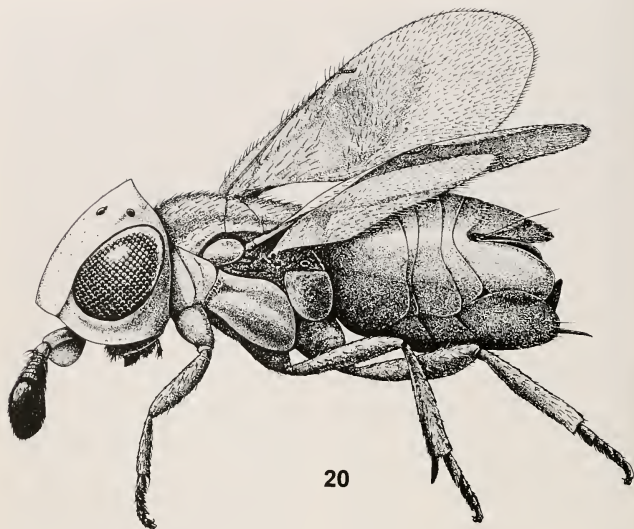
**20**

Fig. 20. *Hambletonia pseudococcina*, female habitus.

Occurs as a bisexual race in Brazil, and as a unisexual race in Colombia and Venezuela, with the males/females ratio in the latter race of about 1:200, and males being unnecessary for reproduction (Bartlett, 1978).

*Economical importance.*—Was used for biological control of the pineapple mealybug. The species had established in Florida, Hawaii, and Puerto Rico, and in Hawaii was found to be a relatively successful control agent of *D. brevipes* (Bartlett, 1978).

*Material examined.*—Holotype ♀: BRASIL: São Paulo, Araras, ex *Pseudococcus brevipes* on pineapple, July 10,1935 (Edson Hambleton) (USNM) (the head of the holotype is missing). *Paratypes*: same data, 2 ♀ and 2 ♂ (1 ♂ labelled "Allotype") (USNM). *Additional material*: same location, 25.ix.1935 (Edson Hambleton), 7 ♀ 3 ♂; RO Fazenda, Rancho Grande, 62 km

S. Ariquemes, 10°32′S 62°48′W, 12–22.xi.1991 (E.M. Fischer), 1 ♀; same location 2.xii.1991 (S.L. Heydon), 1 ♀; same location, goat pasture sweep, 27.xi.1991 (S.L. Heydon), 1 ♀; 14°17.2′S 48°55.5′W, Goiás, Uruaçu, Serra da Mesa Survey, 21–30.v.1996, yellow pan traps, 2 ♀; TRINIDAD: B.W.I., *P. brevipes* on pineapple, v.1953 (Bennett No. 30), 6 ♀; "From F.J. Simmonds, Trinidad to D. Lloyd, Fontana, Jan.15, 53", 4 ♀; B.W.I., 18.vi.1950, ex *Pseudococcus brevipes*, (Wash. EQ # B-5521) (W.B.Wood coll.), 4 ♀; PUERTO RICO: Lajas, ex *Pseudococcus brevipes* on pineapple, 1.vi.1949 (H.K. Plank), 4 ♀; Palmareja, 1.vi.1949 (W. Gaud), 3 ♀; 6.vii.1943 (Lot #1), ~5 ♀ in gelatin capsule; vii.1943 (Lot #2), 60+ ♀ in 2 gelatin capsules; COLOMBIA: Caqueta, I.1936 (E.G. Salas), 3 ♀; Coqueta region, ex *Pseudococcus* on pineapple (E. Garcia Salas), 1 ♀ (36–4471, vial #2); B.W.I.C.R.S. Expedition (D.J. Taylor), 6 ♀; 12°50′S 69°20′W Madre de Dios, Rio Tambopata Res., 1–13.xi.1983 (N.E.Stork), 1 ♀; Cuzco Quillambamba, 24–26.xii.1983 (L. Huggert), 2 ♀ (B.M. 1984-337); Junin Satipo, 24.i.1984 (L. Huggert), 1 ♀ (B.M. 1984-337); ECUADOR: Napo Misahualli,

20.ii.1983 (L. Huggert), 1 ♀ (B.M. 1984-337); Rio Pal-
enque, forest, 4.ii.1983 (L. Huggert), 1 ♀; COSTA
RICA: Puntarenas, R F Golfo Dulce, 24 km W Piedras
Blancas, 200 m, iv–v.1991 (P. Hanson), 1 ♀; DOM-
INICA: W.I. Springfield Plantation, 18–22.vii.1978
(G.C. Steyskal), 1 ♀ (Bredin-Archbold Smithsonian
Bio. Surv. Dominica); St. Paul Parish, Springfield Est.,
505 m, 20–27.xi.1995 (L. Masner), 7 ♀ (B.M. 1995-214);
USA: Florida, Sebring, on pineapple mealybug,
1.vii.1946 (M.R. Osborn), 2 ♀; same location, pine-
apple mealybug, 17.i.1947 (M.R. Osborn), 3 ♀; HA-
WAII: 5.i.1937 (D.T. Fullaway), 22 ♀ (received from
K.A. Bartlett) (P.R. No. 1881); Country unknown, ex
collection of unidentified mealybug on cocoa, Palnura
Valle, Jan. 1953 (D. Taylor), (Bennet coll., vial No. 3),
7 ♀; same data (Bennet coll., vial No. 31), 5 ♀; No
data, 1 ♀ (BMNH, USNM, UCDC, UCRC).

*Diagnosis.*—Close to *H. pilosifrons* n. sp.,
*H. setosifrons* n. sp., *H. roseni* n. sp., and *H.
calvifrons* n. sp. From first two species dif-
fers by the completely naked frontovertex
and eyes (at most few minute hairs can be
present behind the posterior ocelli) (Figs.
13–15, 20). From *H. roseni* n. sp. differs by
the pilose basal cell of the forewing (Fig.
38), and from *H. calvifrons* n. sp. differs by
the convex anterior edge of the frontov-
ertex (Fig. 14) and the presence of several
rows of setae on the dorsal surface of the
costal cell of the forewing (Fig. 38).

### *Hambletonia punctifrons* Sharkov & Woolley, new species
#### (Figs. 1–3, 27, 33)

*Female* (holotype measurements in pa-
rentheses).—Body length 1.42–1.6 (1.6)
mm.

*Relative measurements.*—**Head** width
1.8–1.93× length, 1.24–1.33× height (57:
29.5:43); frontovertex at level of an-
terior ocellus 0.81–0.89× its length, 0.46–
0.49× width of head (28:31.5:57); ocelli in
obtuse triangle, with angle at anterior
ocellus of 111°–154° (128°); POL:OOL:LOL:
OCL = 14:3.5:6.5:1 (in holotype); OOL
0.88–1.14× diameter of posterior ocellus
(3.5:4); distance between antennal toruli
2.08–2.25× distance between torulus and
mouth margin, 0.64–0.71× mouth width
(13.5:6:19); eye oval, maximum diameter
1.27–1.32× minimum diameter (26:20.5);
posterior orbit of eye reaching occipital
margin (dorsal view); antenna as in Fig.
27; scape broadened and flattened, length
2.25–2.29× maximum width (19.5:8.5); fu-
nicle 4-segmented. **Mesosoma** length 1.1–
1.17× width (58.5:53); mesoscutum length
0.47–0.53× width (25:53); Scutellum
length 0.94–0.96× width (30:31); mid tibial
spur 0.95–1.05× as long as mid basitarsus,
0.24–0.27× as long as mid tibia (10:9.5:42);
forewing length 2.11–2.29× maximum
width (110:48). **Metasoma** length 1.19–
1.2× width (70:59); distance from cerci to
base of metasoma 1.15–1.26× correspond-
ing distance to apex of metasoma (37.5:
32.5).

*Color.*—**Head, mesosoma** and **metaso-
ma** brownish orange dorsally, slightly
lighter, yellowish orange to yellow later-
ally and ventrally; frontovertex, when il-
luminated at certain angle, with very
weak purplish or greenish metallic luster;
antenna (Fig. 33) with radicle brownish
yellow, scape brownish orange yellow, its
flange brown in translucent part, pedicel
brown, funicle dark brown, and clava
very dark brown, almost black, with light-
er base and apex; forewing almost hyaline,
or with slight brownish infuscation, es-
pecially in basal ⅓ (similar to *H. pseudo-
coccina*, Fig. 38); legs same color as body;
metasoma dorsally with extremely weak
greenish and purplish metallic shine.

*Sculpture and pubescence.*—**Head** (Figs. 1,
2, 3): frontovertex almost flat, except for
anterior part, which is slightly convex and
raised upwards, with large, shallow,
round to slightly oval punctures, which
are more or less grouped in middle part
of frontovertex between its anterior edge
and anterior ocellus, with few smaller
punctures along eye orbit; surface be-
tween punctures unsculptured, smooth,
with sparse brownish hairs; anterior edge
of frontovertex (dorsal view) slightly con-
vex (Fig. 2); face unsculptured; lower part
of interantennal prominence, and clypeus
with brownish hairs; eyes with short
translucent hairs; gena smooth, with few
scattered translucent hairs. **Mesosoma**:
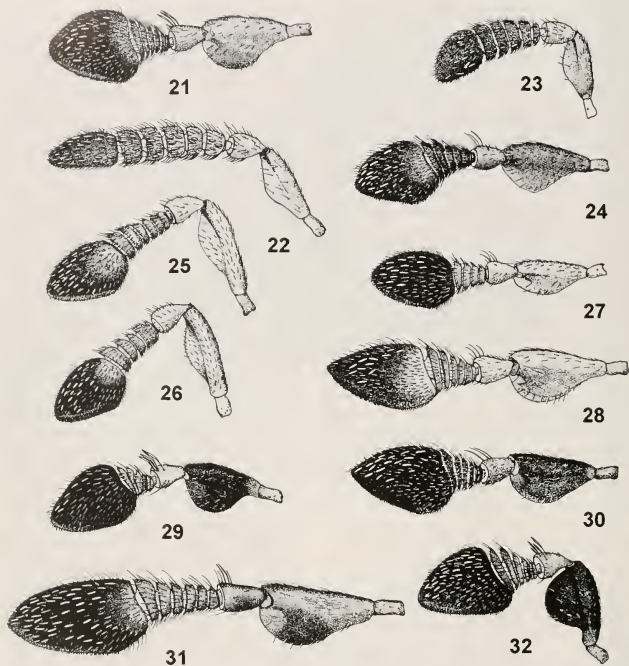
Figs. 21–32. Antennae of *Hambletonia* species. 21, 22. *H. pilosifrons*. 21, female; 22, male. 23, 24. *H. squalicephala*. 23, male; 24, female. 25, 26. *H. marticephala*, females. 27. *H. punctifrons*, female. 28. *H. calvifrons*, female. 29. *H. roseni*, female. 30. *H. setosifrons*, female.
31. *H. undultibiae*, female. 32. *H. pseudococcina*, female.

mesoscutum, axillae and scutellum smooth, with erect brown hairs, with few scattered punctures and one row of punctures along posterior edge of scutellum; prepectus shallowly reticulate; mesopleuron glabrous; forewing setation similar to *H. pseudococcina* and *H. pilosifrons* (Figs. 36, 38); metanotum laterally of dorsellum rugulose; propodeum carinate dorsally, and with rather coarse, irregular sculpture, slightly indicated reticulation, and few short, brown hairs laterally. Metasoma with tergum II (first visible) shallowly coriaceous, shiny, terga III–VIII smooth; posterior edge of terga VI and VII, and anterior part of syntergum VIII with brownish

Fig. 33. *Hambletonia punctifrons*, female habitus.

hairs; posterior part of syntergum VIII with longer hairs, especially so along posterior margin.

*Male.*—Unknown.

*Hosts and Biology.*—Unknown.

*Material examined.*—Holotype ♀: COSTA RICA: Heredia, La Selva BS, 50 m, ii.1991, MT/YPT (J.S. Noyes) (BMNH). *Paratypes:* same data, 2 ♀ (left antenna and left wings of 1 ♀ in microslide # OSU-0012); Heredia, 3 km S Puerto Viejo, OTS-La Selva, 100 m, ii–iii.1993 (P. Hanson), 1 ♀ (BMNH).

*Distribution.*—Costa Rica.

*Etymology.*—The name reflects the presence of large punctures on the frontovertex.

*Diagnosis.*—From *H. pseudococcina* differs by the relatively short, punctate fron-tovertex, and by the presence of hairs on the frontovertex and eyes (Figs. 1–3).

*Hambletonia roseni* Sharkov & Woolley,
new species
(Figs. 29, 40)

*Female* (holotype measurements in parentheses).—Body length 1.4–1.84 (1.84) mm.

*Relative measurements.*—Head width 1.59–1.71× length, 1.11–1.2× height (63.5: 40:57.5); frontovertex width at level of anterior ocellus 0.67–0.73× its length, 0.51–0.54× width of head (33.5:50:63.5); ocelli in obtuse triangle, with angle at anterior ocellus of 96°–116° (112°); POL:OOL:LOL:

**34**



**35**
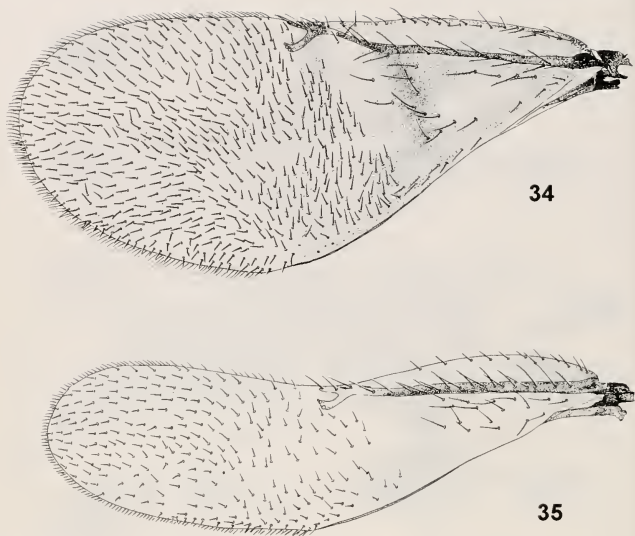
Figs. 34–35.   Forewings of *Hambletonia* species. 34. *H. calvifrons*, female. 35. *H. marticephala*, female.

OCL = 17.5:5:9:3 (in holotype); OOL 1.42–1.71× diameter of posterior ocellus (5:3.5); distance between antennal toruli 2.0–2.6× distance between torulus and mouth margin, 0.6–0.65× mouth width (13:6.5:20); eye oval, maximum diameter 1.5–1.7× minimum diameter (37.5:25); posterior orbit of eye reaching, or almost reaching occipital margin (dorsal view); antenna as in Fig. 29; scape strongly broadened and flattened, length 1.58–1.67× maximum width (20:12); funicle 6-segmented. **Mesosoma** length 1.12–1.23× width (67:60); mesoscutum length 0.46–0.55× width (31:59); scutellum length 0.86–0.94× width (30:35); mid tibial spur slightly shorter or equal to mid basitarsus, 0.28–0.31× as long as mid tibia (12.5:14:45); forewing length 1.96–

2.32× maximum width (120:52); venation and setation as in Fig. 40. **Metasoma** length 1.14–1.2× width (77:64); distance from cerci to base of metasoma 1.32–1.46× corresponding distance to apex of metasoma (45:34).

*Color.*—**Head, mesosoma** and **metasoma** brownish orange dorsally, and slightly lighter, yellowish orange to yellow laterally and ventrally; frontovertex, when illuminated at certain angle, with very weak purple or green metallic luster; antenna (Fig. 29) with radicle brownish yellow, scape dark brown, except its base, pedicel and funicle brownish yellow, clava dark brown, almost black, with lighter apex; axillae and scutellum slightly darker than rest of body (in paratype from Costa
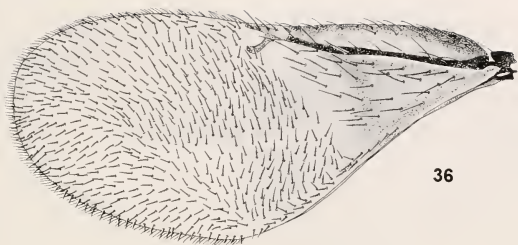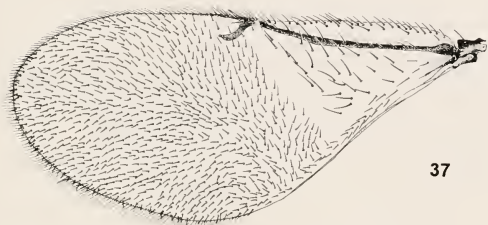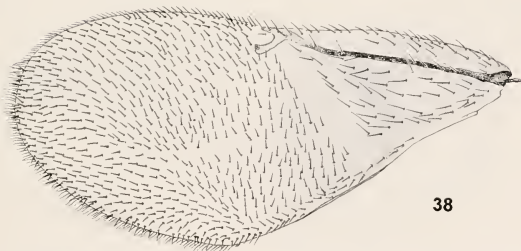
Figs. 36–38. Forewings of *Hambletonia* species. 36, 37. *H. pilosifrons.* 36, female; 37, male 38. *H. pseudococcina,* female.

**39**



**40**



**41**
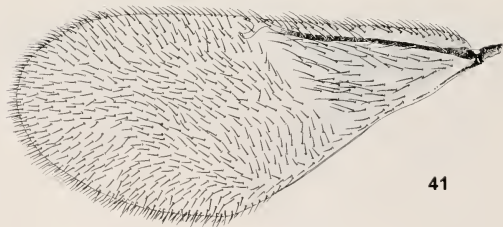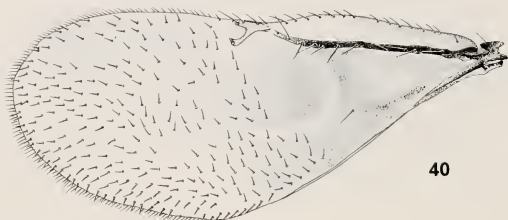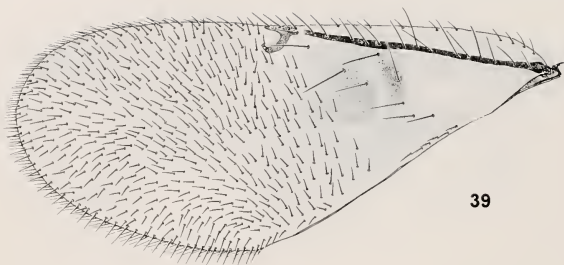
Figs. 39–41. Forewings of *Hambletonia* species. 39. *H. undulitibiae*, female. 40. *H. roseni*, female. 41. *H. squalicephala*, female.

Rica, mesoscutum, except basal ¼ or so, also darker, orange brown, same color as axillae and scutellum); forewing with more or less expressed brownish infuscation, which is stronger in basal half and in anterior part of apical half (Fig. 40); all legs yellow to orange yellow, same color as body, or slightly lighter.

*Sculpture and pubescence.*—Head: frontovertex slightly convex, almost smooth, matt, with scattered minute punctures and very inconspicuous, extremely minute translucent hairs, visible only at higher magnification, at certain angle and illumination; anterior edge of frontovertex (dorsal view) convex; face with short, yellowish to brownish translucent hairs on interantennal prominence, and slightly longer hairs on clypeus; eyes with sparse, extremely minute translucent hairs; gena smooth, with very sparse, extremely minute translucent hairs. Mesosoma: mesoscutum punctulate, with extremely shallow reticulation between punctures, and brownish hairs arising between punctures at angle of about 30° to surface of mesoscutum; axillae and scutellum smooth, with very few scattered punctures, and sparse brownish translucent hairs, similar to hairs on mesoscutum; posterior margin of scutellum with row of deeper punctures; prepectus with reticulate sculpture, which is isodiametric in anterior half, and slightly elongate and shallower in posterior half; mesopleuron glabrous; metanotum laterally of dorsellum irregularly alveolate to rugulose; propodeum dorsally with irregular carinae in callar region and short longitudinal irregular carinae in plical region. Metasoma dorsally almost smooth, except for extremely shallow, transversely reticulate to rugulose sculpture on tergum II (first visible); pubescence consisting of short, scattered, brownish hairs on terga VI and VII and in anterior half of syntergum VIII, and longer brownish hairs in posterior half of syntergum VIII with (especially along its posterior margin).

*Male.*—Unknown.

*Hosts and Biology.*—Unknown.

*Material examined.*—Holotype ♀: PANAMA: Las Cumbres, 1–7.x.1982 (H. Wolda) (BMNH). *Paratypes*: same location, 3–9.xi.1982 (H. Wolda), 1 ♀ (left antenna and left wings in microslide # OSU-0011); Barro Colorado, 20–27.iii.1983 (H. Wolda), 1 ♀; COSTA RICA: Alaj Pv. Fa Sn Gabriel, 600 m, 2 km W Dos Rios, vii.1988 (Gauld & Mitchell), 1 ♀ (BMNH).

*Distribution.*—Panama, Costa Rica.

*Etymology.*—Named after our colleague and friend, the Israeli hymenopterist Dr. David Rosen, who died on January 8, 1997, when this paper was under preparation. Dr. Rosen contributed much to the knowledge of systematics, biology, and practical use of Chalcidoidea.

*Diagnosis.*—Very close to *H. pseudococcina*, from which differs by the almost hairless basal part of the forewing (Fig. 40), and the presence of extremely minute hairs on the frontovertex and eyes.

### *Hambletonia setosifrons* Sharkov & Woolley, new species
(Figs. 9, 30)

*Female* (holotype measurements in parentheses).—Body length 1.78–2.47 (2.25) mm.

*Relative measurements.*—Head width 1.78–1.91× length, 1.12–1.15× height (83: 46.5:74); frontovertex× width at level of anterior ocellus 0.58–0.60× its length, 0.43–0.44× width of head (36.5:63:83); ocelli in obtuse triangle, with angle at anterior ocellus of 113°–114° (114°); POL:OOL:LOL: OCL = 23:3.5:11:7 (in holotype); OOL 0.64–0.82× diameter of posterior ocellus (3.5:5.5); distance between antennal toruli 1.80–1.86× distance between torulus and mouth margin, 0.67–0.77× mouth width (18:10:23.5); eye maximum diameter 1.24–136× minimum diameter (47:35); posterior orbit of eye reaching occipital margin (dorsal view); antenna as in Fig. 30; scape strongly broadened and flattened, length 1.56–1.67× maximum width (27.5:16.5); funicle 6-segmented. Mesosoma length 0.99–1.2× width (77:78); mesoscutum length 0.49–0.55× width (38:77.5); scutellum length 0.88–0.94× width (42:44.5);

mid tibial spur 0.80–0.84× as long as mid basitarsus, 0.27–0.28× as long as mid tibia (17.5:22:64); forewing length 2.13–2.23× maximum width (151.5:68). **Metasoma** length 1.15× width (85:74); distance from cerci to base of metasoma 1.22–1.29× corresponding distance to apex of metasoma (56:46).

*Color.*—**Head:** frontovertex brownish orange, at certain illumination with slight pink or purple metallic luster; face yellow to orange yellow; gena yellow; occiput yellow to orange yellow; antenna (Fig. 30) with radicle yellow, scape black except for yellowish brown base, pedicel and funicle brownish yellow, clava black, with brownish-white truncation. **Mesosoma:** pronotum dorsally, mesoscutum, and axillae brownish orange to orange brown or dark brown, with darker posterior margin of mesoscutum and interior corner of axillae; scutellum brownish orange, slightly darker anteriorly; sides of pronotum brownish yellow; tegulae translucent, slightly brownish; forewing with slight infuscation in basal ⅓ or so, and almost inconspicuous infuscation anteriorly, beyond postmarginal vein (similar to *H. pseudococcina* and *H. pilosifrons* n. sp., Figs. 36, 38); mesopleuron orange brown; all legs yellow, with brownish-yellow coxae; metanotum and propodeum dorsally and laterally brownish yellow to yellowish brown. **Metasoma** yellow to brownish yellow, very slightly darker posteriorly.

*Sculpture and pubescence.*—**Head** (Fig. 9): frontovertex convex, smooth, matt, with erect translucent brownish hairs; vertex between and behind posterior ocelli extremely shallowly minutely transversely reticulate; anterior edge of frontovertex (dorsal view) convex (similar to *H. pseudococcina*, Fig. 14); face smooth, hairless except for translucent brownish hairs on interantennal prominence and longer hairs on clypeus; eyes with translucent hairs; gena smooth, with small piliferous punctures and scattered brownish hairs; posterior margin of gena with low carina

separating it from occiput. **Mesosoma:** pronotum and mesoscutum with extremely shallow, minute, transverse reticulation, and few scattered, minute punctures; axillae and scutellum smooth, with very few scattered minute punctures; pronotum, mesoscutum, axillae and scutellum with semiappressed to semierect brownish hairs; mesopleuron glabrous; forewing venation similar to *H. pseudococcina* and *H. pilosifrons* n. sp. (Figs. 36, 38); metanotum laterally of dorsellum with several oblique and one transverse carinae; propodeum laterally with irregular uneven surface in upper half, dorsally with mainly longitudinal, irregular carinae, with few short, slightly curved hairs dorsolaterally. **Metasoma** smooth, with few short hairs on lateral part of terga IV and V, appressed short hairs on posterior edge of terga VI and VII, and more numerous, longer hairs on syntergum VIII.

*Male.*—Unknown.

*Hosts and Biology.*—Unknown.

*Material examined.*—*Holotype* ♀: COSTA RICA: Puntarenas, RF Golfo Dulce 3 km SW Rincon, 10 m, xi.1992, (P. Hanson) (BMNH). *Paratypes:* Cartago, Turrialba, CATIE, 22.vi.1994 (P. Hanson), 2 ♀ (left antenna and left wings of 1 ♀ in microslide # OSU-0019) (BMNH).

*Distribution.*—Costa Rica.

*Etymology.*—The name reflects the presence of setae on the frontovertex.

*Diagnosis.*—Close to *H. pseudococcina* and *H. pilosifrons* n. sp. From *H. pseudococcina* differs by the presence of hairs on the frontovertex and eyes (Fig. 9), and from *H. pilosifrons* n. sp. differs by more elongated clava, and completely black scape (Fig. 30).

### *Hambletonia squalicephala* Sharkov & Woolley, new species
### (Figs. 16–18, 23, 24, 41, 42)

*Female* (holotype measurements in parentheses).—Body length 1.54–1.55 (1.55) mm.

*Relative measurements.*—**Head** width 1.58–1.65× length, 1.24–1.27× height (64: 40.5:50.5); frontovertex width at level of
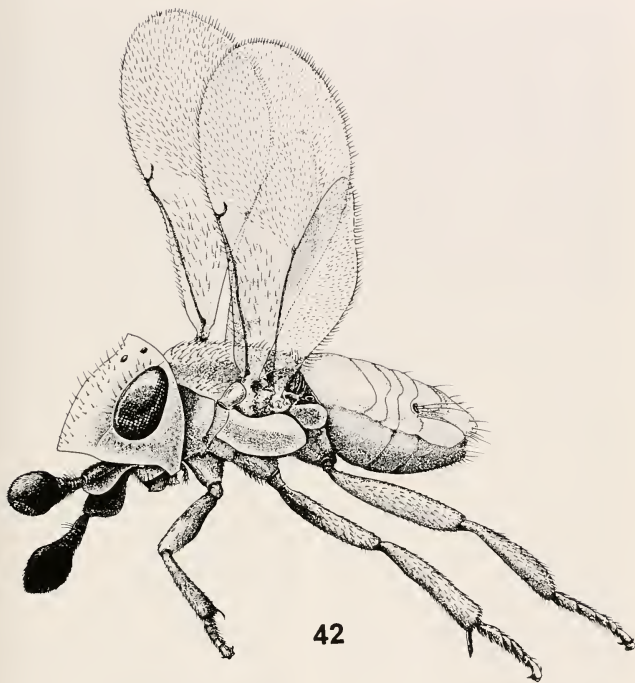
Fig. 42. *Hambletonia squalicephala*, female habitus.

anterior ocellus 0.78–0.79× its length, 0.59–0.6× width of head (38:48:64); ocelli in obtuse triangle, with angle at anterior ocellus of 126°–131° (126°); POL:OOL:LOL: OCL = 17:8.5:8.5:2.5 (in holotype); OOL 2.29–2.43× diameter of posterior ocellus (8.5:3.5); distance between antennal toruli 1.73× distance between torulus and mouth margin, 0.55× mouth width (13: 7.5:23.5); eye maximum diameter 1.57–1.63× minimum diameter (27.5:17.5); pos-

terior orbit of eye almost reaching occipital margin (dorsal view); temple very short (2); antenna as in Fig. 24; scape strongly broadened and flattened, length 1.71–1.74× maximum width (20:11.5); funicle 5-segmented. **Mesosoma** length 1.04–1.09× width (56:54); mesoscutum length 0.43–0.45× width (23:54); scutellum length 0.7–0.73 width (23:33); mid tibial spur 0.96× as long as mid basitarsus, 0.26× as long as mid tibia (12:12.5:45);

forewing length 2.38–2.44× maximum width (122:50); venation and setation as in Fig. 41. **Metasoma** length 1.14–1.24× width (65.5:57.5); distance from cerci to base of metasoma 0.95–1.02× corresponding distance to apex of metasoma (33:32.5).

*Color.*—Head, **mesosoma** and **metasoma** yellowish brown, head slightly lighter than other body parts; frontovertex, when illuminated at certain angle, with light purple and green metallic luster; antenna (Fig. 24) with radicle yellowish brown, same color as face, scape very dark brown, almost black, distal part of its flange slightly lighter, pedicel dark brown, funicle and clava very dark brown, almost black; forewing with diffuse brownish infuscation, which is stronger expressed in basal part (proximad of linea calva) (Fig. 41); legs same color as body, with darker mid tibial spur.

*Sculpture and pubescence.*—**Head** (Figs. 16–18): frontovertex in anterior part almost flat, in posterior part, especially in area of anterior ocellus, slightly concave, with occipital edge slightly raised upwards, smooth, more or less glossy, with minute erect hairs (visible only at certain angle and illumination), and one row of longer erect brownish hairs along each inner eye orbit; anterior edge of frontovertex (dorsal view) convex (Fig. 17); face smooth; lower part of interantennal prominence and clypeus with short translucent hairs; eyes with minute translucent hairs; gena smooth, glossy, with few short brown hairs. **Mesosoma:** pronotum, mesoscutum, axillae and scutellum smooth, glossy, with appressed and semierect brownish hairs; mesoscutum with scattered small punctures, scutellum with few punctures along posterior margin; mesopleuron glabrous, glossy; metanotum laterally of dorsellum with several carinae in posterior part directed from its lateral (outer) margin toward dorsellum; propodeum laterally smooth, with irregular surface, its callar region carinate, and plical region smooth. **Metasoma** dorsally smooth, glossy, with extremely shallow and extremely weakly expressed transversal coriaceous sculpture on tergum II (first visible); terga V–VII with appressed short brownish hairs along posterior edge; syntergum VIII with rather long translucent brownish hairs.

*Male.*—Body length 1.13–1.29 mm.

*Relative measurements* (measurements in parentheses refer to one of the paratypes).—**Head** width 2.02× length, 1.18–1.19× height (49.5:24.5:42); frontovertex width at level of anterior ocellus 1.06× its length, 0.56–0.57× width of head (27.5:26: 49); ocelli in obtuse triangle, with angle at anterior ocellus of 121°–125°; POL:OOL: LOL:OCL = 12.5:5.5:6.5:1.5 (in one paratype); OOL 1.25–1.38× diameter of posterior ocellus (5.5:4); distance between antennal toruli 1.85–2.1× distance between torulus and mouth margin, 0.57–0.58× mouth width (12.5:5.5:215); eye maximum diameter 1.22–1.31× minimum diameter (21:16); posterior orbit of eye almost reaching occipital margin (dorsal view); temple very short (2); antenna as in Fig. 23; scape broadened and flattened, length 2.19–2.54× maximum width (17.5:8). **Mesosoma** length 0.86–1.15× width (56.5:59.5); mesoscutum length 0.37–0.44× width (26: 59.5); scutellum length 0.78–0.79× width (24:30.5); mid tibial spur 0.81–0.86× as long as mid basitarsus, 0.22–0.24× as long as mid tibia (12:12.5:45); forewing length 2.12–2.23× maximum width (107:50.5). **Metasoma** length 0.95–1.1× width (50: 45.5); distance from cerci to base of metasoma 0.7–0.85× corresponding distance to apex of metasoma (23:27).

*Color.*—**Head:** frontovertex very dark brown to almost black, at certain illumination with weakly expressed purplish and bluish metallic luster; face very dark brown, with darker, almost black middle ⅓ above interantennal prominence; gena very dark brown; temples and occiput very dark brown to almost black; antenna (Fig. 23) with radicle light brown, scape light brown to brown, very slightly darker

than radicle, pedicel, funicle and clava brown; mouth parts very light brown to brownish yellow. **Mesosoma:** pronotum dorsally, mesoscutum, axillae and scutellum very dark brown, almost black; sides and ventrum brown to dark brown; forewing almost hyaline, with extremely weak brownish infuscation in basal ⅓ or so; all legs brown, with femora and tibiae gradually becoming light brown toward apex, tarsi very light brown; mid tibial spur dark brown; metanotum and propodeum brown to dark brown. **Metasoma** dark brown to very dark brown dorsally, slightly lighter laterally and ventrally.

*Sculpture and pubescence.*—**Head:** frontovertex almost flat (very slightly convex), with very shallow coriaceous sculpture, almost smooth around anterior ocellus, with numerous semierect brown hairs; face smooth, lower part of interantennal prominence and clypeus with semiappressed light brown hairs; eyes with minute translucent hairs; gena smooth, with few scattered short brown hairs. **Mesosoma:** pronotum dorsally, mesoscutum, axillae and scutellum smooth, with few scattered, small punctures on mesoscutum; scutellum almost flat; axillae fused with scutellum, with traces of sutures slightly indicated laterally by lines of small punctures; pubescence of dorsum consisting of rather dense, semiappressed to semierect, brownish hairs on pronotum, mesoscutum, axillae and scutellum, and erect, longer hairs on apex of scutellum; pronotum laterally shallowly reticulate; prepectus, mesopleuron, and sides of propodeum smooth; metanotum and callar region of propodeum with several irregular carinae. **Metasoma** dorsally with tergum II shallowly transversely reticulate, terga V–VII smooth, with appressed short hairs along their posterior edge; syntergum VIII with longer (especially posteriorly) brown hairs.

*Hosts and Biology.*—Unknown.

*Material examined.*—*Holotype* ♀: COSTA RICA: San Vito, 1500 m, Las Cruces. Wilson Bot. Gdns, 18–22.iii.1990 (J.S. Noyes) (BMNH). *Paratypes:*

same data, 2 ♀ and 2 ♂ (1 ♀ in microslide; left antenna and left wings of second ♀ in microslide # OSU-0014; left antenna and left wings of 1 ♂ in microslide # OSU-0015) (BMNH).

*Distribution.*—Costa Rica.

*Etymology.*—The name reflects the shape of the head, which in lateral view resembles the head of a shark (from the Latin words *squalus*, the shark, and *cephalon*, the head).

*Diagnosis.*—From *H. pseudococcina* differs by the relatively wider and flatter frontovertex, smaller eyes, and the presence of hairs on the frontovertex and eyes (Figs. 16–18). Males differ from all other *Hambletonia* species by the fusion of the axillae and scutellum.

### *Hambletonia undulitibiae* Sharkov & Woolley, new species
(Figs. 10–12, 31, 39, 43)

*Female* (holotype measurements in parentheses).—Body length 1.96–2.52 (2.08) mm.

*Relative measurements.*—**Head** width 1.85–2× length, 1.23–1.3× height (78:39:60.5); frontovertex width at level of anterior ocellus 0.67–0.88× its length, 0.42–0.45× width of head (32.5:40:78); ocelli in obtuse triangle, with angle at anterior ocellus of 109°–117° (114°); POL:OOL:LOL: OCL = 16:4:8:2 (in holotype); OOL 0.67–1.1× diameter of posterior ocellus (4:5); distance between antennal toruli 2.06–2.5× distance between torulus and mouth margin, 0.7–0.8× mouth width (18.5:8:26.5); eye maximum diameter 1.21–1.44× minimum diameter (38:30); posterior orbit of eye almost reaching occipital margin (dorsal view); temple very short (1.5); antenna as in Fig. 31; scape strongly broadened and flattened, length 1.54–1.83× maximum width (28:16.5); funicle 6-segmented. **Mesosoma** length 1.09–1.16× width (83:76); mesoscutum length 0.47–0.49× width (36:76); scutellum length 0.8–0.94× width (39.5:45); mid tibial spur 0.66–0.83× as long as mid basitarsus, 0.21–0.24× as long as mid tibia (12.5:19:

**43**
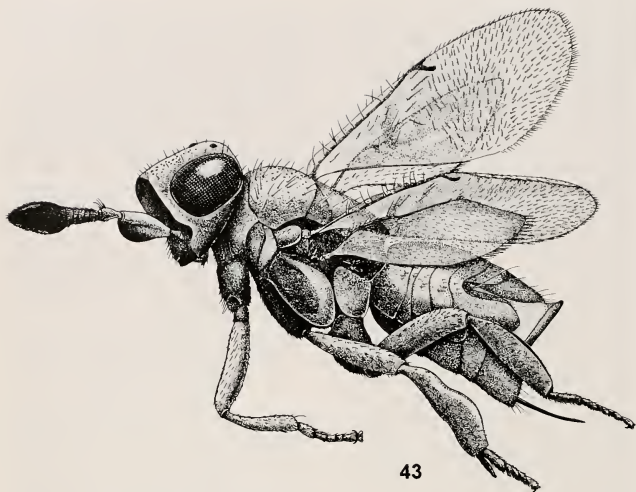
Fig. 43. *Hambletonia undulitibiae*, female habitus.

60); forewing length 2.21–2.41× maximum width (147:61); venation and setation as in Fig. 39. **Metasoma** length 1.16–1.22× width (88:76); distance from cerci to base of metasoma 1.35–1.61× corresponding distance to apex of metasoma (46:34).

*Color.*—**Head, mesosoma** and **metasoma** yellow orange to brownish orange dorsally and laterally, sometimes with slightly darker axillae and anterior part of mesoscutum, without any metallic luster, slightly lighter, orange yellow to yellow ventrally; antenna (Fig. 31) with radicle orange to brownish orange, scape brownish orange to brownish yellow (with slightly brownish flange) to completely very dark brown, almost black, pedicel yellowish orange to orange brown, with darker base, funicle yellow orange to orange brown, clava in basal approximately ¼ same color as fu-

nicle, gradually becoming black in apical ⅔ or so, slightly lighter at apex; forewing weakly, more or less uniformly infuscate with brownish yellow, with slightly stronger infuscation in basal half, and diffuse darkening along line of hairs delimiting distal margin of basal cell (Fig. 39); legs same color as body, or slightly lighter.

*Sculpture and pubescence.*—**Head** (Figs. 10–12): frontovertex slightly convex, smooth, more or less glossy, with numerous small punctures, and erect brown hairs; anterior margin of frontovertex (dorsal view) slightly concave (sometimes, almost straight), in middle very thin and translucent (Fig. 11); face minutely superficially reticulate; lower part of interantennal prominence, and clypeus with short, brownish hairs; eyes with translucent hairs; gena minutely, extremely shallowly

reticulate, with scattered erect brown hairs; posterior margin of gena with more or less expressed carina, separating it from occiput. **Mesosoma:** lateral part of pronotum and prepectus reticulate; mesoscutum minutely, very shallowly, isodiametrically reticulate, with scattered punctures; axillae minutely, extremely shallowly reticulate; scutellum smooth, with very few scattered, minute to small punctures, its apex with inconspicuous, shallow, coriaceous sculpture; dorsum of metasoma with erect brown hairs, hairs longer on apex of scutellum; mesopleuron with glabrous upper part, and vertically coriaceous lower part; metanotum laterally of dorsellum with several long oblique carinae directed from its outer margin toward dorsellum, and several short, very weakly indicated longitudinal carinae directed posteriad from its anterior margin; propodeum laterally reticulate, with carinate callar region, and longitudinally carinate plical region; mid tibia characteristically thickened, slightly flattened laterally, undulate dorsally, and slightly undulate ventrally (in one specimen these features, especially undulation, are weakly expressed); hind tibia slightly thickened, flattened laterally, and carinate dorsally (Fig. 43). **Metasoma** with tergum II (first visible) very shallowly transversely coriaceous, shiny, terga III–VIII almost smooth; pubescence consisting of brown hairs on lateral part of all terga, shorter brownish hairs on posterior edge of terga V–VII, and longer brownish hairs of syntergum VIII.

*Male.*—Unknown.

*Hosts and Biology.*—Unknown.

*Material examined.*—Holotype ♀: COSTA RICA: 10°25'N 84°01'W, Heredia, 3 km S Puerto Viejo, OTS La Selva, 100 m, iii.1991 (P. Hanson) (INBio). *Paratypes:* Heredia, La Selva BS, 50 m, ii.1991, MT/YPT (J.S. Noyes), 1 ♀; Alajuela, Peñas Blancas, viii.1987 (E. Cruz), BM 1988-119, 1 ♀ (left antenna and left wings in microslide # OSU-0013); Guanacaste Pv., Sta Rosa NP, Sn. Emilio-8-C, 8.ii–1.iii.1986 (Janzen & Gauld), 1 ♀ (BMNH).

*Distribution.*—Costa Rica.

*Etymology.*—The name reflects the un-

dulate shape of the dorsal edge of the mid tibia.

*Diagnosis.*—From *H. pseudococcina* differs by the longer funicle and clava (Fig. 31), the presence of brown erect hairs on the frontovertex and brownish translucent hairs on the eyes, the concave anterior edge of frontovertex (Fig. 10–12), the almost naked basal cell of the forewing (Fig. 39), the thickened, flattened and undulate mid tibia, and the carinate dorsal margin of the hind tibia (Fig. 43).

## *Hambletonia* spp.

We were unable to assign four female specimens to any of the above species. Each of them apparently belongs to a separate species, and differs in some features from all other species. However, the material was insufficient to assess the consistency of those differences, and to determine the specific status of the specimens.

*Material examined.*—COSTA RICA: Cartago, Turrialba, CATIE, 22.vi.1994 (P. Hanson), 1 ♀; ECUADOR: Napo Misahualli, 20.ii.1983 (L. Huggert), 1 ♀, BM 1984-337; Napo Tena, 16.ii.1983 (L. Huggert), 1 ♀; PERU: Madre de Dios, Rio Tambopata Res., 12°50'S 69°20'W, 1–13.xi.1983 (N.E. Stork), 1 ♀ (BMNH).

## ACKNOWLEDGMENTS

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# Antero-lateral Abdominal Scent Glands of Braconine Wasps (Hymenoptera: Braconidae)

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*Abstract.*—Virtually all members of the Braconinae possess one, two or three pairs of sac-like, glandular invaginations of the unsclerited lateral cuticle between the terga and sterna of their 1st and 2nd metasomal (2nd and 3rd abdominal) segments. These antero-lateral abdominal glands (ALAGs) are present in both sexes, are often partially evaginated when the wasps are disturbed (e.g. handled), and are the source of an odoriferous secretion characteristic of the subfamily. The external surfaces of the exposed glands are typically highly corrugated providing a large evaporative surface area. Light and transmission electron microscopy show the thin cuticular intima of the glands to be lined internally by a layer of squamous epithelial cells overlain on the inner most part of the invagination by irregularly shaped secretory cells which are associated with transcuticular ducts. Overlying all these cells are large pigment-containing cells. The function(s) of the ALAG secretions are at present unknown, but they do not serve as a deterrent to vertebrate predators such as some lizards.

Braconid wasps possess a diversity of exocrine glands (Teles da Silva & Palma 1986; Williams *et al.* 1988; Buckingham and Sharkey 1988; Quicke 1990), mostly located toward the posterior of the metasoma. Aside from those associated with the reproductive tract or with mating (Weseloh 1980; Tagawa 1977, 1983; Field and Keller 1994), little as yet is known about the function of these glands (Quicke 1997). Some odoriferous glands in the related family Ichneumonidae (Townes 1939) and in the ant-mimicking, adeliine braconid *Paradelius* De Saeger (Whitfield 1988) may be protective in function, while the Hagen's glands of male opiine braconids may have mixed courtship and protective roles (Buckingham 1964; Buckingham and Sharkey 1988; Williams *et al.* 1988).

Many museum specimens of braconine wasps have puffy membranous protrusions between the tergites and sternites of the 1st to 3rd metasomal segments. These have previously gone unreported, even in the detailed anatomical studies by Alam (1953). Observations on living wasps and dissections of their metasomas have shown that these structures are sac-like scent glands which are partially evaginated when wasps are handled or otherwise disturbed. This particular set of glands appears to be unique to the Braconinae, a large subfamily containing well over 2000 described species, and no equivalent ones in structure and location have been found in any other subfamily of Braconidae. A pair of antero-lateral glands have been described in the pine sawfly, *Diprion similis* (Hartig), but these open via a vertical orifice in the intersegmental membrane between the 2nd and 3rd abdominal terga, and they are only found in females (Mertins and Coppel 1972). These glands are therefore unlikely to be homologous with those found in the Braconinae. In this paper we describe the structure and distri-

bution of these antero-lateral abdominal glands (ALAGs) and report on some observations relating to their possible function.

## MATERIALS AND METHODS

Histological and morphological studies were carried out on specimens of *Atanycolus ulmicola* (Viereck) collected in College Station, Texas, *Digonogastra kimballi* Kirkland and *Bracon mellitor* Say, both reared for biological control studies at Texas A&M University, *Habrobracon hebetor* (Say) reared for biological control in Egypt, an unidentified *Bracon* species collected in Budapest, Hungary and an unidentified *Iphiaulax* species collected in North Queenland, Australia. The distribution of ALAGs among other Braconidae and other genera of Braconinae was determined using aqueous KOH treatment and subsequent dissection of dry museum specimens.

Material for light microscopy was embedded in paraffin wax (*Atanycolus*) or resin (*Bracon, Digonogastra* and *Habrobracon*). Wax-embedded material was fixed in alcoholic Bouin's solution, dehydrated through alcohols, double embedded in celloidin/paraffin wax and sectioned at 5 μm. Sections were stained with haematoxylin/eosin. Resin embedded material was fixed in glutaraldehyde followed by osmium tetroxide, embedded in Spurr's resin and sectioned at 0.5 μm. Sections were stained with 1% Toluidine blue in 1% aqueous sodium borate.

Material for transmission electron microscopy was dissected in insect saline (Ephrussi and Beadle 1939) and fixed for 6 hours in 2% glutaraldehyde, 2% paraformaldehyde, 2% acrolein and 1.5% dimethyl sulphoxide in 0.133 M sodium cacodylate (pH 7.4). After washing, material was post fixed in 2% osmium tetroxide (Hayat 1989). Following fixation the material was embedded in Araldite 502-EM-BED 812 Embedding Medium (Mollenhauer 1964). Material was sectioned with

a diamond knife using an ultramicrotome from LKB (Ultrotome type 4801 A). 50–70 nm thin sections were post-stained with alcoholic uranyl acetate solution for 30 minutes followed by Reynolds' lead citrate (Reynolds 1963) for 10 minutes. Sections were examined and photographed using a Zeiss 10C transmission microscope at 60 kV on Kodak Electron Microscope Film 4489 (ESTAR Thick Base).

The internal morphology of the ALAG was determined both by the dissection of fresh wasps in 70% ethanol or physiological saline, and by dissecting wasps fixed in alcoholic Bouin's solution. The latter material was dehydrated after dissection, critical point dried, sputter coated with gold and examined using a Cambridge scanning electron microscope (SEM).

The external sculpturing of the ALAG was examined by SEM. Specimens of *Atanycolus*, *Bracon*, and *Digonogastra* were killed by placing them into alcoholic Bouin's fixative or Carnoy Fluid. Metasomas were removed, dehydrated and critical point dried. Some individuals treated this way died with their ALAGs everted. The specimen of *Myosoma nyanzaensis* Quicke & Wharton illustrated is a museum specimen which had died in culture.

Preliminary tests were run to determine whether gland products function as a predator deterrent. Both spiders (Salticidae) and lizards (Iguanidae) were used as potential predators. Predators were placed in cages with male and female *D. kimballi* and with individuals of the doryctine braconid, *Allorhogas pyralophagus* Marsh, which are similarly sized and coloured to *D. kimballi* but lack ALAGs. Interactions between predators and prey were recorded.

## RESULTS

*Distribution among genera.*—ALAGs were only found in members of the Braconinae and not in any specimens of the related subfamilies Doryctinae, Pambolinae, Rhyssalinae, Exothecinae, Hormiinae,

Rogadinae, Mesostoinae, Histeromerinae, Gnamptodontinae, Opiinae or Alysiinae that were examined (list of taxa sampled available from senior author upon request). Within the Braconinae, ALAG's were present in the vast majority of genera examined, viz. *Angustibracon* Quicke, *Aphrastobracon* Ashmead, *Archibracon* Saussure, *Atanycolus* Foerster, *Bacuma* Cameron, *Baryproctus* Ashmead, *Bathyaulax* Szépligeti, *Bicarinibracon* Quicke & Walker, *Bracon* Fabricius, *Calcaribracon* Quicke, *Callibracon* Ashmead, *Campyloneurus* Szépligeti, *Compsobracon* Ashmead, *Compsobraconoides* Quicke, *Cratobracon* Cameron, *Cratocnema* Szépligeti, *Cyclaulax* Cameron, *Cyclaulacidia* Quicke, *Digonogastra* Viereck, *Eunesaulax* Tobias, *Euurobracon* Ashmead, *Euurobraconoides* Quicke, *Euvipio* Szépligeti, *Fraterarchibracon* Quicke, *Gammabracon* Quicke, *Glyptomorpha* Holmgren, *Gronaulax*, Cameron, *Habrobracon* Ashmead, *Hemibracon* Szépligeti, *Hybogaster* Szépligeti, *Iphiaulax* Foerster, *Ischnobracon* Baltazar, *Lapicida* Quicke, *Lasiophorus* Haliday, *Leptobracon* Szépligeti, *Ligulibracon* Quicke, *Macrobracon* Szépligeti, *Megalommum* Szépligeti, *Merinotus* Szépligeti, *Mesobracon* Szépligeti, *Mollibracon* Quicke, *Monilobracon* Quicke, *Myosoma* Brullé, *Nedinoschiza* Cameron, *Nesaulax* Roman, *Odesia* Cameron, *Odontoscapus* Kriechbaumer, *Paranesaulax* Quicke, *Philomacroploea* Cameron, *Plaxopsis* Szépligeti, *Pseudovipio* Szépligeti, *Psittacibracon* Quicke, *Pycnobracon* Cameron, *Rhadinobracon* Szépligeti, *Rhytimorpha* Szépligeti, *Rostraulax* Quicke, *Serraulax* Quicke, *Shelfordia* Cameron, *Sobrinarchibracon* Quicke, *Sororarchibracon* Quicke, *Stenobracon* Szépligeti, *Stigmatobracon* Turner, *Sylvibracon* Quicke, *Undabracon* Quicke, *Vipiellus* Roman, *Vipio* Latreille, *Vipiomorpha* Tobias, *Virgulibracon* Quicke, *Virgulibraconoides* Quicke, *Vomeribracon* Quicke, *Zaglyptogastra* Ashmead and *Zanzopsis* van Achterberg.

The only Braconinae examined in which ALAGs appeared to be absent are *Meso-*

*braconoides psolopterus* (Wilkinson) and a *Pseudoshirakia* species, both belonging to the *Mesobracon* Szépligeti group of genera (Quicke 1987; Sarhan and Quicke 1990), and a *Rhamnura* species of the Rhamnurini.

In most genera there were two or three pairs of ALAG sacks but in a few, for example in *Lasiophorus*, *Leptobracon* and *Sobrinarchibracon*, only one was apparent. The ALAG in *Coeloides* is poorly developed and is also more or less unilobular. Details of gland number and sculpture may prove useful in future phylogenetic analysis of the relationships between the genera of Braconinae.

*Behaviour.*—As with many Apocrita, including both aculeates and terebrants, male and female braconines often raise their metasomas vertically and flex them when handled. In the case of females of some braconines, particularly those with a moderately short, robust ovipositor (e.g. some *Iphiaulax* Foerster and *Digonogastra* Viereck), this may result in stinging (Quicke *et al.* 1992). For many species (and all males) pseudo-stinging behavior is mimetic (see Rothschild 1984; Quicke 1986a, b). In both male and female Braconinae, this abdominal flexion is also frequently accompanied by various degrees of eversion of the ALAG (Figs. 1–4) and the latter is associated with the release of a distinctive odour. However, eversion of the glands does not always accompany metasomal flexion and flexion itself is probably principally concerned with applying the metasomal apex to the source of disturbance as part of the stinging or pseudo-stinging behaviour. In living *D. kimballi*, small droplets of a clear fluid can be observed on the everted ALAG and this liquid can be collected by touching the end of a fine glass capillary to the droplets. The liquid appears to contain both highly volatile and less volatile components since the droplet rapidly volatilizes in air, but leaves a sticky residue. Some alcohol-preserved specimens of this and many other
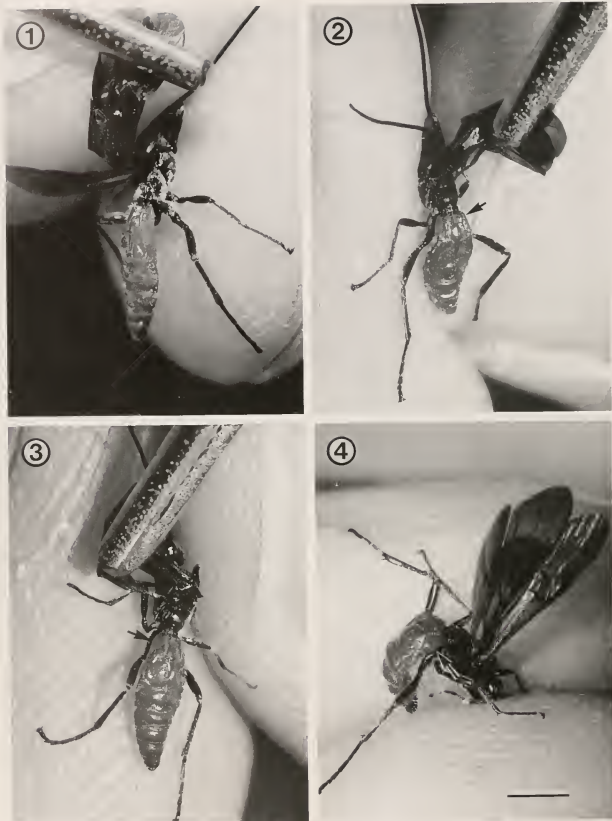
Figs. 1–4.  Photographs of live male *Digonogastra kimballi* being handled so as to evoke eversion of the antero-lateral abdominal glands (arrows in Figs. 2–4), and pseudo-stinging posture (Fig. 4). Scale bar approximately 2 mm.

species of Braconinae have their ALAGs filled with a pale grey precipitate similar to that observed by Buckingham in the intersegmental, tergal glands of similarly preserved *Bracon* species (Buckingham 1964).

*Palatability of braconines.*—Despite their distinctive odour and the aposematic coloration of many of the larger species (Quicke 1986a; Quicke et al. 1992), at least *Atanycolus simplex* and *Digonogastra kimballi* appear to be palatable to several potential predators. One of us (DLJQ) has eaten *A. simplex*, which have a weak but not unpleasant flavour. Lizards (*Sceloporus cyanogens*) presented with male and female *D. kimballi* consume them readily, but spiders (*Platycryptus undata* (DeGeer)) release the wasps rapidly after an attack. A wasp and spider will both remain alive for a week if placed together in a small vial even if the spider has no alternative food source. However, the doryctine *A. pyralophagus* elicited a similar response, and other observations have shown that several non-braconine Braconidae are also unpalatable to spiders (Wharton 1984).

*Morphology and histology of glands.*—Dissections and SEM of the external surface of the ALAG revealed that there are one, two or three discrete pairs of evaginations (Figs. 5–12). In freshly dissected material of *D. kimballi* or *A. ulmicola*, the inner surface of these evaginations is covered by large red-pigment-containing cells and there are no obvious muscular attachments to the ALAG membrane (Figs 11, 12).

Externally, the surface of the ALAG in each of the five genera examined (*Atanycolus, Bracon, Digonogastra, Habrobracon* and *Myosoma*) was highly corrugated although there were marked differences in the detailed form of the surface sculpture between them (Figs. 5–10). No pores were apparent on evaginated sacs under the SEM, however, cuticular ducts were usually discernible in chlorazol black-stained, KOH-treated sac cuticle. Ductules were

also observed in some semi-thin sections when these were examined carefully at $200 \times$ magnification (Fig. 15). In most genera of Braconinae, these ducts were located on the innermost portion of the sac. In semi-thin sections they were specifically associated with a patch of irregularly-shaped subepidermal cells whose cytoplasm stained darkly with toluidine blue (Fig. 16; S).

Transverse light microscope sections through ALAGs showed a deeply invaginated chitinous membrane (intima). The chitin lining the sac was thinner and less densely staining with toluidine blue than that of the adjacent entrance slit to the sac which was in turn thinner than the adjacent cuticle that was never invaginated into the gland sac (Fig. 14). Light microscope sections also revealed ducts running from the cell layer lining the ALAG membrane and the external surface of the gland (Fig. 15 arrow). These secretory ductules appear to pass directly from epithelial to secretory cells and therefore the latter can be classified as Type 3 gland cells as defined by Noirot and Quennedey (1974) and Quennedey (1975).

The secretory gland cells themselves are characterized by the possession of a complex, elongate, microvilli-lined secretory invagination or end apparatus (Figs. 17–20). Running along the center of the invagination is a cuticular structure which in cross-section shows a thin and frequently interrupted circumferential layer within which is a thicker zone of longitudinally-orientated, cuticular filaments. Usually a discrete lumen can be discerned surrounded by microvilli (Fig. 19).

The secretory gland cell cytoplasm contains numerous elongate to irregular mitochondria and is densely packed with small, (0.04–0.08 µm), irregular, membrane-bounded vesicles (Figs. 18, 19). There are free ribosomes and dilated rough endoplasmic reticulum (indicating an active phase) within the cytoplasm. Microtubules can be detected more frequent-
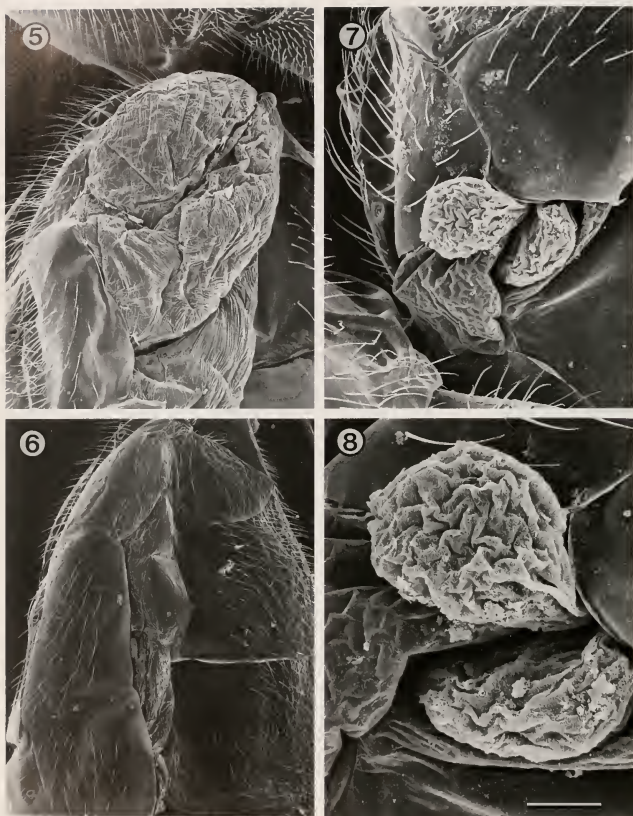
Figs. 5–8. SEMs of external appearance of ALAGs: 5, 6, right anterior metasoma, *Digonogastra kimballi* showing, everted (5) and uneverted, resting (6) condition. 7, 8, left anterior metasoma, *Bracon mellitor* showing everted ALAGs. Scale bar on Fig 8 applies to all figures on plate. Scale bar applied to: 5, 6 = 0.25 mm; 7 = 0.1 mm; 8 = 0.05 mm.
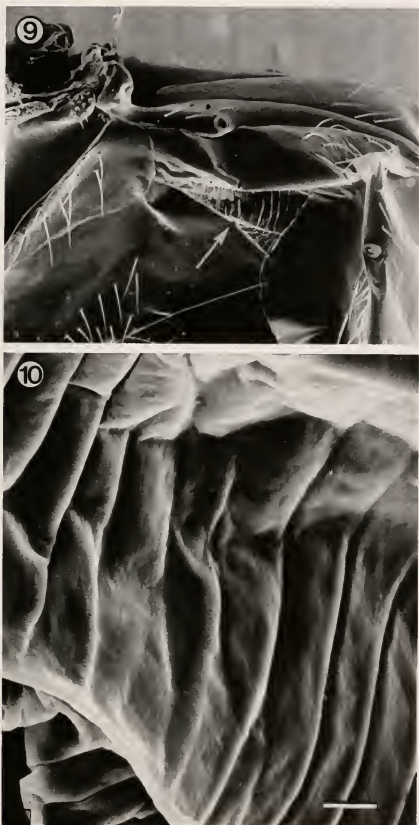
Figs. 9–10. SEMs of external appearance of partially everted ALAG of *Myosoma nyanzaensis* showing surface sculpture at two magnifications. Scale bar on Fig. 10 applies to both figures on plate. Scale bar applied to: 9 = 0.1 mm; 10 = 0.01 mm.
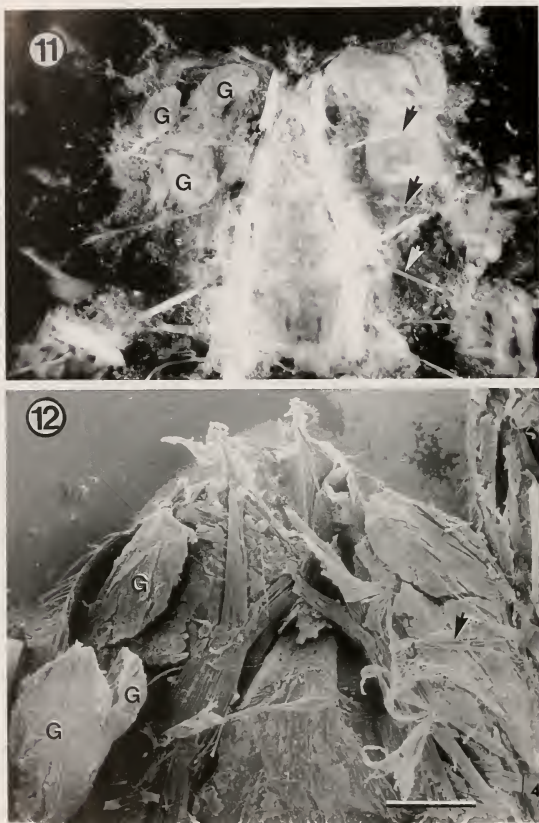
Figs. 11–12. Light and scanning electron micrographs of dissected anterior metasomas (anterior at top) of *Digonogastra kimballi* (9) and *Iphiaulax* sp. (10), showing internal appearance of non-evaginated ALAGs. Abbreviations: G = gland sac; arrows indicate segmental muscle strands overlying gland sacs. Scale bar on Fig. 12 applies to both figures on plate. Scale bar applied to: 11 = 0.5 mm; 12 = 0.25 mm.
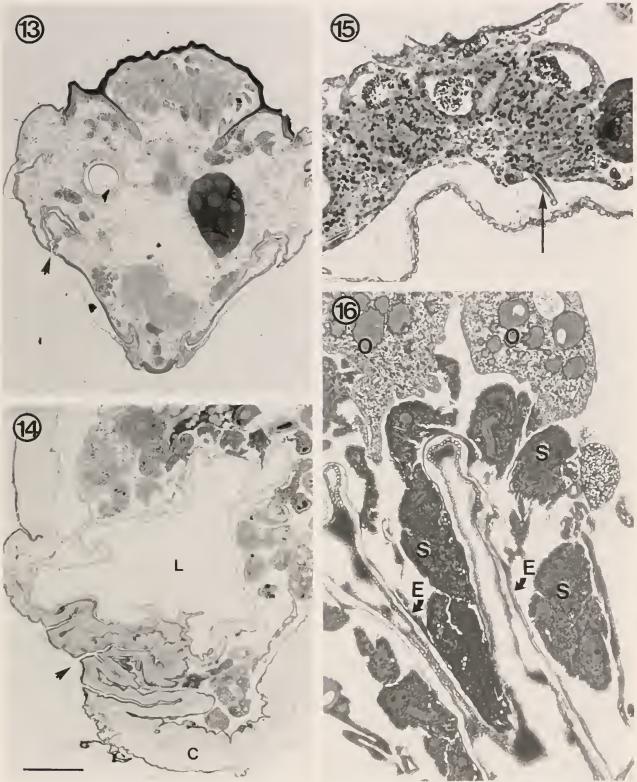
Figs. 13–16. Light photomicrographs of semi-thin, resin-embedded, transverse sections of ALAGs in *Bracon* sp. (13, 14) and *Digonogastra kimballi* (15, 16). Abbreviations: C = cuticle; E = epithelial cell; L = lumen of ALAG; O = oenocyte/pigment cell; S = secretory cell; arrows in 13 and 14 indicate opening of ALAG sac to exterior; arrow in 15 shows pore through glandular cuticle. Scale bar on Fig. 14 applies to all figures on plate. Scale bar applied to: 13 = 0.1 mm; 14, 15 = 0.05 mm; 16 = 0.025 mm.
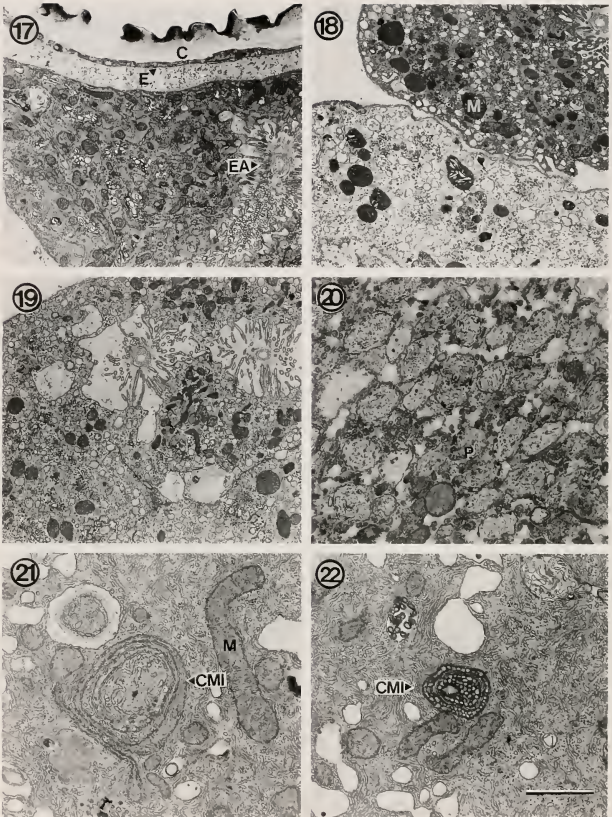
Figs. 17–22.  Transmission electron micrographs showing ultra-structure of ALAG and related cells in *Digono-gastra kimballi*. 17, secretory cell (note microvilli-lined ductule) separated from cuticle with associated epithelial cell; 18, 'dark' secretory cell (upper right and translucent type of secretory cell with numerous large pale inclusions (lower left); 19, secretory cell with looped end apparatus ductule sectioned twice, note the numerous mitochondria; 20, pigment cell; 21 and 22, oenocytes showing extensive smooth endoplasmic reticulum, elongate mitochondria and membranous structures. Abbreviations: C = cuticle; CMI = complex membranous inclusion; E = epithelial cell; EA = end apparatus; M = mitochondrion; P = putative pigment inclusion. Scale bar on Fig. 22 applies to all figures on plate. Scale bar applied to: 17, 19 = 1.0 μm; 18 = 0.5 μm; 20–22 = 2.0 μm.

ly near the base of the microvilli, next to invaginations. Numerous Golgi complexes were discernible, located at some distance from the secretory ductule. Some secretory cells appeared rather less electron lucid than others (Fig. 18; upper right *cf* lower left) but all had a similar complement of subcellular organelles.

The gland cells, and on the more peripheral part of the gland sac, the epithelial cells, are overlain by large pigment-containing lipid cells (Figs. 11, 12, 16). Under the transmission electron microscope these pigment-containing cells were packed with large, weakly-staining, membrane-bounded droplets (Fig. 20; P) which we interpret as being a lipid-based pigment. Between these, the cytoplasm has extensive and relatively dark-staining smooth endoplasmic reticulum. Scattered over and among the pigment cells were a number of another category of large cells which SEM revealed to be oenocytes (Fig. 14). These were densely packed with smooth endoplasmic reticulum interspersed with elongate mitochondria (0.5–2.0 μm long by 0.2–0.4 μm). The oenocyte sections also showed a number of complex membranous inclusions (Figs. 21, 22).

## DISCUSSION

The present paper describes a set of unique, eversible, sac-like glands, the ALAGs, that are located laterally at the anterior end of the metasoma in virtually all members of the braconid subfamily Braconinae. These glands are the source of a distinctive odour which is characteristic of members of the Braconinae (Quicke 1988) and they are everted and release their secretory product notably when the wasps are disturbed in some way, such as when they are handled or caught in an insect net. The end apparatus of the gland cells and vesicular organelles are very similar to those of the venom glands and other glands associated with reservoirs suggesting that the anterolateral glands may be very active secretory structures.

Undoubtedly, some parasitic wasps (including ichneumonids and braconids) produce volatile secretions that render them unpalatable to potential predators (Townes 1939; Buckingham & Sharkey 1988; Wharton 1984). The function of the ALAGs in the Braconinae is still obscure, however. Although the product seems to be released when the wasps are disturbed, it does not appear to render the wasps unpalatable to vertebrates. Although braconines are rejected by salticid spiders, members of several other braconid subfamilies that do not have an obvious odour and lack ALAGs are similarly rejected. A sex pheromone function for the ALAGs does not seem likely since the glands are well-developed in both sexes, and, in addition, members of both sexes have a similar odour to humans. However, in a behavioral study on *Habrobracon*, Grosch (1948) showed that males were attracted more by the anterior of the female metasoma than by its posterior part. If the gland in females does serve as a male attractant, then the question still remains as to what the role of the ALAGs might be in male braconines. Perhaps the ALAG product has a more general intra-specific signalling role such as an aggregation or alarm pheromone.

## ACKNOWLEDGMENTS

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# Activity Patterns in a Nesting Aggregation of *Sphex pensylvanicus* L. (Hymenoptera: Sphecidae)

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*Abstract.*—Daily observations were made on 22 individually marked females of *Sphex pensylvanicus* L. in upstate New York in 1981 and 1982. Wasps nested in soil at the bottom of a storm sewer drain, obtained nectar from flowers, slept on the stems of forbs, and hunted and captured prey in trees on a nearby hillside. Their nourishment, nesting and predatory activities incorporated a distinct temporal series of flights to and from nests including (1) early to mid-morning returns from sleeping roosts; (2) periodic inspection returns; (3) exits to feed, hunt, and bask in sun; (4) prey transport; (5) returns to enlarge nests; (6) returns to nests at dusk; and, (7) exits to sleeping roosts. One-half of exits that followed morning or afternoon visits to nests, only one in three exits after placing prey in the nest, and fewer than one in five exits following nest enlargement or entry near dusk gradually transformed into orientation flights. Females spent more time inside their nests following pre-darkness returns than after morning returns from sleeping roosts, periodic inspection returns, or taking in prey.

Species of the sphecid genus *Sphex* comprise large, thread-waisted, ground-nesting wasps. Aside from *Sphecius speciosus* (Drury), the cicada killer, *Sphex pensylvanicus* Linnaeus is the largest sphecid in eastern North America. The females average nearly 30 mm in body length, are all black with black erect hairs on the head and thorax, and have violaceous tinted black wings (Bohart and Menke 1963). This species, the "Great Black Wasp" of John Bartram, is of historic significance as it was the first solitary digger wasp described from the United States (Rau 1944). *Sphex pensylvanicus* has a rather broad geographic distribution ranging transcontinentally across the United States into northern Mexico, except for the northwestern states (Bohart and Menke 1976). Some of the species of *Sphex* appear to be strictly solitary nesters. Females of other species such as *Sphex ichneumoneus* (Linnaeus), the Great Golden Digger Wasp (Ristich 1953), nest close together with two or more wasps rarely sharing the same nest (Brockmann

and Dawkins 1979). Females of *Sphex pensylvanicus* also nest close together but it is uncertain whether they share a common nest.

Although the basic features of the nesting behavior of *Sphex pensylvanicus* have been studied in some detail, little is known about the daily periodic activities of the females. Reinhard (1929) and Frisch (1938), working together on this species, published separate articles under the name *Ammobia pennsylvanica* (L.). Their reports contained information on geographic distribution, seasonal occurrence, aggregation, nesting habitat, nest structure and dimensions, cell contents, prey selection, prey paralysis, prey transport, egg placement, and description and duration of egg, larva, cocoon, parasites, and hyperparasites. Rau (1944) described seasonal flight period, habitat, aggregation size, burrow construction, nest dimensions, cell contents, prey type, paralysis of prey, prey transport, nest entry, and egg placement of this species under the name *Chlorion*

*pennsylvanicum* (L.). Krombein (1955) reported on the prey transport, prey paralysis, and provisions of one "*C. pennsylvanicum*" nesting among a dozen individuals in a bluff along a beach. Rigley and Hays (1977) noted flight period, aggregation size, reuse of old nests, burrow excavation including sound production and sonagram, prey type, and male activity of this species.

The objectives of my paper are to sequentially delineate some of the periodic daily activities of *Sphex pensylvanicus* in relation to time of day, air temperature, and season. Only sparse information of this kind exists for sphecid wasps and, therefore, such observations should be valuable to future researchers in this field. A recent study on *Sphex argentatus* Fabricius in India by Belavadi and Mohanraj (1996) comes closest to approximating the goals of the present paper. These authors delineated nest structure and dimensions, indicated time spent for various activities including provisioning and types of closures, and gave a flow diagram of nest building components. They presented a detailed time table for various daily activities but, unfortunately, did not define the activities listed in the table such as grooming, sitting alert, sitting, and chasing predators. Belavadi and Mohanraj (1996) found that excavating the main burrow, hunting for prey, and making the permanent closure utilized more than three-fourths of a female's observed activities. Brockmann and Dawkins (1979) prepared a time budget for *Sphex ichneumoneus* and found similarly that burrow excavation, searching for prey, and closing the nest utilized a considerable portion of a female's available time.

## LOCATION OF NESTS

The aggregation of *Sphex pensylvanicus* I studied nested during 29 July–30 August 1981 and 27 July–1 September 1982 inside of a storm sewer drain situated in an asphalt driveway beside the Marcellus Se-

nior High School, Marcellus, N.Y. (Fig. 1). The 70 × 70 cm iron drain cover had grates large enough to permit ready entry and exit by the provisioning and orienting wasps. In 1981 a total of 10 females nested inside this sewer drain. One of the wasps nested in the loosened mortar between the bricks of one wall of the drain. The nest entrance, 2 cm in diameter, was situated 41 cm below the driveway surface. The tumulus to this nest, consisting of pebble-sized pieces of mortar and measuring 10 cm long, 13 cm wide, and 5 cm high, was positioned 29 cm beneath the nest entrance at the bottom of the drain, or 70 cm below the driveway. The other nine wasps nested in a single aggregation in soil beneath a sewer tile located at the bottom of the drain. These females used the intact mouth of the tile, which was one-third filled with gravel and broken in several places, as a common vestibule. A torrential downpour on 2–3 September 1981 filled the bottom of the drain and submerged all of the nests except for the one in the brick wall. There was no sign of female activity at this site in 1981 following the rain. Nonetheless, 12 wasps emerged and nested beneath the same drain tile in 1982. On 12 August 1982, I discovered two additional nesting aggregations of this species inside sewer drains in the high school parking lot, 30 and 80 m NE of the first site. These wasps were not studied in detail because of the distance from the first aggregation.

## METHODS

Individual wasps were observed daily, weather permitting, from 0730 to 2100, except for one day (19 August 1982) when I arrived at the nesting site as early as 0600 hrs (EDT). Their behaviors were arbitrarily separated into functional categories as defined under "Female Activity." Each wasp was color-coded to facilitate following her daily and seasonal activity. This was accomplished by marking the mesoscutum with Testor's model paint using a

Figs. 1–2. 1, Storm sewer drain in which females of *Sphex pensylvanicus* nested. Wasps entered and exited through openings in the drain cover. 2, Black locust stand and adjacent field of flowers where females of *Sphex pensylvanicus* hunted, fed on nectar, and slept.

tiny paint brush from which most of the hairs had been removed. Maximum longevity of females was 35 days for one wasp marked yellow. Only three of 22 wasps lived for longer than a month. One male and one female each were collected before individually marking them and placed as voucher specimens in the insect museum of the State University of New York College of Environmental Science and Forestry, Syracuse, New York.

## FEMALE ACTIVITY

From early to mid-morning, *Sphex pensylvanicus* females left the upright vegetation on which they slept, flew to nests, entered, and exited with or without orienting or fed briefly or basked in the sun before arriving at the nest. Some females left sleeping roosts and returned to nests as early as daybreak. Individuals periodically visited nests during the day, entered, exited, and then fed on honeydew or nectar of nearby flowers, basked in the sun, or hunted, captured and transported prey. Nest enlargement frequently took place toward evening and preceded exits and flights to sleeping roosts. Females not enlarging burrows returned to nests at dusk, entered, exited, and flew to sleeping roosts (Fig. 3).

Female activity at or near nests arbitrarily was separated into the following components for analysis: (1) morning flights to nests from sleeping roosts, feeding stations, or basking places, entry, and exit; (2) orientation flights; (3) periodic flights to nests probably for the purpose of nest inspection and/or reorientation, entry, and exit; (4) nectar feeding; (5) prey transport flights, entry, and exit; (6) entry, nest enlargement, and exit; (7) pre-darkness flights to nests and entry; and, (8) exit flights to sleeping roosts. A companion paper examines the territoriality and mating behavior of this species (Kurczewski in prep.).

*Returns from sleeping roosts.*—Ninety-three observations of females returning from sleeping roosts, which comprised upright vegetation [predominantly *Melilotus alba* (white sweet clover)] on a hillside 55 m from the nesting area (Fig. 2), indicated that most returns were made between 0829 and 1038 hrs (EDT) on warm sunny mornings (Fig. 5). However, three females returned from sleeping roosts on 19 August 1982 as early as 0635, 0647 and 0655 hrs at an air temperature as low as 10°C. The earliest of these returns was made before sunrise. Successively later sunrises induced increasingly later morning returns to nests in females nesting over a period of several weeks. On rainy mornings, 17 flights (N=9 wasps) were made to nests within 48–69 min after cloud cover dissipated and the sun reappeared, regardless of time of day.

Females returning from sleeping roosts flew into the sewer drain more slowly than those returning to inspect their nests later in the day when temperatures were higher. Eighty-eight of 93 entries were made through the grates without hesitation. Five times wasps approached the drain cover, hovered near it, flew off, returned in flight 3–8 sec later, and entered. Once inside the drain, females inspected the opening into the drain tile by flying from left to right and vice versa while facing it. After entering the opening and disappearing from view, females stayed inside nests 7–59 min ($\bar{x}$=16.9, N=93) before reappearing inside the drain. They then spent 1–4 min ($\bar{x}$=1.5) flying in front of the opening, as described above, before exiting through the grates. Forty-eight of 93 exits gradually transformed into what I interpreted to be orientation flights. Forty-five times, the wasps abruptly flew away without making repetitive aerial maneuvers. Five of the females that did not orient made an orientation flight the previous evening. Other wasps that did not make orientation flights may have done so before I arrived at the nesting site.

*Orientation flights.*—Wasps made orientation flights during practically any time
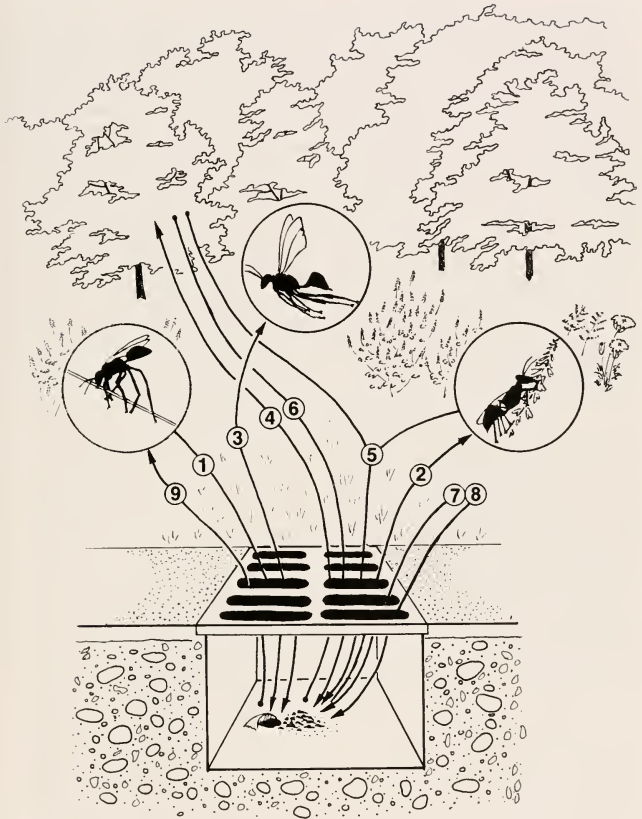
Fig. 3. Summary of daily flight activities of females of *Sphex pensylvanicus*. Numbered arrows designate flights as follows: (1) from sleeping roost; (2) to feed on nectar; (3) orientation; (4) to hunt in trees; (5) periodic return from flowers or trees; (6) prey transport; (7) return to enlarge burrow; (8) dusk inspection return; and, (9) to sleeping roost. Wasps in circles are sleeping and feeding on white sweet clover, respectively, and making an orientation flight (center).

of day, except around the noon hour (EST), and prior to or following different activities. Such flights varied in degree of complexity and occurred from 0859 to 2004 hrs (Fig. 4), usually after females spent many minutes below ground in their nests. The flights followed nest entry and exit after morning returns to nests from sleeping roosts, periodic daytime returns to nests with or without prey, nest enlargement at dusk, and pre-darkness returns to nests. Some flights were brief and lasted only 10–30 sec, whereas others were extensive and occupied 5–6 min. The briefest flights usually followed placement of prey in a nest and many wasps, after provisioning, left without making flights. The longest and most intricate flights followed morning visits inside nests and preceded initial prey capture and transport.

Such flights began inside of the drain, near the bottom, the wasps flying back and forth in front of the tile opening while facing it. These flights gradually extended to include much of the space inside the sewer drain, the wasps flying alternately toward and away from the opening. Females then exited through the sewer grates and repetitively flew back and forth outside of the drain, interspersed with occasional entries through the grates but not into the drain tile. Outside, the flights involved flying straight toward the drain, momentarily hovering near it, turning 180°, flying directly away from the drain, and then repeating this pattern. Most sallies away from the drain were in the direction of the hunting grounds, a stand of black locust trees on a hillside 60 m away (Fig. 2). However, some sallies alternated between this and the opposite direction. Flights increased in height as the wasps flew away from and decreased in height as they flew toward the drain.

The duration and complexity of such flights varied with different females. For example, one wasp began her air-borne maneuvers outside the drain by making two 15 cm-long sallies, then three 30 cm-long sallies, four 75 cm-long sallies, three 150 cm-long sallies, one 300 cm-long sally, one 13 m-long sally around a pine tree and, finally, a 60 m-long sally into the stand of black locust trees. Nearest the drain, the height of the flight approximated 15 cm, whereas at the pine tree, 13 m away, the flight attained a height of at least 3 m. Another female alternated between flying inside and outside the drain. She made 18 sallies outside the drain in the direction of the hunting grounds interspersed with 27 much shorter ones inside the drain, or a total of 45 sallies. Variation in duration and composition of orientation flights seemed to be related to type of activity rather than time of day (see above). The average number of straight line sallies made outside of and away from the drain during an orientation episode was 16.5 (11–31, N=45 episodes; 9 females) following morning return trips from the sleeping roosts.

*Periodic visits to nests.*—Periodic visits to nests probably for the purposes of inspection and reorientation did not include morning returns from sleeping roosts or evening returns. Periodic nest entries preceded and followed nectar feeding, feeding on honeydew, basking in the sun, and prey transport. Periodic returns to nests without prey, followed by entry, were made between the hours of 0934 and 1638 (N=114, Fig. 4). Subsequent exits from the nests occurred between 0939 and 1641 hrs. Females spent 1–30 min ($\bar{x}$=9.5, N=114) inside nests before exiting. Fifty-eight of 114 exits following such nest entry slowly transformed into orientation flights. Wasps abruptly flew away without making lengthy aerial maneuvers 56 times. Forty-seven (84%) of these exits were made by wasps that oriented earlier in the day.

*Nectar feeding.*—Females frequently visited flowers in nearby fields to obtain nectar. They were seen on flowers mostly during the late morning (1100–1200) and mid- to late afternoon (1400–1700) hours

(N=39, Fig. 5). Flowers most visited by the wasps in order of frequency were (1) white sweet clover, (2) goldenrod (*Solidago* spp.), (3) Queen Anne's lace or wild carrot (*Daucus carota*), and (4) white clover (*Trifolium repens*). Frequency of specific flower visits corresponded to the relative abundance of the plant species located between the nesting site and hunting ground.

*Prey transport.*—Females with prey were observed flying to nests between 1032 and 1924 hrs on warm sunny days (Fig. 4). More prey (14 katydids) were brought to nests at air (shade) temperatures of 27–29°C than at other temperatures. Some wasps provisioned their nests with katydids at air temperatures as high as 33°C. No prey were brought to nests at temperatures below 23°C. Some females (n=4) preferred to provision in the morning, some (n=6) in the afternoon, and others (n=2) more or less continuously throughout the day. Combined observations on nine wasps bringing prey to their nests showed peak provisioning activity between the hours of 1030 and 1300, 1400 and 1500, and 1630 and 1900 (Fig. 4). These females spent an average of 43 min (11–72, N=20 trips) between consecutive returns with prey from 1054 to 1924 hrs. One of the wasps that provisioned at 1032 hrs took 110 min from exit to entry with prey. The nine females utilized 2–17 min ($\bar{x}$=8.4, N=21 trips) between taking prey into nests and exiting through the grates. They oriented in flight seven times after placing prey inside nests. They exited without making extensive aerial maneuvers 14 times. Eleven of the 14 exits involved females that made orientation flights previously during that day.

Most females with prey flew directly to their nests. In late July and early August, some provisioning wasps were pursued and jostled in flight by males attempting to mate. Nonetheless, these females retained their grasp of the prey and entered their nests. During mid-August, four wasps nesting inside the two sewer drains

in the high school parking lot were followed in flight, harassed, and robbed of their prey by house sparrows (*Passer domesticus*). Three such sparrows sat on the asphalt pavement near the drains throughout much of the day and successfully stole prey items from the provisioning females as they attempted to fly between the grates. The sparrows fed on the prey, leaving only the wings and legs behind on the asphalt surface. On 18 August 1982, sparrows robbed four incoming wasps of 13 prey items they attempted to bring into the drains. In addition, four prey unwittingly relinquished by the provisioning females were observed lying at the bottom of one of the drains on the earthen floor. Such opportunistic activities on the part of the sparrows probably led to the demise of both *Sphex pensylvanicus* aggregations, as wasps did not nest in these drains in 1983.

Details of prey transport were as described by Reinhard (1929), Rau (1944), and Rigley and Hays (1977). Transport was invariably in flight despite the large sizes and heavy weights (566–716 mg, N=7) of the prey. Three provisioning females each landed once on the edge of the drain and paused momentarily before entering, but six others invariably flew directly inside. Twenty prey were brought in flight from the direction in which the orienting wasps had left and only one katydid was flown in from a different direction.

*Prey.*—Seven prey collected from incoming provisioning wasps were identified as females of *Scudderia septentrionalis* (Serville) (Orthoptera: Tettigoniidae). This katydid species is primarily arboreal and was seen ovipositing on the black locust trees mentioned above.

Prey paralysis included periodic movements of the antennae, mouthparts, and, rarely, legs, and rhythmic breathing movements of the abdomen. Similar descriptions of the paralysis of prey were
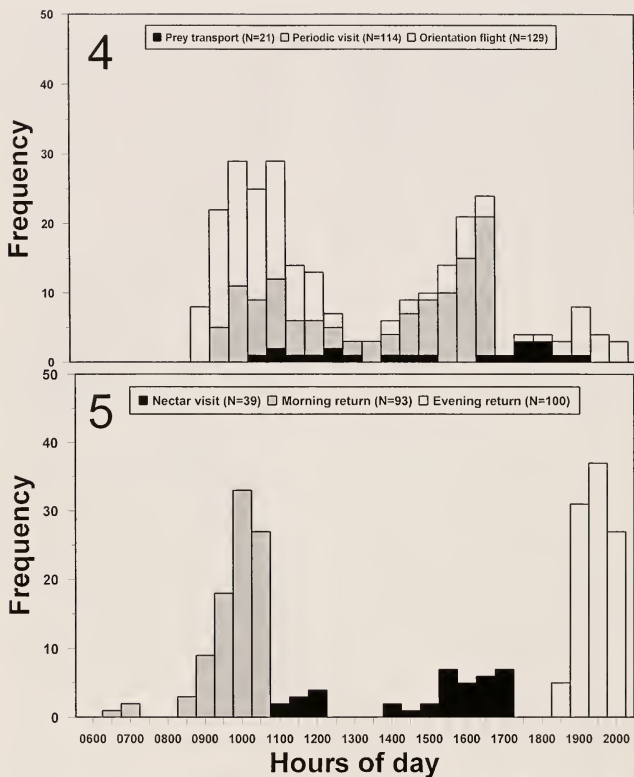
Figs. 4–5. 4, Time distribution diagram of prey transport flights, periodic visits to nests, and orientation flights of *Sphex pensylvanicus* females. 5, Time distribution diagram of floral visits to obtain nectar, morning returns from sleeping roosts, and evening returns prior to departing for sleeping roosts of *Sphex pensylvanicus* females.

given by Reinhard (1929) and Frisch (1938).

*Nest enlargement.*—Components of nest enlargement were as described by Reinhard (1929), Rau (1944), and Rigley and Hays (1977), including the manner of soil removal, except that females were unable to characteristically distribute the soil of the tumulus due to the vertical attitude of one nest and the space constraints imposed by the broken pieces of sewer tile of the other nests. Audible sounds accompanied nine nest enlargements. One wasp periodically made sounds for 56 min while enlarging her nest. Individual bursts of sound in this female lasted 1–5 ($\bar{x}$=3.1, N=18) min. These sounds evidently are a by-product of the wasps excavating with their mandibles in a hardened substrate. In this species, they may serve as an audible repellent to conspecific females attempting to gain access to pre-existing burrows (Rigley and Hays 1977).

Nest enlargement often occurred just prior to darkness. Four wasps that began enlarging nests after 1800 did not finish until well after 1900 hrs. Rigley and Hays (1977) noted that wasps dug as late as 2100 with most such activity occurring between 1100 and 1800 hrs.

*Exits to sleeping roosts.*—Females without prey returned in flight to nests between 1826 and 1948 hrs (Fig. 5), flew into the drain, entered the tile opening, and stayed min 6–40 min ($\bar{x}$=23.8, N=26) before exiting. Such returns coincided with the sun beginning to disappear over a nearby hill and thus wasps returned to nests progressively earlier as daylength shortened. Some females arrived at the drain almost simultaneously, e. g., on 23 August 1981 two wasps arrived at 1844, 3 sec apart, and two others arrived at 1855, only 1 sec apart. By twilight, usually all but one or two of the females were inside burrows. Wasps then began leaving the drain by flying between the sewer grates, sometimes hesitatingly. The exit times of 22 females ranged from 1832 to 2008 hrs

(N=100). After exiting, the wasps flew to their sleeping roosts, often on white sweet clover, 84 times without exhibiting any form of orientation. Seventy-eight (93%) of these exits were made by females that oriented previously that day. The wasps made air-borne orientation movements 16 times prior to flying to sleeping roosts. All of these flights were observed in females that made similar flights earlier in the day. Some females left, turned 180°, entered, and exited one or a few times, or occasionally circled once or twice, and then flew toward the sleeping roosts. Just as they flew to nests almost simultaneously, two pairs of females flew away only 3–5 sec apart on 23 August 1981.

## DISCUSSION

Rigley and Hays (1977) noted that females of *Sphex pensylvanicus* used the same nesting site for at least three consecutive years by cleaning and renovating pre-existing conspecific burrows. In my study, females of this species reused 1980 burrows in 1981 and 1982. Twenty-one of 22 wasps utilized an enlarged common entrance and upper main burrow (broken drain tile) during these years. Use of pre-existing conspecific burrows by subsequent generations of wasps probably saved females considerable time and energy in excavation. The use of a common main burrow by more than one wasp and the reuse of burrows by siblings represent initial steps in the direction of semisocial behavior of aculeate Hymenoptera (Brockmann and Dawkins 1979).

*Sphex ichneumoneus* proceeds farther than this in preadaptation toward semisocial behavior. Burrows that are excavated and then abandoned by some females are adopted as useable nests by other wasps. The females adopting and renovating the nests of conspecifics save much time, often nearly two hours (Brockmann 1980), and energy that otherwise would have been unnecessarily invested in digging. Wasps that accidentally enter con-

specific burrows evidently cannot distinguish between empty, abandoned burrows and those being actively provisioned (Brockmann and Dawkins 1979). Rarely, a female of *Sphex ichneumoneus* deposits a paralyzed katydid in a neighboring female's nest. The two wasps thus temporarily share the same burrow and cell. The intruder may even oviposit on a prey in the cell and fill the burrow, but eventually she returns to her own nest and finishes it (Brockmann and Dawkins 1979).

*Sphex pensylvanicus* incidentally may have evolved a behavior that lessens accidental intrusion into and takeover or sharing of conspecific nests. Rigley and Hays (1977) believed that sound produced by excavating females of this species acts as an auditory repellent to nest entry by conspecifics nesting nearby or investigating burrows. Females were often repulsed from entering nests in which previously taped, conspecific sounds were being replayed (Rigley and Hays 1977). Although they termed this sound "stridulation," implying in the classical sense of the definition that it was produced by two body parts rubbing together, it seems more likely that the sound was made as a by-product of the mandibles digging in a compact substrate. Such sound was produced intermittently by females adding side burrows and cells to their nests (pers. obs.).

Why do females of *Sphex pensylvanicus* return to their nests from sleeping roosts, feeding stations, or basking places each morning? The wasps could immediately begin searching for prey in the trees near the sleeping roosts and thus make better use of their time and energy. First, temperatures in the morning are too cool to facilitate searching for prey (see below). Second, females probably return to their nests every morning to examine the area for disturbance. Why waste valuable time and energy hunting, capturing and transporting prey if the nest has been destroyed or parasitized? Females probably also return to the nesting site each morn-

ing to reacquaint themselves with the surroundings in order to expedite subsequent returns to the nest with prey. More than half of the wasps made orientation flights upon returning to their nests the next morning.

Females of *Sphex pensylvanicus* spent, on average, more time inside nests following pre-darkness returns than after morning returns from sleeping roosts, feeding stations, or basking places, periodic inspection returns, or taking in prey unless engaged in subsequent nest enlargement. The shorter amount of time spent inside nests during midday may be related to increased temperature or absence of certain subterranean activities such as oviposition and burrow excavation.

About one-half of exits that followed morning or afternoon visits to nests progressed to orientation flights. In contrast, only one in three exits after placing prey in the nest and fewer than one in five exits following evening nest enlargement or pre-darkness returns and entries evolved into some form of orientation. The majority of wasps that did not orient following a visit to the nesting site either oriented previously following a morning return from their sleeping roost, feeding station, or basking place or subsequently fed on honeydew or nectar or basked in the sun instead of searching for prey. Certain wasps that did not orient following morning visits inside their nests had done so the previous evening. Other wasps that did not make an orientation flight may have done so earlier in the morning before I arrived at the study site. Change in temperature may partly regulate the duration and extent of an orientation flight as the wasp's movements noticeably increased in rapidity with increased temperature during midday.

Although orientation flights have been described for a number of sphecid species (Evans 1966), few authors conclusively ascertained the function(s) of these flights. Tinbergen (1932, 1935) and some of his

colleagues probably came closest to as-cribing a specific function to them, that of familiarization with landmarks in the vicinity of the nest to facilitate subsequent provisioning activities. In *Sphex pensylvanicus* the purpose of orientation flights seemingly is to acquaint or reacquaint the female with her surroundings, but as the sallies of some wasps extended a great distance (>13 m) from the nesting site it was difficult to separate the final stage(s) of such flights from the longer (55–60 m) flights to the hunting area. By familiarizing herself with her immediate environs, a female probably facilitates an expeditious straight-line return to the nest with a large and heavy prey. Otherwise, much time and energy would be expended in aerially searching, more or less at random, for the nesting site.

Orientation flights in *Sphex pensylvanicus* were observed only in conjunction with an active nest. They usually decreased in duration and complexity as the wasps made successive trips to and from their nests. Females usually flew to the nesting site with prey from the direction in which they made orientation sallies and left. Females became disoriented upon their return when foreign objects or obstacles were placed near the storm sewer drain cover. If orientation flights served for parasite avoidance rather than reconnaissance (McCorquodale 1986), as one anonymous reviewer suggested, then shouldn't they be made while transporting prey to the nest rather than when exiting it?

Weather clearly influenced the nesting and provisioning activities of females of *Sphex pensylvanicus*. Wasps did not appear at the nesting site on rainy or excessively overcast days. However, on cloudy mornings, females appeared at the nesting site usually within 1 hour after the cloud cover had dissipated. Females arrived at their nests from sleeping roosts on cool, sunny mornings as early as 0635 hrs at an air temperature as low as 10°C. Wasps pro-visioned their nests with katydids at air (shade) temperatures as high as 33°C.

Certain activities of *Sphex pensylvanicus* females regularly occurred from mid-morning through the afternoon, and, in the case of orientation flights and prey transport, into early evening (Fig. 4). Orientation flights preceded or followed many wasp activities and, although somewhat bimodally distributed around the hottest period of the day, were observed from 0859 to 2004 hrs. Periodic visits to nests, also somewhat bimodally distributed around the hottest hours of the day, began at 0934 but were not seen after 1638 hrs probably because females were feeding on honeydew or nectar, basking in the sun, or searching for prey after that time. Provisioning flights were seen interspersedly from late morning (1032 hrs) to early evening (1924 hrs) on sunny days, except for around the noon hour (EST). They were evidently temperature regulated, as they occurred only between 23 and 33°C peaking at 27–29°C. Provisioning times (1030–1300, 1400–1500, 1630–1900 hrs) were sandwiched around times when the wasps were either feeding, basking in the sun, or undertaking some other activity.

In contrast to the somewhat broadly but bimodally distributed orientation flights, periodic visits to the nesting site, and prey transport flights, morning returns to nests from the sleeping roosts and arrivals at the nests before dusk followed by departures for sleeping roosts were strongly pulsed because of the specific functions of these activities (Fig. 5). Flights from sleeping roosts to nests occurred only from 0635 to 1038 hrs and returns to sleeping roosts near dusk took place only between 1832 and 2008 hrs. The latter behavior seemed to be highly synchronized because conspecifics sometimes both arrived at the nesting site and departed from it in pairs only one or a few seconds apart. Feeding on the nectar of flowers was mildly bimodally distributed (1100–1200, 1400–1700 hrs) during late morning and mid- to

late afternoon. Such synchronized feeding could have been governed by temperature, light intensity, and/or nectar availability.

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# Family-Group Names in Sphecidae
## (Hymenoptera: Apoidea)

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*Abstract.*—The known family-group names for Sphecidae are listed with their authors and dates of publication. The status and proper spelling of these names are reviewed. The only major change is that Bembicinae Latreille 1802 has priority over Nyssoninae Latreille 1804. The subtribe Gastrosericina André 1886 has priority over Tachytina G. Bohart 1951. Alyssontini and Chloriontini are the correct spellings for Alyssonini and Chlorionini, respectively. Crabronidae is shown to be the correct name for the Larridae of recent authors; Larridae being a younger name. The gender of the genus *Pison* is discussed, and is regarded as neuter. Some recent developments in the classification of Sphecidae are reviewed.

Usage of family-group names is governed by priority just as with generic and species level names. The stability of subfamily and tribal names is as important as that of species and genera, but all too often the status of family-group names is ignored. Unfortunately this was the case when *Sphecid Wasps of the World* was published (Bohart and Menke 1976). In the last 20 years work on Sphecidae has intensified, and phylogenetic research currently in progress by several scientists may result in rearrangements of some higher taxa. Thus a review of family-group names in Sphecidae that will enable others to determine priorities is very appropriate now. Family-group names for Pompilidae were treated by Day (1981) and those for bees by Michener (1986).

Various problems arise in a study of family-group names. The first is finding all of the names in the vast literature available, and another is determining the earliest (oldest) use of any particular name. A third problem is determining the actual dates of publication of two or more works appearing the same year. I have tried my best to locate all family-group names for Sphecidae, and have enlisted the help of others in this endeavor. Yet, some may have been missed. I would appreciate hearing from anyone who knows of omitted names. Family-group names of fossil taxa are included as a separate section.

A good starting point when searching for family-group names is Handlirsch (1925). He cited many names although I found occasional errors and the original source for each one must be checked. Dalla Torre's (1897) catalog is another useful source of family-group names; he also gave derivations of generic names.

During this study I became curious about who first proposed identifying family names with the ending -idae. William Kirby (1813:88), in a long footnote in his paper on Strepsiptera, suggested using the suffix -idae to denote subsections of insect orders [i.e., families]. Subsequent workers adopted Kirby's proposal and -idae became the standard family suffix.

## THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE

Other authors have presented rather exhaustive discourses on how the Code ap-

plies to family-group names and various problems that can arise: Fitton and Gauld 1976, Michener 1986, Sabrosky (in press). The following notes outline the more important provisions of the 3rd edition of the International Code of Zoological Nomenclature (1985) that govern family-group names in Sphecidae.

1. Family-group names must be based on the stem of a generic name (Art. 11f). The stem is based on the genitive (possessive) case of the generic name. Some commonly used names in Sphecidae have had to be emended because they were not derived from correct stems. For example, Alyssontini is correct, not Alyssonini. Names not based on genera are unavailable. Examples of these are found in Ohl (1996).

2. Family-group names based on the same type-genus take the same author and date regardless of rank (Art. 36). Latreille (1802b) proposed Sphegimae [correctly Sphecinae]. Thus Sphecidae, Sphecinae and Sphecini all take Latreille 1802 as their author.

3. Family-group names are subject to the rules of priority (Art. 23) but there are rare exceptions (Art. 40b) that have to do with usage. For example, Pelopoeinae Leach 1815 was based on the genus *Pelopoeus* Latreille which became a synonym of *Sceliphron* Klug. Ashmead (1899) proposed the family-group name Sceliphrinae, and since then it has been nearly universally used for the group. Art. 40b permits maintenance of the younger name, and it takes the date of the older name it has replaced. Thus Sceliphrinae is dated 1815. Although I understand the reason for emending the date of publication in this way, I personally dislike the practice.

4. New family-group names have appeared in theses or their abstracts (Budrys 1988, Ohl 1993), but Art. 8b indicates that any work that includes a disclaimer (i.e., Budrys 1988) is not pub-

lished. The same Article may apply in the case of Ohl (1993) and Art. 9(11) may also be relevant in his case; deposition of a thesis in a library does not constitute publication.

5. Family-group names based on vernaculars such as in Lepeletier 1845 (French: Cercérites) may be available under the provisions of Article 11f iii. It is difficult to determine if names are French vernaculars if no accent is present because the ending -ites is sometimes correct in both Latin and French. So I have also given the first recognizable Latin version of such names in brackets.

## CHRONOLOGICAL LIST OF FAMILY-GROUP NAMES IN SPHECIDAE

This list starts with the oldest author proposing family-group names. Under each author are all of the names proposed in that publication followed by the page where the name or names are found. This is followed by the type genus and the stem upon which the family-group name should be based. Whenever necessary I have clarified spellings or provided other information in brackets. Complete citations for each author are in the Literature Cited.

### Latreille 1802a (April):

Apiariae, p. 425. *Apis* Linnaeus 1758, Ap-.

### Latreille 1802b (November):

Sphegimae, p. 331. *Sphex* Linnaeus 1758, Sphec- [Spheg- is incorrect, see Discussion below].

Melliniores, p. 337. *Mellinus* Fabricius 1790, Mellin-.

Crabronites, p. 340 [printed as "140" in error in some copies of the book]. *Crabro* Fabricius 1775, Crabron-.

Bembiciles, p. 343. *Bembex* Fabricius 1775 [recte *Bembix*], Bembic-.

Philantores, p. 365. *Philanthus* Fabricius 1790, Philanth-.

## Latreille 1804:

Nyssonii [recte Nyssonini], p. 180. *Nysson* Latreille 1802, Nysson- [The correct stem has a t after the n, however, the International Commission on Zoological Nomenclature in Opinion 1115 (1979) ruled that Nyssoninae should be maintained and the name was added to the Official List of Family-Group Names in Zoology. Hence the legal stem is Nysson-. For explanation of the grammatically correct stem see Discussion below].

## Latreille 1810:

Larratae, p. 289, 438. *Larra* Fabricius 1793, Larr-.

## Leach 1815:

Pelopaeida [recte Pelopoeida], p. 150. *Pelopaeus* Latreille 1802 [recte *Pelopoeus*], Pelopoe-.

Oxybellida [recte Oxybelida], p. 152. *Oxybelus* Latreille 1797, Oxybel-.

## Dahlbom 1835:

Pemphedronides, p. 2, 6, 8 [recte Pemphredonides]. *Pemphredon* Latreille 1797, Pemphredon- [Corrected to Pemphredonides in Isis von Oken 1836, Heft 4, col. 288, and cited as Pemphredonidae in Dahlbom 1842, p. 1. According to Don Cameron, *Pemphredon* is a feminine Greek word that means 'a kind of wasp'. Hence the correct stem is Pemphredon-.]

## Shuckard 1840:

Ampulicidae, p. 178, 180. *Ampulex* Jurine 1807 [not specifically listed], Ampulic-.

## Dahlbom 1842:

Dolichuridae, p. 3. *Dolichurus* Latreille 1809, Dolichur-.

## Lepeletier 1845:

Cercérites, p. 1. *Cerceris* Latreille 1802, Cercer-. [Thomson 1870, p. 207 and 247 gave the latinized spelling Cerceridae]

Gorytites, p. 54. *Gorytes* Latreille 1804, Goryt-. [Costa 1859, p. 3, 26 and 55, gave the spelling Goritini but this may have been an Italian vernacular. The proper spelling would have been Gorytini. Dalla Torre 1897 (October), p. 535, gave the latinized spelling Gorytinae. Acloque 1897, p. 80, used the name Gorytesii.]

Trypoxylites, p. 224. *Trypoxylon* Latreille 1797, Trypoxyl-. [Thomson 1870, p. 207 and 250 gave the latinized spelling Trypoxylidae. The genitive of the neuter name *Trypoxylon* is Trypoxyl-, not Trypoxylon-. Incorrect use of the last stem resulted in the improperly spelled tribal name Trypoxylonini in many publications.]

Astatites, p. 231. *Astata* Latreille 1797, Astat-. [de Saussure 1867, p. 65, gave the latinized spelling Astatii which should have been spelled Astatini].

## Costa 1858:

Psenini, p. 4, 21. *Psen* Latreille 1797, Psen-.

## Costa 1859:

Stizini, p. 2, 4, 55. *Stizus* Latreille 1802, Stiz-.

## André 1886:

Ammophilidae, p. 50. *Ammophila* Kirby 1798, Ammophil-

Gasterosericidae [recte Gastrosericidae] p. 51. *Gastrosericus* Spinola 1838, Gastroseric- [Spelled correctly by André 1888, p. 211].

## Cresson 1887:

Mimesidae, p. 119. *Mimesa* Shuckard 1837, Mimes-.

## de Saussure 1892:

Podiites, p. 419. *Podium* Fabricius 1804, Podi- . [Ashmead 1899, p. 348, gave the latinized spelling Podiinae].

Larradidae, p. 471. *Larrada* Smith 1856, Larrad-.

### Fox 1895:

Lyrodini, p. 302. *Lyroda* Say 1837, Lyrod-.

Diploplectrini, p. 302. *Diploplectron* Fox 1893, Diploplectr-.

Miscophini, p. 302. *Miscophus* Jurine, 1807, Miscoph-.

Bothynostethini, p. 302. *Bothynostethus* Kohl 1884, Bothynosteth-.

Dinetini, p. 305. *Dinetus* Panzer 1806, Dinet-.

### Dalla Torre 1897:

Exeirinae, p. 534. *Exeirus* Shuckard 1838, Exeir-.

Entomosericinae, p. 557. *Entomosericus* Dahlbom 1845, Entomoseric-.

Alysoninae [recte Alyssontinae], p. 562. *Alyson* Panzer 1806 [recte *Alysson*], Alyssont- [see Discussion below for explanation of correct stem].

Sericophorinae, p. 577. *Sericophorus* Smith 1851, Sericophor-.

Nitelinae, p. 697. *Nitela* Latreille 1809, Nitel-.

### Ashmead 1899:

Anacrabroninae, p 163. *Anacrabro* Packard 1866, Anacrabron-.

Lindeniinae, p. 163. *Lindenius* Lepeletier and Brullé 1834, Lindeni-.

Thyreopinae [recte Thyreopodinae], p. 164. *Thyreopus* Lepeletier and Brullé 1834, Thyreopod-. [According to Don Cameron, *Thyreopus* is a compound Greek word meaning 'shield-foot' and the proper stem is thus Thyreopod-.]

Rhopalinae, p. 164. *Rhopalum* Stephens 1829, Rhopal-. [This name is a possible junior homonym of the heteropteran family-group name Rhopalidae Amyot & Serville, 1843, based on *Rhopalus* Schilling, 1827.]

Pisoninae [recte Pisinae], p. 241. *Pison* Jurine 1808, Pis-. [According to Don Cameron, it is impossible to know the true derivation of Jurine's genus *Pison*. If the name is based on the Latin word for pea, pisum, gender neuter, then the

proper stem is Pis-. However, if the name was the Greek spelling of the common Roman proper family name Piso, gender masculine, then the correct stem is Pison-. See my comments on the gender of *Pison* under Discussion farther on. Currently this family-group name is treated as a synonym of Trypoxylini.]

Sceliphroninae [recte Sceliphrinae], p. 349. *Sceliphron* Klug 1801, Sceliphr-. [According to Don Cameron, *Sceliphron* is from the neuter of a Greek adjective meaning lean, slender; hence the correct stem is Sceliphr-].

### Fernald 1905:

Chlorioninae [recte Chloriontinae], p. 166. *Chlorion* Latreille 1802, Chloriont-. [See Discussion below for explanation of correct stem].

### Turner 1914:

Paranyssoninae [recte Paranyssontinae], p. 337. *Paranysson* Guérin-Méneville, 1844, Paranyssont-. [see comments under Nyssonii Latreille 1804 above].

### Turner 1915:

Arpactinae, p. 67. *Arpactus* Panzer 1805, Arpact-.

### Rohwer 1916:

Hoplisini, p. 654, 656. *Hoplisus* Lepeletier 1832, Hoplis-.

### Börner 1919:

Palarini, p. 185. *Palarus* Latreille 1802, Palar-.

### Handlirsch 1925:

Heliocausini, p. 807. *Heliocausus* Kohl 1892, Heliocaus-.

### Bradley 1926:

Soleniini, p. 1029. *Solenius* Lepeletier and Brullé 1835, Soleni-

**Brues and Melander 1932:**

Dimorphidae, p. 503. *Dimorpha* Panzer 1806, Dimorph-.

**Pate 1935:**

Pemphilidae [recte Pemphilididae], p. 246. *Pemphilis* Risso 1826, Pemphilid-.

**Pate 1936:**

Karossiini, p. 151. *Karossia* Arnold 1929, Karossi-.

**Bohart, G. E. 1951:**

Tachytini, p. 945. *Tachytes* Panzer 1806, Tachyt-.

**Evans 1959:**

Ammoplanini, p. 182, 189. *Ammoplanus* Giraud 1869, Ammoplan-.

**Bohart and Menke 1963:**

Prionyxina [recte Prionychina], p. 94, 141. *Prionyx* Vander Linden 1827, Prionych-.

**Bohart, R. M. 1966:**

Aphilanthopsina [recte Aphilanthopina], 158. *Aphilanthops* Patton 1881, Aphilanthop-.

**Menke 1967:**

Odontosphecini, p. 144. *Odontosphex* Arnold 1951, Odontosphec-.
Pseudoscoliini, p. 147. *Pseudoscolia* Radoszkowski 1876, Pseudoscoli-.
Eremiaspheciini, p. 148. *Eremiasphecium* Kohl 1897, Eremiaspheci-.
Philanthinina, p. 148. *Philanthinus* de Beaumont 1849, Philanthin-.

**Menke 1968:**

Scapheutina, p. 91. *Scapheutes* Handlirsch 1887, Scapheut-.

**Gittins 1969:**

Psenuli [recte Psenulina], p. 50. *Psenulus* Kohl 1897, Psenul-.

**Nagy 1969:**

Heterogynidae [emended to Heterogynai-dae in Opinion 1445, Intern. Comm. Zool. Nomencl. 1987:150–151], p. 7. *Heterogyna* Nagy 1969, Heterogyna-

**Bohart and Horning 1971:**

Stictiellina, p. 1. *Stictiella* Parker 1917, Stictiell-.

**Bohart and Menke 1976:**

Stangeellina, p. 87. *Stangeella* Menke 1962, Stangeell-.
Stigmina, p. 175, 185. *Stigmus* Panzer 1804, Stigm-.
Laphyragoginae, p. 217. *Laphyragogus* Kohl 1889, Laphyragog-.
Xenosphecinae, p. 437. *Xenosphex* Williams 1954, Xenosphec-.

**Lomholdt 1985:**

Mesopalarina, p. 22. *Mesopalarus* Brauns 1899, Mesopalar-.

**Budrys 1988:**

Several family-group names in Pemphredoninae were proposed in this brief, printed summary of his thesis, and it does not qualify as a publication because the cover has a disclaimer in Russian, "to be considered a manuscript" (see Art. 8b of the International Code of Zoological Nomenclature.)

**Menke 1989:**

Spilomenina, p. 740. *Spilomena* Shuckard 1838, Spilomen-.

**Ohl 1993:**

A number of suprageneric names were introduced in this work but some are not based on generic names and are therefore not available (Art. 11f). Also Ohl's printed thesis may not qualify as a publication under Art. 8b or Art. 9(11) of the Code.

**Ohl 1996a:**

The suprageneric names first proposed by Ohl (1993) are validly published here but some are unavailable because they are not based on generic names. The names in

question are Lutifera, Eusphecinomorpha, and Acutoclypeata. However, three of Ohl's names, Sphecinomorpha, Palmodomorpha, and Ammophilomorpha, could be construed as valid since they are based on generic names with -morpha endings. The suffix -morpha has been used in some insect orders to designate infraorders, as in the Heteroptera (Nepomorpha and others). However the Code does not govern ordinal-group names.

### Nemkov and Lelej 1996:

Clitemnestrina, p. 11. *Clitemnestra* Spinola 1851, Clitemnestr-.

Olgiina, p. 11. *Olgia* Radoszkowski 1877, Olgi-.

Argogorytina, p. 11. *Argogorytes* Ashmead 1899, Argogoryt-.

Handlirschiina, p. 12. *Handlirschia* Kohl, 1897, Handlirschi-.

### DISCUSSION

*Stem of some Greek generic names ending in -on:* According to Don Cameron a "t" has to be inserted after the "n" in *Alysson* and *Nysson* for the stem to be correct grammatically. The explanation is that these generic names are masculine nominative participles of Greek verbs. The genitive of *Alysson* is alyssontos, of *Nysson* nyssontos, thus the tribal names are Alyssontini and Nyssontini (as noted earlier, the spelling Nyssoninae (without a t) was conserved in Opinion 1115 of the International Commission on Zoological Nomenclature (1979). Paranyssonini is properly emended to Paranyssontini (a synonym of Miscophini). The genitive of *Chlorion*, based on the Greek word for the color green, is chloriontos, thus the tribal name is Chloriontini.

The correct stems for *Pemphredon* and *Trypoxylon* have been explained earlier in this paper.

*Gender of the genus* Pison: Jurine (in Spinola 1808) did not indicate the derivation of his new genus *Pison*, and there is no evidence in the description of its gender.

The only included species was a patronym, *jurini* Spinola. Shuckard (1838) appears to have been the next author to treat the genus, and he clearly regarded it as masculine. Subsequent workers followed Shuckard until Kohl (1884, 1885) who interpreted the gender as neuter (earlier de Saussure, 1867, described one new species, *tahitense*, that indicates he regarded *Pison* as neuter). Although some of his contemporaries continued to treat *Pison* as masculine, Kohl's interpretation of the genus as neuter would prevail. Kohl was, after all, the foremost sphecid worker of his time. Dalla Torre (1897) in his world catalog of Sphecidae, considered *Pison* as neuter, and this, with minor exceptions, has remained its gender for the last 100 years. A considerable number of taxonomic papers published during this period have all treated the genus as neuter.

The Code does not seem to directly deal with this problem. Article 30 (d) addresses the gender of non-Latin and Greek names, but *Pison* is from one of these languages according to Don Cameron. Under the principle of first revisor, Shuckard (1838) could be interpreted as having established the gender of *Pison* as masculine. However, the principle of stability argues for maintenance of *Pison* as neuter, and this is my position. Thus the correct stem for Ashmead's (1899) "Pisoninae" becomes Pis- and his family group name becomes Pisinae. Ironically it is clear from the suffixes of the three species Ashmead (1899:251) listed under *Pison* that he had no clear idea of its gender (*laevis, conformis, fasciatum*).

*Sphecidae versus Sphegidae:* Authors of the last century often spelled the family Sphegidae following Latreille's (1802b) original grammatical error in using Spheg- as the stem for the family-group name. Leach (1815) used the correct stem Sphec- and Tillyard (1926) was one of the first people to clearly explain why this was correct. According to Don Cameron (in litt to Menke) the genitive of the Greek word "wasp" is sphêkos. To quote Cameron,

"You get the stem of the word by removing the genitive singular ending -os leaving the stem sphek-''. Latinized this becomes Sphec-.

*Sceliphrini versus Pelopoeini:* Pelopoeus Latreille was made a junior synonym of *Sceliphron* Klug by Kohl (1890:102), and apparently because of this, Ashmead (1899) proposed the name Sceliphrini. This name has been universally used all of this century instead of the older Pelopoeini Leach 1815, and Article 40b of the International Code of Zoological Nomenclature permits maintenance of Sceliphrini. Article 40b also states that the younger name (Sceliphrini) takes the date of the name it has replaced (Pelopoeini), in this case 1815. Thus Podiini de Saussure, 1892 is a synonym of Sceliphrini 1899 (1815).

## SOME COMMENTS ON CURRENT SPHECID CLASSIFICATION

*Apoidea versus Sphecoidea:* A growing consensus of workers share the belief that sphecids and bees form a monophyletic group and thus belong in one superfamily (see for example, Brothers 1975, Gauld and Bolton 1988, Finnamore and Michener 1993, Hanson and Gauld 1995). Michener (1986) demonstrated that Apoidea is an older name than Sphecoidea.

*Status of Heterogynaidae:* The status of this group has vacillated recently between a subfamily of Sphecidae or as a family. In the most recent phylogenetic analysis, Brothers and Carpenter (1993) treated the group as a family.

*Ohl's classification of Sphecinae:* Ohl's (1996a) phylogenetic analysis has resulted in some changes in the way genera are grouped in this subfamily. The genus *Stangeella* is shown to be most closely allied to Sphecini. Unfortunately instead of simply using existing family-group names with appropriate tribal and subtribal endings, he introduced a few new names that are not based on existing genera. Thus they are unavailable. Also he was apparently unaware of priorities among existing

family-group names. An approximation of his classification is shown below using available family-group names; the result is five tribes instead of the usual three. However, my interpretation may not accurately express Ohl's own ideas. Included genera are in parentheses. Ohl's new family-group names are included in brackets. The ending -ina indicates subtribe. No valid family-group names are available for two of his names, Palmodomorpha and Acutoclypeata.

Chloriontini (*Chlorion*)
Sceliphrini [Lutifera]
    Podiina (*Dynatus, Penepodium, Trigonopsis, Podium*)
    Sceliphrina (*Chalybion, Sceliphron*)
Stangeellini (*Stangeella*)
Sphecini [Eusphecinomorpha]
    Sphecina (*Sphex, Isodontia*)
    Prionychina (*Prionyx, Palmodes, Chilosphex*) [the last two genera are grouped under Palmodomorpha]
Ammophilini
    [Acutoclypeata] (*Hoplammophila, Eremnophila*)
    Ammophilina [Ammophilomorpha] (*Podalonia, Parapsammophila, Eremochares, Ammophila*)

In a more recent paper, Ohl (1996b) reiterated the monophyly of *Dynatus, Penepodium, Trigonopsis* and *Podium* and he called the assemblage the ''Podiinae'' which he regards as a subgroup of ''Sceliphrina''. I interpret his Podiinae as identical with Podiina in the outline I have just given for Ohl (1996a), and his Sceliphrina as coordinate with Sceliphrini. Ohl (1996b) says his unorthodox hierarchical system that ignores traditional family-group name suffixes follows Hennig (1969). To quote Ohl: '' . . . no use is made of any Linnaean categories (familia, subfamilia, tribus, etc.) to characterize the absolute rank of monophyletic taxa, but I refer to a certain taxon [by] assigning a proper name instead.'' Ohl admits '' . . . that abandoning the Linnaean categories leads

to the loss of any information tradionally implied by the suffixes formerly associated with certain categories (e.g. -idae for the category 'family')".

Lauterbach (1996) introduced the use of standard suffixes for the various family-group taxa in Ohl (1996a), namely -ozoa and -zoon. Consideration of Lauterbach's proposal is outside the scope of the present paper.

*Current interpretation of Crabroninae:* This subfamily includes the Larrinae following Lomholdt (1985), Menke (1988), Hanson and Menke (1995), and Menke and Fernández (1996).

*Status of Mesopalarina:* The affinities of *Mesopalarus* have always been problematical (Bohart and Menke, 1976; Lomholdt, 1985) until Gess (1996) described the hitherto unknown male. Gess's study demonstrated a close relationship with *Palarus*. Because of that, I have placed Mesopalarina as a subtribe of Palarini. However, monotypic subtribes are probably unwarranted in Palarini.

*Subtribes in Gorytini:* Nemkov and Lelej (1996) analyzed this tribe cladistically and recognized six subtribes, four of which were new. I have provisionally adopted their classification here.

RESULTS OF FAMILY-GROUP NAME SURVEY

The following tabulation outlines the correct names for all higher taxa. Junior synonyms are listed in parentheses. There are only three name changes, one of which is simply a minor spelling correction, and these are indicated in boldface. The only one of major consequence is Bembicinae for the Nyssoninae. The subfamily arrangement used here basically follows Bohart and Menke (1976) although it reflects some subsequently published opinions of groupings. Finnamore (1993) elevated most subfamilies to families and regrouped some taxa. Laphyragoginae was included in Astatidae; Xenosphecinae in Mellinidae; and Entomosericinae in Nys-

sonidae. I have not attempted to reflect Finnamore's classification here. Subtribes are identified by the suffix -ina.

Lomholdt (1982) divided the family into two families: Sphecidae and Larridae, the latter containing all but the Ampulicinae and Sphecinae. However Larridae is not the oldest available name for this group sensu Lomholdt. The family name would have to be chosen from one of the following established by Latreille (1802b), i.e., Mellinidae, Crabronidae, Bembicidae, and Philanthidae. Acloque (1897) recognized two apparent families, Crabronidi and Sphegidi, the first essentially the same as Larridae sensu Lomholdt. However Acloque's Sphegidi also included pompilids and thus is not comparable to Sphecidae of Lomholdt. Nevertheless I think Acloque should be considered as the first person to use Crabroninae and thereby establish it as the name for Crabronidae sensu Lomholdt.

Apoidea Latreille 1802a (Sphecoidea Latreille 1802b)
Heterogynaidae Nagy 1969 (originally spelled Heterogynidae)
Sphecidae Latreille 1802b
Ampulicinae Shuckard 1840
  Ampulicini Shuckard 1840
  Dolichurini Lepeletier 1845
Sphecinae Latreille 1802
  Sceliphrini Ashmead 1899 (1815—Art. 40b.i) (Pelopoeini Leach 1815, Podiini de Saussure 1892, Chloriontini Fernald 1905)
    Sceliphrina Ashmead 1899 (1815) (Pelopoeini Leach 1815, Podiini de Saussure 1892, Chloriontini Fernald 1905)
    Stangeellina Bohart and Menke 1976
  Sphecini Latreille 1802
    Sphecina Latreille 1802
    Prionychina Bohart and Menke 1963
    Ammophilini André 1886
Pemphredoninae Dahlbom 1835
  Psenini Costa 1858 (Mimesini Cresson 1887)

Psenina Costa 1858 (Mimesina Cresson 1887)

Psenulina Gittins 1969

Pemphredonini Dahlbom 1835

Pemphredonina Dahlbom 1835

Stigmina Bohart and Menke 1976

Spilomenina Menke 1989

Ammoplanina Evans 1959

Astatinae Lepeletier 1845

Astatini Lepeletier 1845 (Diploplectrini Fox 1895, Dimorphini Brues and Melander 1932)

Dinetini Fox 1895

Laphyragoginae Bohart and Menke 1976

Crabroninae Latreille 1802 (Larrinae Latreille 1810)

Larrini Latreille 1810 (Gastrosericini André 1886, Larradini de Saussure 1892)

Larrina Latreille 1810 (Larradina de Saussure 1892)

**Gastrosericina** André 1886 (Tachytina Bohart 1951)

Miscophini Fox 1895 (Lyrodini Fox 1895, Sericophorini Dalla Torre 1897, Nitelini Dalla Torre 1897, Paranyssontini Turner 1914)

Palarini Börner 1919

Palarina Börner 1919

Mesopalarina Lomholdt 1985

Trypoxylini Lepeletier 1845 (Pisini Ashmead 1899)

Bothynostethini Fox 1895

Scapheutini Menke 1968

Oxybelini Leach 1815

Crabronini Latreille 1802 (Anacrabronini Ashmead 1899, Lindeniini Ashmead 1899, Thyreopodini Ashmead 1899, Rhopalini Ashmead 1899, Soleniini Bradley 1926, Pemphilidini Pate 1935, Karossiini Pate 1936.)

Entomosericinae Dalla Torre 1897

Xenosphecinae Bohart and Menke 1976

**Bembicinae** Latreille 1802 (Nyssoninae Latreille 1804)

Mellinini Latreille 1802

Heliocausini Handlirsch 1925

**Alyssontini** Dalla Torre 1897

Nyssonini Latreille 1804 (spelling conserved in Opinion 1115)

Gorytini Lepeletier 1845 (Arpactini Turner 1915, Hoplisini Rohwer 1916)

Clitemnestrina Nemkov and Lelej 1996

Olgiina Nemkov and Lelej 1996

Argogorytina Nemkov and Lelej 1996

Exeirina Dalla Torre 1897

Handlirschiina Nemkov and Lelej 1996

Gorytina Lepeletier 1845 (Arpactina Turner 1915, Hoplisina Rohwer 1916)

Stizini Costa 1859

Bembicini Latreille 1802

Bembicina Latreille 1802

Stictiellina Bohart and Horning 1971

Philanthinae Latreille 1802

Eremiaspheciini Menke 1967

Odontospheciini Menke 1967

Philanthini Latreille 1802

Aphilanthopini Bohart 1966

Pseudoscoliini Menke 1967

Cercerini Lepeletier 1845

## FOSSIL FAMILY-GROUP NAMES

Alexander Rasnitsyn provided me with family-group names of fossil taxa. Each family-group name is followed by the genus on which it is based, and the proper stem.

Angarosphecidae Rasnitsyn (1975:109). *Angarosphex* Rasnitsyn 1975, Angarosphec-

Baissodidae Rasnitsyn (1975:122). *Baissodes* Rasnitsyn 1975, Baissod-

Rasnitsyn (1980) synonymized Angarosphecidae under Sphecidae, reducing it to a subfamily of the latter. Rasnitsyn (in litt. to Menke) states that Baissodidae should be synonymized under Angarosphecinae, but he has yet to publish this change.

## ACKNOWLEDGMENTS

name for this subfamily. This germ of information finally prodded me to dig into the family-group names of Sphecidae. Don Cameron, a Latin and Greek scholar at the University of Michigan, Ann Arbor, graciously took the time to examine most of the type-genera of family-group names and verify the proper stems for them. He also discussed various problems with me on the telephone. Curt Sabrosky, Medford, New Jersey, and Chris Thompson, Systematic Entomology Lab., USDA, Washington D.C., both gave their expertise on thorny nomenclatorial problems that I encountered. Sabrosky let me examine his huge MS on the family-group names of Diptera (Sabrosky in press), and Thompson let me examine Evenhuis' monumental MS on the literature of Diptera (Evenhuis in press). Woj Pulawski, California Academy of Sciences, San Francisco, reviewed several versions of my MS, constantly bugging me to do better. He also discovered names I had missed and furnished copies of literature not available to me. Charles Michener and Gabriel Melo, University of Kansas, Lawrence discovered other missed names in their review of the MS. I. M. Kerzhner, Zoological Institute, St. Petersburg; Curtis Sabrosky; Alexander Rasnitsyn, Paleontological Institute, Moscow; James Carpenter, American Museum of Natural History, New York; and Colin Vardy, The Natural History Museum, London, read the MS and offered many suggestions. Rasnitsyn also furnished me with family-group names of fossil taxa. Eric Grissell, Systematic Entomology Laboratory, USDA, Washington D.C., sent me copies of Kirby (1813), Thomson (1870), and Acloque (1897).

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# A Review of New Guinean *Ochleroptera* Holmberg 1903 (Hymenoptera: Sphecidae)

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*Abstract.*—The New Guinean species of *Ochleroptera* Holmberg are reviewed, and a key for their identification is provided. *Ochleroptera novaguineensis* Bohart is redescribed, and the following three new species are described: *gendeka, nigroclypeata,* and *obscura.*

*Ochleroptera* Holmberg is a bembicine genus of 12 known species, of which one occurs in North America, one in the Caribbean, 9 in Central and South America, and one in New Guinea (first reported from that island by Bohart 1970). Subsequent to Bohart and Menke (1976), *pygmaea* Brèthes has been transferred to *Pluto* (van Lith 1979), and *sanambrosiana* Pérez D'Angello (1980) was added. During my fieldwork in New Guinea in 1987 and 1988, I collected specimens of an undescribed species, and Colin R. Vardy, then at the British Museum (Natural History), London, United Kingdom, kindly provided additional material. The total number of species is thus brought to 15. All New Guinean species of *Ochleroptera* are reviewed below.

*Ochleroptera* is similar to *Clitemnestra* Spinola 1851, and Bohart and Menke (1976) separated them only by the shape of the first gastral segment, which is comparatively broad in the latter, but elongate in the former. There are several problems with this classification. First, some undescribed Neotropical forms appear to be intermediate, making the distinction of the two genera tenuous (Colin Vardy, pers. comm.). Menke and Fernández (1996:59) concur that the abdominal characters used to separate these two

genera are unreliable in Neotropical species and that *Ochleroptera* may prove to be a synonym. Second, the broad gastral base appears to be plesiomorphic within Gorytini, hence recognition of *Ochleroptera* may make the other genus paraphyletic. Third, elongation of gastral segment I may well have occurred more than once, hence there is no certitude that the New World and New Guinean *Ochleroptera* developed from a single ancestor. Solving these problems, however, is beyond the scope of this paper.

## SOURCES OF MATERIAL

The specimens examined belong to the following institutions:

ANIC: Australian National Insect Collection, c/o Commonwealth Scientific and Industrial Research Organization, Canberra, A.C.T., Australia.

BMNH: British Museum (Natural History), London, United Kingdom; currently: Natural History Museum.

BISHOP: Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

CAS: California Academy of Sciences, San Francisco, California, USA.

UCD: Bohart Museum of Entomology, University of California, Davis, California, USA.

KEY TO NEW GUINEAN SPECIES OF *OCHLEROPTERA*

1. Propodeum adjacent to enclosure with well-defined punctures; setae of head and thoracic dorsum longer (e.g., genal setae at least as long as midocellar diameter) . . . . . . . . . . . . . . 2
– Propodeum adjacent to enclosure with microscopically small, evanescent punctures, practically unsculptured; setae of head and dorsum shorter (e.g., genal setae shorter than midocellar diameter) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2. Thorax and gastral segments II–IV with no yellow markings; legs brownish red (all or largely so); tergum I proportionately longer (Fig. 3) . . . . . . . . . . . . . . *obscura* Pulawski, sp. n.
– At least pronotal collar, metanotum (except laterally), and tergum II marked with yellow; legs black or with yellow markings; tergum I proportionately shorter (Fig. 2) . . . . . . . . . .
   . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *gendeka* Pulawski, sp. n.
3. Clypeus yellow except for narrow brown strip along free margin; female: preepisternal area of mesonotum yellow; tergum I proportionately longer (Fig. 3) . . . . . . . . . . . . . . . . . . . . . *novaguineensis* Bohart
– Clypeus largely black; mesopleuron and propodeum all black; tergum I proportionately shorter (Fig. 2) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *nigroclypeata* Pulawski, sp. n.

## DESCRIPTIONS OF SPECIES

The following characters that vary in other *Ochleroptera* are shared by all four New Guinean species: clypeus flat (not step-like near free margin); scutum with two types of punctures and two types of setae: short setae emerging from small punctures, longer setae emerging from larger punctures (larger punctures sparser than small ones); subalar fossa not marginate below; propodeal enclosure unsculptured, shiny; tergum I with no oblique, basal carinae; laterotergite I absent anteriorly, conspicuously narrow posteriorly; male sternum VIII broadly truncate apically; and yellow are: scapal venter, frons bellow antennal sockets, and narrow paraorbital band extending up to about one third or half of frons height.

### *Ochleroptera gendeka* Pulawski, sp. n.

*Derivation of name.*—Named after the Gendeka people of the Madang Province, Papua New Guinea, in whose territory the type locality is located.

*Diagnosis.*—As in *obscura*, the setae on the interocellar area and scutum anteriorly are longer than a midocellar diameter in *gendeka*. In *gendeka*, however, at least the pronotal collar, metanotum (except later-

ally); and tergum II are marked with yellow rather than being black; the legs are all black or marked with yellow; and tergum I is proportionately shorter (Fig. 2).

*Description.*—Propodeum adjacent to enclosure with well-defined punctures. Tergum I as in Fig. 2. Sternum I not ridged or with rudimentary ridges basally. Clypeus yellow (except narrow, black fascia along free margin) to largely black (see Variation below). Flagellum black or flagellomeres I and II brown ventrally (at most weakly so in males). Thorax black, but the following are yellow: pronotal collar, pronotal lobe (all black in some females), preepisternal area of mesonotum in many females and most males, metanotum (except laterally), scutellum in many males (see also Variation below). Gaster black, with yellow apical fascia on terga I and II (fascia on tergum II continuous to broadly interrupted mesally). Female terga III–VI all black or terga III–V fasciate apically and tergum VI yellow laterally (a frequent combination includes black terga III and IV and fasciate tergum V). Male terga III–VI varying from all black (Western Highlands specimens) to fasciate apically (most specimens from Madang Province); tergum VII either yel-

Fig. 1.  Collecting localities of *Ochleroptera* in New Guinea.

low or black. Femora all black or with apicoventral spot (all venter yellow in some males). Foretibia black except outer surface yellow (also inner surface in some females); mid- and hindtibiae all black, or yellow basodorsally or dorsally, or brown or yellow ventrally. Foretarsus varying from black to yellow, mid- and hindtarsi varying from black to brown.

*Variation.*—In most specimens examined, the clypeus is largely yellow, with only a narrow black band along the free margin (width of black band varying from about half antennal socket diameter to more than one diameter mesally in some females), and the female scutellum is all black. The single female specimen from Goilala in the Owen Stanley Range, has the clypeus largely black, yellow only along frontoclypeal margin (width of yellow band about equal to antennal socket), and a narrow yellow strip adjacent to scutellar hindmargin.

*Prey.*—Three females were collected as they were flying with prey. All three prey are adult Cicadellinae, two of which are Dorycephalini (det. Norman D. Penny).

*Records.*—(Fig. 1).—Holotype: ♀, Papua New Guinea: Madang Province: 5 air km NE Mundiai Pass at 5°46′S 145°09′E, 2500 m, 14 May 1988, W.J. Pulawski (CAS). Paratypes: PAPUA NEW GUINEA: Madang Province: 5 air km NE Mundiai Pass, circa 8°16′S, 146°59′E, 21–31 Dec 1957, W.W. Brandt (1 ♀, BISHOP). Madang Province: 5 air km NE Mundiai Pass at 5°46′S 145°09′E, 2500 m, W.J. Pulawski, 14 May 1988 (3 ♀, 2 ♂, CAS) and 17 May 1988 (1 ♀, 11 ♂, CAS); Pandambai, 6 air km W Bundi at 5°38′S 145°11′E, 2300 m, W.J. Pulawski, 10–13 May 1988 (7 ♀, 9 ♂, CAS), 15 May 1988 (2 ♀, CAS), and 18 May 1988 (30 ♀, CAS), 31 May 1988 (7 ♂, CAS), 1 June 1988 (3 ♂, CAS). Central Province: Goilala at Loloipa River in Owen Stanley Range, circa 8°16′S, 146°59′E, 21–31 Dec 1957, W.W. Brandt (1 ♀, BISHOP). Morobe Province: upper Gumi [Creek] near Wau [7°12′S 146°25′], 20 Mar 1981, H. Roberts (2 ♂, BMNH); Wau, 1000 m, Oct 1979, I. Gauld (1 ♀, BMNH). Western Highlands: Mt. Hagen Range: Murmur Pass, 8700 ft [= 2870 m], 27 Oct–20 Dec 1961, W.W. Brandt (7 ♀, 3 ♂, ANIC).

## *Ochleroptera nigroclypeata*
Pulawski, sp. n.

*Derivation of name.*—The Neolatin feminine adjective *nigroclypeata* is coined from two Latin words: niger (for black) and clypeus.

*Diagnosis.*—The female of *nigroclypeata* (the male is unknown) can be recognized

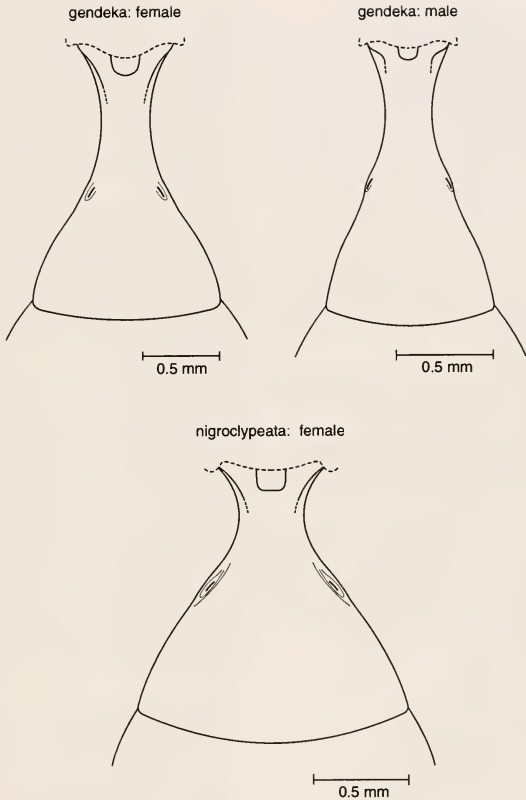Fig. 2. *Ochleroptera gendeka* and *nigroclypeata*: outline of tergum I.

by the combination of the clypeus largely black, propodeum practically unsculptured adjacent to the enclosure, and the setae adjacent to the hypostomal carina shorter than a midocellar diameter. In the other New Guinean species, the clypeus is all yellow except largely black in some *gendeka*. Also, tergum I of *nigroclypeata*

(Fig. 2) is proportionately shorter than in the other New Guinean species.

*Description* (female only).—Propodeum adjacent to enclosure with microscopically small, evanescent punctures, practically unsculptured. Tergum I as in Fig. 1. Sternum I irregularly ridged on basal half. Antennal flagellum yellowish basoventrally. Yellow are: clypeus along frontoclypeal suture, pronotal collar (pronotal lobe black), metanotum (except laterally), apical fascia on tergum I; also small apicolateral spot on tergum II and narrow, apicomesal fascia on tergum III in one specimen examined. Legs reddish brown in one specimen; in the other, femora as well as mid- and hindtibiae largely dark, almost black.

Male unknown.

*Prey*.—The holotype female is pinned with a cicadellid nymph, presumably her prey (det. Norman D. Penny).

*Records* (Fig. 1).—*Holotype*: ♀, Papua New Guinea: Morobe Province: NE Wau at 1150 m, 19 Sept 1971, J. Sedlacek (BISHOP). *Paratype*: PAPUA NEW GUINEA: same locality as holotype, 7 Dec 1972, O.W. Richards (1 ♀, BMNH).

## *Ochleroptera novaguineensis* R. Bohart

*Ochleroptera novaguineensis* R. Bohart, 1970:387, ♂. Holotype: ♂, Papua New Guinea: Madang Province: Finisterre Range: Matoko Village in the Saidor area; not Wau in Morobe Province (BISHOP), **present correction**, examined.— Bohart and Menke, 1976:490 (listed).

*Correction of type locality.*—Bohart apparently confused the locality labels of the two specimens he examined. According to the original description, the holotype (deposited at BISHOP) came from Wau, and the single paratype (deposited at UCD) from the Saidor area. In reality, the holotype's locality label indicates the Saidor area as its origin, and the paratype's label (at UCD) gives Wau. The two specimens can be easily identified by the differences indicated in the original description: the holotype has both flagella missing and no yellow markings on tergum IV, whereas

the paratype has one flagellum preserved (glued to a piece of cardboard now) and a broken yellow line on tergum V. Although the International Code of Zoological Nomenclature provides no guidelines for this situation, I treat as the holotype the specimen from BISHOP so labeled by the author and agreeing with the description (i.e., the male from the Saidor area, not the one from Wau).

*Diagnosis.*—This species differs from the other New Guinean *Ochleroptera* in having a light brown rather than black stripe along the clypeal free margin, a pair of yellow spots on the propodeum, and a yellow, apicolateral spot on tergum II. The yellow preepisternal area of the mesopleuron, typical of *novaguineensis*, is also found in some *gendeka*.

*Description.*—Propodeum adjacent to enclosure with microscopically small, evanescent punctures, practically unsculptured. Sternum I transversely ridged on basal half. Tergum I as in Fig. 3. Antennal flagellum yellow brown basally. Yellow are: pronotal collar, pronotal lobe, scutellum mesally, metanotum (except laterally), a pair of spots on propodeum, broad apical fascia on tergum I, a pair of lateral spots on tergum II, and a narrow apical fascia on tergum III. Femora brown, becoming yellowish toward apex; foretibia and foretarsus yellow or foretibia brown on inner surface, midtibia and midtarsus yellow or brown, hindtibia and hindtarsus brown.

*Records* (Fig. 1).—PAPUA NEW GUINEA: **Madang Province**: Northeastern Finisterre Range: Matoko Village (5°41′S 146°33′E, 1500 m alt.) in Saidor area (1 ♂, BISHOP, holotype of *novaguineensis*). **Morobe Province**: Wau (1 ♀, BMNH; 1 ♂, UCD, paratype of *novaguineensis*), Mt. Missim, 7°13′S, 146°49′E, 1600 m (1 ♀, 1 ♂, BISHOP).

## *Ochleroptera obscura* Pulawski, sp. n.

*Derivation of name.*—*Obscura*, a Latin feminine adjective for dark, refers to the coloration of this species.

*Diagnosis.*—*Ochleroptera obscura* has an all black thorax and gastral segments II–
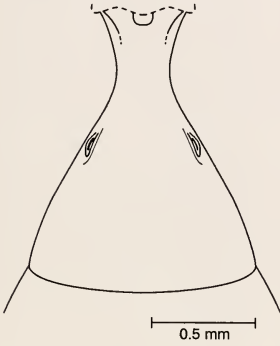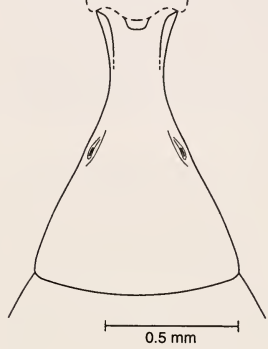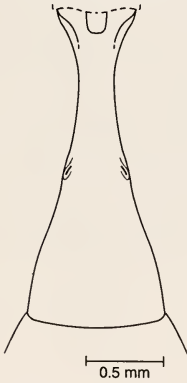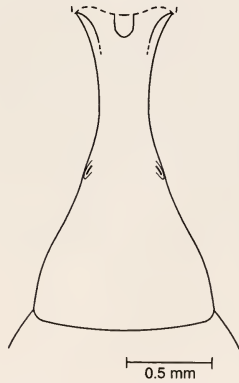
Fig. 3. *Ochleroptera novaguineensis* and *obscura*: outline of tergum I.

V, and reddish tergum I (at least in apical half). In the other three species, at least the pronotal collar, metanotum (except laterally), and tergum II are marked with yellow, and tergum I is black except for apical, yellow fascia. In addition, tergum I of *obscura* is proportionately longer than in the other *Ochleroptera* from New Guinea (Fig. 3).

*Description.*—Propodeum adjacent to enclosure with well-defined punctures. Tergum I as in Fig. 3. Sternum I microsculptured, but with no rugae or ridges. Antennal flagellum reddish brown in female, black in male. Pronotal lobe yellowish brown in female, black in male. Clypeus yellow except narrow black strip along free margin. Legs brownish red in female; in male, forefemur entirely and midfemur largely brownish red, hindfemur, tibiae, fore- and midtarsi brownish red (foretibial outer surface yellow), hindtarsus black. Gaster black except tergum I brownish red (entirely so in female, between spiracles and hindmargin in male); tergum I in male with narrow, apical fascia that is narrowly interrupted mesally.

*Records* (Fig. 1).—*Holotype:* ♀, Indonesia: Irian Barat: Vogelkopf Peninsula: Sururai SW Lake Anggi Giji at 1°24'S 133°55'E, 1900 m, 27 Feb 1963, R. Straatman (BISHOP). *Paratype:* PAPUA NEW GUINEA: **Central Province:** Guar'l [almost certainly a mistake for Guari at 8°07'S 146°51'S], 1900–2100 m, Oct 1968, N.L.H. Krauss (1 ♂, BISHOP).

## ACKNOWLEDGMENTS

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# A Revision of *Protophotopsis* Schuster (Hymenoptera: Mutillidae)

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*Abstract.*—*Protophotopsis*, a rare and incompletely known genus of Sphaeropthalmina, is revised. The following new synonymies are established: *Huacotilla* Casal, female = *Protophotopsis* Schuster, male; *Huacotilla diaguita* Casal, female, and *Huacotilla hepperi* Casal, female = *Protophotopsis* (*Protophotopsiella*) *humeralis* Schuster, male; *Protophotopsis* (*Protophotopsiella*) *humeralis rugosa* Schuster, male = *Protophotopsis* (*Protophotopsiella*) *sulcifrons* (André), female, new combination for *Ephuta sulcifrons* André, incertae sedis; *Protophotopsis* (*Protophotopsis*) *scudderi* Schuster, male = *Protophotopsis* (*Protophotopsis*) *venenaria* (Melander), female. *Protophotopsis* (*Protophotopsis*) *clauseni* n. sp., described and illustrated from Costa Rica and Panama, is the first known Neotropical species of the nominotypical subgenus. A key for the two subgenera and for the males and females of the four species of *Protophotopsis* s. s. is provided. *Protophotopsis* (*Protophotopsiella*) *sulcifrons* and *P.* (*Protophotopsis*) *venenaria* are recorded for the first time from Bolivia and Mexico respectively. The inferred generic relationships are discussed.

The sphaeropthalmine genus *Protophotopsis* was established by Schuster in 1947 for *P. scudderi* Schuster, based on five males collected in Texas and Colorado, USA (he mentioned one additional male from Kansas in 1949). Schuster (1949) and Krombein (1979: 1301), thought that *Mutilla venenaria* Melander, 1903, might be the female sex of *Protophotopsis scudderi*, based on coincident geographic distributions. Schuster described (1949) a South American subgenus of *Protophotopsis*, *Protophotopsiella*, with one additional species with two subspecies: *P. humeralis humeralis* Schuster, from Argentina, and *P. humeralis rugosa* Schuster, from Brazil; their females were unknown. Based on an unspecified "larger number of features in common," Schuster (1958) considered *Protophotopsis* to be closer to his nebulous "Dasymutilline and Pseudomethocine complexes" instead of his "Sphaeropthalmine complex" (*Sphaeropthalma*), as suggested in 1949. Brothers (1975) included *Protophotopsis* in the subtribe Sphaeropthalmina of the tribe

Sphaeropthalmini. The present revision, the first of this poorly collected genus, is based on 31 specimens in addition to the 16 previously known (including Casal's females of *Huacotilla*).

We follow the scutum terminology suggested by Menke (1993) instead of parapsidal furrows (Schuster 1958). We use calcaria to refer to tibial spurs, following previous usage for mutillids. Acronyms for institutions where specimens are deposited are: University of Minnesota Insect Collection (UMIC); American Museum of Natural History, New York (AMNH); U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); The James Entomological collection, Washington State University (WSU); Museum of Comparative Zoology, Harvard University (MCZ); Museo de Invertebrados G.B. Fairchild (MIUP); Muséum National d'Histoire Naturelle, Paris (MNHN); Instituto Nacional de Biodiversidad, Heredia, Costa Rica (INBio).
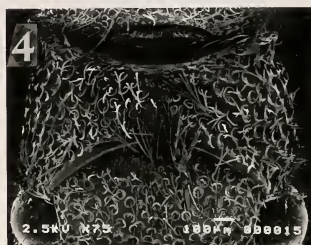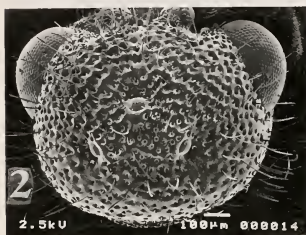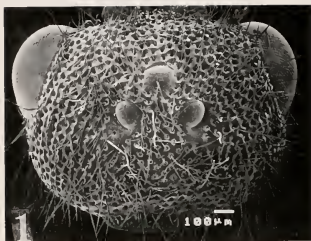
Figs. 1–2. Head of *Protophotopsis* (*Protophotopsis*), males, dorsal view. 1, *P. clauseni*. 2, *P. venenaria*.





Figs. 3–4. Pronotum of *Protophotopsis*, male, dorsal view. 3, *P.* (*Protophotopsis*) *clauseni*. 4, *P.* (*Protophotopsiella*) *sulcifrons*.

## *Protophotopsis* Schuster

*Protophotopsis* Schuster 1947:693–694. Type species: *Protophotopsis* (*Protophotopsis*) *scudderi* Schuster 1947, by original designation and monotypy.

*Huacotilla* Casal 1962:259–261. Type species: *Huacotilla diaguita* Casal 1962, by original designation. **New Synonymy.**

*Diagnosis.*—*Protophotopsis* is the only genus in the Sphaeropthalmina with males that have the anterior pronotal margin distinctly emarginate (Figs. 3, 4). The females of *Protophotopsis* are recognized by the following combination of characters: smooth pygidial area not delimited by lateral carinae, segment I of the gaster sessile with the second (Figs. 7, 8), mandibles bidentate distally, and integument of head and thorax punctate.

Females of the sister genus *Nanotopsis* Schuster (1949) differ from those of *Protophotopsis* in having mandibles edentate distally and the integument of head and thorax reticulate. The diurnal males of both genera share the following characters: felt line on sternum II, and body pubescence of simple and microserrated setae (serrations are visible only at high magnification). The males of *Nanotopsis* are recognized by the following apomorphy: integument of basal half of tergum II finely, longitudinally striate.

The following additional characters will help to recognize *Protophotopsis* within the Sphaeropthalmina: males with anterior margin of clypeus without teeth; mandibles tridentate distally, without a

ventral basal tooth; parapsidal lines and notauli absent (Fig. 5); mesosterna without teeth or projections; gastral segment I distinctly petiolate (Fig. 6); penis valve with two large apical teeth (Figs. 11–14). Females with genal carinae absent; anterior margin of clypeus without teeth; proboscidal fossa large, extending to base of mandibles; thorax subrectangular (Figs. 7, 8); pubescence simple and microserrate.

*Remarks.*—It is clear that a sister group relationship exists between *Protophotopsis* and *Nanotopsis* (we are conducting a worldwide phylogenetic analysis of the genera of Sphaeropthalmina). Only one additional genus in the Sphaeropthalmina has females with segment I of the gaster sessile with the second: *Photomorphus* Viereck (1903), which most likely is the sister group of (*Protophotopsis* + *Nanotopsis*). These three genera form a holophyletic group. The males of *Photomorphus* differ from those of *Protophotopsis* and *Nanotopsis* in having a basal ventral tooth on each mandible, and a modified mesosternum, with teeth or tubercles. Females of *Photomorphus* differ in having the pygidial area well delimited laterally, and with the surface sculptured.

*Synonymy.*—The discovery of an undescribed species of *Protophotopsis* (*Protophotopsis*) in Costa Rica and Panama, permitted us to recognize the female sex of this genus. We then discovered that this female was congeneric with females of *P. venenaria* (Melander) and with females of the Argentinian genus *Huacotilla* Casal (1962) (a genus including two nominal species, and known only from three female specimens). Examination of the female type of *Ephuta sulcifrons* (André), incertae sedis recognized here as a *Proto-*
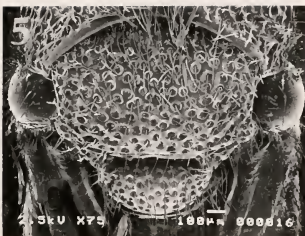




Figs. 5–6. 5, Mesonotum and scutellum of *Protophotopsis* (*Protophotopsiella*) *sulcifrons*, male, dorsal view. 6, Gaster of *Protophotopsis* (*Protophotopsis*) *clauseni*, male, terga 1 to 3, dorsal view.

*photopsis*, and representing a new distribution record for that species, from Bolivia, helps us clarify the distribution of the genus.

*Distribution.*—*Protophotopsis* ranges from Colorado, southern Arizona, and Texas, south to Brazil and Argentina. Krombein (1979) lists California for *P. venenaria* but we have not been able to locate specimens from that state.

KEY TO MALES OF *PROTOPHOTOPSIS*

1. Humerus conspicuously, sharply produced (Fig. 4), armed with sharp ventral carina; genitalia with distinct process on lateral half of penial valve, basad to distal teeth (Fig. 11); apical tooth of penis valve shorter than subapical one (Figs. 11 and 14); South America . . . . . . . . . . . . . . . . . . *Protophotopsis (Protophotopsiella)* . . . . . . . . . . . . . . . . . . . 2
−. Humerus not at all produced, not carinate (Fig. 3); genitalia with penial valve bidentate, without distinct lobe or ventro-lateral process basad to distal teeth (Fig. 12); apical tooth of penis valve longer than subapical one (Figs. 12 and 13); North and Central America . . . . . . . . . . . . . . . . . . . . . *Protophotopsis (Protophotopsis)* . . . . . . . . . . . . . . . . . . . . . . 3
2. Tubercle of antennal scrobes with delicately margined, truncate, outer face; sculpture of frons and vertex punctate, punctures nearly confluent; Argentina . . . . . *humeralis* Schuster
−. Tubercle of antennal scrobes dentiform, not margined, outer face not truncate; sculpture of frons and vertex exceedingly coarse, more or less rugose; Brazil and Bolivia . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *sulcifrons* (André)
3. Metanotum punctate throughout; hind ocelli very small (Fig. 2), maximum diameter 0.14× own distance from inner eye margin; hind ocelli with near vertical insertion, on postero-lateral margin of low ocellar tubercle (Fig. 2); scutellum slightly gibbous; USA, Mexico . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *venenaria* (Melander)
−. Metanotum with median, smooth area; hind ocelli larger (Fig. 1), maximum diameter 0.2× own distance from inner eye margin; hind ocelli with oblique insertion on very low ocellar tubercle (Fig. 1); scutellum totally flat; Costa Rica and Panama . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *clauseni* Cambra and Quintero, n. sp.

KEY TO FEMALES OF *PROTOPHOTOPSIS*

1. Dorsal face of propodeum with transverse row of denticles, lateral margins with two small denticles (Figs. 7, 9); tergum III with pair of lateral, pale integumental spots; South America . . . . . . . . . . . . . . . . . *Protophotopsis (Protophotopsiella)* . . . . . . . . . . . . . . . . . . 2
−. Dorsal face of propodeum without transverse row of denticles (Fig. 8), lateral margins without denticles; tergum III with or without pair of lateral, pale integumental spots; North and Central America . . . . . . . . . . *Protophotopsis (Protophotopsis)* . . . . . . . . . . 3
2. Sides of propodeum almost smooth, with only few, sparse punctures; integument red under sparse pale pubescent band on posterior margin of tergum I; tergum II red . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *humeralis* Schuster
−. Sides of propodeum densely punctured; integument pale under dense pale pubescent band on posterior margin of tergum I; tergum II black . . . . . . . . . . . . . *sulcifrons* (André)
3. Humeral angles of pronotum with sharp carina (Fig. 8); tergum III with pair of lateral, pale integumental spots; apex of tergum I with pale pubescence; integument of tergum II red; head covered with dense pale-golden pubescence . . . . . . . . . . *venenaria* (Melander)
−. Humeral angles of pronotum without a sharp carina; tergum III without pale integumental spots; apex of tergum I with black pubescence; integument of tergum II red, except the apical third, black; head covered with sparse pale-golden pubescence . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *clauseni* Cambra and Quintero, n. sp.

Subgenus **Protophotopsis** s. s.

**Protophotopsis (Protophotopsis)
clauseni** Cambra and Quintero,
New Species
(Figs. 1, 3, 6, 10, 12, 13, 15)

*Description of male.*—Integument black,
clothed with long, erect and recumbent
white pubescence, except the last tergum
of gaster with some infuscated setae.
Head rounded—subquadrate, its width
slightly less than width of thorax (Fig. 1);
clypeus convex, without denticles; scape
with a strong longitudinal carina be-
neath; pedicel and flagellomere I sub-
equal, short, transverse; front, vertex and
genae coarsely punctate; ocelli small, its
maximum diameter 0.2× its distance
from the inner eye margin; hind ocelli
with oblique insertion on very low ocellar
tubercle (Fig. 1). Thorax with close punc-
tures (Fig. 3), about the size of those on
head, except the metanotum, with a me-
dian, smooth area; propodeum strongly
reticulate; tegulae smooth; scutellum to-
tally flat; coxae without teeth or keels;
calcaria pale. Gaster with segments I and
II with median punctures, mostly 2 punc-
ture diameters apart (Fig. 6); segments III
to VI with small, close punctures; apical
half of pygidium smooth; felt line on ter-
gum II 0.54× as long as lateral margin of
tergum; felt line on sternum II 0.36× as
long as lateral margin of sternum; wings
infuscated; forewing with two well de-
fined submarginal cells and traces of a
third. Parameres as in Fig. 10, penis valve
as in Figs. 12 and 13, apical tooth distinc-
tively longer than subapical. Length: 7.2
mm.

*Description of female.*—Integument red,
except the apical third of tergum II, black.
Head with deep, close punctures; anten-
nal tubercles set distinctly apart; flagel-
lomere I short, 0.73× as long as flagello-
mere II; head covered with sparse pale-
golden pubescence. Alitrunk with mod-
erate, dense punctures, except metapleu-
ron, smooth; humeral angle of pronotum

without a sharp carina; sides of mesono-
tum and propodeum without denticles;
coxae without teeth or carinae; alitrunk
and legs covered with sparse pale-golden
pubescence, except the posterior half of
pronotum and metanotum with sparse
black pubescence. Gaster with terga and
sterna I–II with dense, near confluent,
median punctures; terga and sterna III–V
with fine, close punctures; tergum III
without pale integumental spots; sternum
I with a strong elevated, median, longi-
tudinal carina; gaster with pale-golden
pubescence, except the apex of tergum I
and apical third of tergum II (the apical
fringe pale-golden pubescence) with
black pubescence. Length: 6.3 mm.

*Types.*—Holotype ♂: PANAMA, Pana-
ma Prov.: Chorrera, Río Perequete, Corr.
Playa Leona (in hard clay trail, yellow
trap), 27 Feb 1991, R. Cambra (MIUP).
Paratypes: PANAMA, Panama Prov.:
same data as holotype, 1 ♂ (UMIC); same
data but: 18–20 Mar 1991, 3 ♂ (USNM,
AMNH, MIUP); 25 Jan 1992, I. Henry, 1
♀ (MIUP); 26 Feb 1991, R. Cambra, 1 ♂
(MIUP); 17 Jan 1992, R. Cambra, 2 ♂
(MIUP, MNHN-Paris). COSTA RICA,
Guanacaste Prov.: 3 km NO of Nacaome,
100 m, P.N. Barra Honda, Mar 1993, M.
Reyes, 4 ♂ (INBio, MIUP); P.N. Barra
Honda, 100m, Nov 1993, M. Reyes, 1 ♂
(INBio); Est. Palo Verde, 10 m, P. N. Palo
Verde, 25 Mar–21 Apr 1992, A. Gutiérrez,
1 ♂ (INBio).

*Distribution* (Fig. 15).—Known from
lowlands on the Pacific slopes of Costa
Rica and Panama.

*Remarks.*—*Protophotopsis clauseni* was
found in open areas with patches of dry
forest, close to or in cattle fields (potre-
ros), in Panama and Costa Rica. This new
species of *Protophotopsis* is the first Neo-
tropical species reported for the nomino-
typical subgenus, *Protophotopsis*. The 14
male types vary in body length from 5.1
to 7.2 mm, and lack any noticeable varia-
tions in structure and coloration.

*Etymology.*—Named in honor of Dr.
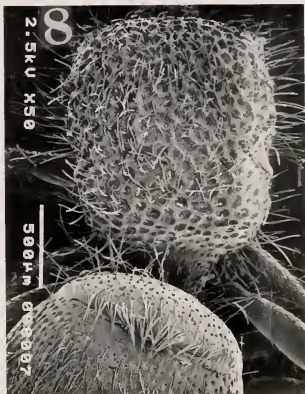
Figs. 7–10. 7, *Protophotopsis* (*Protophotopsiella*) *humeralis*, female, head, thorax, first and second gastral terga, dorsal view. 8, *Protophotopsis* (*Protophotopsis*) *venenaria*, female, thorax, first and second gastral terga, dorsal view. 9, *Protophotopsis* (*Protophotopsiella*) *humeralis*, female, details of propodeum with transverse row of denticles and lateral margins with two denticles, dorsal view. 10, Male genitalia of *Protophotopsis* (*Protophotopsis*) *clauseni*, dorsal view.
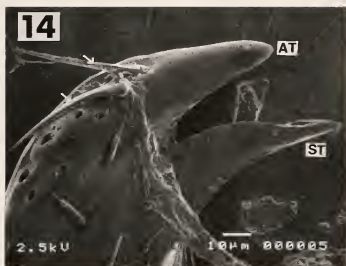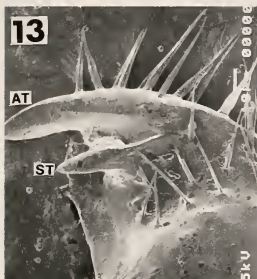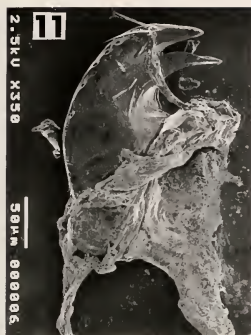
Figs. 11–14. Penis valves of *Protophotopsis*, males, dorsal view. 11, *P. (Protophotopsiella) sulcifrons*. 12, *P. (Protophotopsis) clauseni*. 13–14, detail of anterior half. AT = apical tooth; ST = subapical tooth. 13, *P. (Protophotopsis) clauseni*. 14, *P. (Protophotopsiella) sulcifrons*, setae removed except for two, marked with arrows.

Philip Clausen, Insect Collection, University of Minnesota, for his great encouragement to our research, for providing numerous loans of mutillids for many years, and for his hospitality during two visits by the junior author.

### *Protophotopsis (Protophotopsis) venenaria* (Melander)
(Figs. 2, 8, 15)

*Mutilla venenaria* Melander 1903:320. Fedor [Lee Co.], Texas, Rev. G. Birkman col. Lec-

totype ♀ (Fedor, Texas, April 29 1898), MCZ-Harvard Type 8978, present designation.

*Protophotopsis (Protophotopsis) scudderi* Schuster 1947:694–697. Holotype ♂: Fedor [Lee Co.], Texas, May 29 1902, Birkman col. (MCZ-Harvard University, Type 30514), and 2 paratopotypes. **New synonymy.**

*Notes on Synonymy.*—Schuster (1949) mentioned that *venenaria* might be the female of *scudderi*. The synonymy is based on the fact that this is the only known

species of the genus in North America, that both types were collected from the same locality in Texas, and that none of the other three known species of *Protophotopsis* lives in sympatry.

*Material Examined.*—Three of the original four syntype females were located: two females (one designated lectotype, and one paralectotype), in MCZ; one female, in WSU (Type 145), without locality label but with a Melander identification label, a paralectotype. The paratype of *P. scudderi* listed as deposited in the USNM was not found there, and appears to be lost.

The finding of *Protophotopsis (Protophotopsis) venenaria* in Mexico represents a new country record, as this species was known previously only from the USA. MEXICO: NUEVO LEON: Monterrey, 15 Jun 1941, H. S. Dybas, 1 ♀ (MIUP). USA: TEXAS: La Salle Co., Cotulla, 15 Apr 1906, F.C. Pratt col, 1 ♂ (UMIC); Bastrop Co., Duval col., 1 ♀ (UMIC); COLORADO: Boulder, Jul 12 1910, T.D.A. Cockerell col, 1 ♀ (UMIC); ARIZONA: Sta. Rita Mts, May 15 1940, Bryant col, 1 ♀, without head (UMIC); Cochise Co., Texas Canyon, 11 mi. W. Apache, Aug 8 1967, E. S. Schlinger col, 1 ♂, without head (UCRC).

*Distribution* (Fig. 15).—USA (Texas, Colorado, Arizona) and Mexico (Nuevo León).

*Remarks.*—Schuster's (1947) composite drawing of the male genitalia of *P. venenaria* (as *P. scudderi*), erroneously shows that the apical tooth of the penis valve is shorter than the subapical one. Using dissections and the SEM, we have found that the apical tooth is longer than the subapical one in *venenaria*. The single female specimen of *venenaria* collected in Mexico, some 320 km south of the closest known specimen from the USA, Cotulla, Texas, measures 3.8 mm in body length. Two females from the USA measured 5.2 mm (Texas) and 6.0 mm (Colorado). Although it is shorter in body length, we have been unable to recognize in the Mexican female any differences in structure and coloration from *venenaria* specimens from the USA.
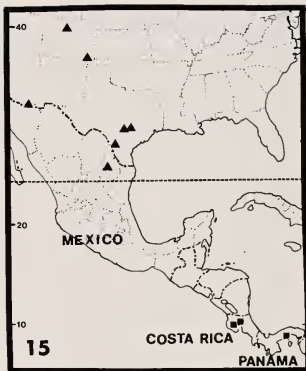


Fig. 15. Distribution of *Protophotopsis (Protophotopsis): venenaria* (triangles); *clauseni* (squares).

### Subgenus **Protophotopsiella** Schuster

*Protophotopsis (Protophotopsiella)* Schuster 1949. Type species: *Protophotopsis (Protophotopsiella) humeralis humeralis* Schuster.

### *Protophotopsis (Protophotopsiella) humeralis* Schuster, New Status
(Figs. 7, 9, 16)

*Protophotopsis (Protophotopsiella) humeralis humeralis* Schuster 1949:85–89. Holotype ♂: Capilla de Monte, Córdoba, Argentina (Zoologische Staatssammlung, Munich, Germany).

*Huacotilla hepperi* Casal 1962:261–263. Holotype ♀: Argentina, Córdoba, Morteros (AMNH), examined. **New synonymy.**

*Huacotilla diaguita* Casal 1962:263–265. Holotype ♀: Argentina, La Rioja Prov., Patquía (AMNH), examined. **New synonymy.**

*Notes on Synonymy.*—*Protophotopsis (Protophotopsiella) humeralis* Schuster is the only species of *Protophotopsis* known from Argentina, and the recognition of the female sex was based on coincident geographic distribution. A study of the female type specimens of *Huacotilla hepperi* Casal and *Huacotilla diaguita* Casal convinced us

Fig. 16. Distribution of *Protophotopsis* (*Protophotopsiella*): *sulcifrons* (triangles); *humeralis* (circles).

that they are synonymous. Casal (1962) points out that *H. diaguita* differs from *H. hepperi* in the following trivial coloration differences: head integument coloration, ochreous with tints of pale red, while *H. hepperi* is dark red, almost black; tergum III lacks integumental maculae, present in *H. hepperi*, and tergum II has two inconspicuous maculae of pale pubescence, longitudinally oval, while *H. hepperi* lacks these inconspicuous maculae. The head integument coloration is variable even among specimens from a single locality, from red to dark brown, near black; the holotype of *H. diaguita* has a pair of pale integumental maculae on tergum III, thus the description given by Casal is erroneous; in two of four females from Alemania, Salta, and in two of three females from Cordoba, we found that the highly inconspicuous pubescent maculae on tergum II are absent. Thus, we consider these variations in coloration and pubescence as

part of the intraspecific variability of the species.

*Additional Material Examined.*—ARGENTINA: Buenos Aires Prov.: Alberdi (sic, Alberti), Dec 11 1910, 1 ♂ (UMIC). Salta Prov.: Alemania, Jan 1983, Fritz, 1 ♀ (AMNH); Alemania, Feb 1983, Fritz, 4 ♀ (AMNH, MIUP). Córdoba Prov.: 3 ♀ (AMNH).

*Distribution* (Fig. 16).—Andean foothills and pampasic regions of Argentina, between 26 and 35 degrees of latitude South. Casal (1962) mentions that two females (as *H. hepperi*) were collected walking on grass in the gardens surrounding a private aerodome, in Monteros, Argentina, about 3 PM.

### *Protophotopsis* (*Protophotopsiella*) *sulcifrons* (André), New Combination (Figs. 4, 5, 11, 14, 16)

*Ephuta sulcifrons* André 1906:164–165. Holotype ♀: Brazil, Goiás (as Goyaz), Muséum National d'Histoire Naturelle, Paris, examined. *Incertae sedis:* Nonveiller 1990:89.

*Protophotopsis (Protophotopsiella) humeralis rugosa*
Schuster 1949:89. Holotype ♂: Brazil, Cha-
pada, Mato Grosso, about 14°8'S (Carnegie
Museum, Pittsburgh), examined. **New Syn-
onymy.**

*Material Examined.*—The finding of *Protopho-
topsis (Protophotopsiella) sulcifrons* in Bolivia represents
a new country record, as this species was previously
known only from the holotype from Brazil. BOLIVIA:
El Beni, Beni Stn., Palm Camp, Savannah, 31 Jul 1988,
1 ♂ (MIUP).

*Distribution* (Fig. 16).—**Known from
Brazil and Bolivia.**

*Remarks.*—The structural differences in
integumental sculpturing on the sides of
the propodeum in females and on the
frons and vertex of males, are justification
for recognizing *P. sulcifrons* and *P. humer-
alis* as separate species. Thus we consider
*sulcifrons* to be a distinct species, and not
just a subspecies of *humeralis*.

We have been unable to compare the
genitalia of *sulcifrons* (Figs. 11, 14) with
those of *humeralis* because we did not dis-
sect the genitalia of the only male exam-
ined and, apparently, the genitalia of the
holotype of *humeralis* was neither dissect-
ed nor discussed by Schuster.

## ACKNOWLEDGEMENTS

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# An Analysis of Host Range in the *Diadegma nanus* group of Parasitoids in Western Europe, with a Key to Species (Hymenoptera: Ichneumonidae: Campopleginae)

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*Abstract.*—From a base of 768 rearings from microlepidoptera, host range characteristics are recorded and analysed for 24 Western Palaearctic species of *Diadegma* (Ichneumonidae: Campopleginae) that may represent one or more natural groups. Some speculations on the evolutionary ecology of host range and speciation are made. A key to these species, and a further six that have not been reared, is provided. *D. germanicum* Horstmann 1973 is synonymised with *D. longicaudatum* Horstmann 1969, and *D. consumptor alpestrator* Aubert 1971 with *D. consumptor consumptor* (Gravenhorst 1829).

The genus *Diadegma* Förster (Ichneumonidae: Campopleginae) is a very large genus of koinobiont endoparasitoids of Lepidoptera, attacking the host in its larval stage and killing it in its cocoon. *Diadegma* has a worldwide distribution, and an overall host range centred on smallish moths in the "lower ditrysian" superfamilies (sensu Scoble 1992), forming a large part of the traditional "microlepidoptera". Several species are important natural enemies of pest Lepidoptera.

The purpose of this paper is to examine the host ranges of Western Palaearctic species in a defined part of the genus *Diadegma* (the *nanus* group) and to provide a key to the included species. We also summarise the known distribution of each species, and make some taxonomic remarks. It has been pointed out by Fitton & Walker (1992), writing on several economically important *Diadegma* species, that hitherto there have been neither careful taxonomic revisions within *Diadegma* nor sufficiently critical assessments of species-level host range, with the consequence that the body of literature on given species is of very limited worth.

A considerable quantity of reared material of the *Diadegma nanus* group has been obtained, most of it recently, and carefully evaluated. Although 63% of this material is in the National Museums of Scotland, we have made efforts to source all available material. As well as trying to understand and express the host ranges of particular species from fairly rich quantitative data (altogether 768 rearings) there is the opportunity to try to analyse the patterns seen between species from the perspective of evolutionary ecology. In particular, from evidence seen in a braconid genus *Aleiodes* (Rogadinae), it has been hypothesised (Shaw 1994) that there is a tendency in some koinobionts to broaden their host ranges, and that this can precede the birth of new species as extreme specialists. While we will argue that a formal test of the hypothesis remains out of reach, the *Diadegma* data can certainly be used to revisit some of its general predictions.

The *Diadegma nanus* group of the subgenus *Nythobia* Förster, as defined here, includes the species groups I and II in

Horstmann (1969: 421 ff.), but without the species that subsequently have been transferred to the genera *Campoplex* Gravenhorst (*maculifemur* (Strobl), syn. *anthracostoma* (Strobl)), *Enytus* Cameron (*apostatus* (Gravenhorst), *neoapostatus* (Horstmann), *parvicanda* (Thomson)), *Eriborus* Förster (*dorsalis* (Gravenhorst)), *Lathrostizus* Förster (*monilicornis* (Thomson)) and *Tranosemella* Horstmann (*praerogator* (Linnaeus), syn. *interrupta* (Holmgren), syn. *lacticrus* (Thomson)) or to the subgenus *Diadegma* Förster s. str. (see Horstmann 1969: 429 ff.). It is characterized within the genus *Diadegma* Förster s. l. by the hind tibiae being whitish or yellow basally and usually having a darker ring or patch subbasally, and in the female sex by the caudal edge of the sixth and seventh tergites of the gaster being not or only very slightly incised dorsally.

No claim can be made that the *nanus* group overall is monophyletic. However, four subgroups might be distinguished and, although the differences between them are poorly characterised, there is a better prospect that further research could show these to be monophyletic:

1. **Diadegma nanus subgroup:** Ovipositor sheaths 0.3–1.5 times as long as the first tergite of the gaster, ovipositor weakly upcurved. Claws inconspicuously pectinate (as in Fig. 7), the subapical teeth less than half as long as the apical one. The foregoing characters are probably symplesiomorphies, but possible synapomorphies are small size coupled with parasitism principally of leaf mining microlepidoptera. Species: *anurum* (Thomson), *brevivalve* (Thomson), *callisto* Horstmann, *crassum* (Bridgman), *crataegi* Horstmann, *duplicatum* Horstmann, *elishae* (Bridgman), *exareolatum* Aubert, *holopygum* (Thomson), *laricinellum* (Strobl), *lithocolletis* Horstmann, *melanium* (Thomson), *micrurum* (Thomson), *nanus* (Gravenhorst), *pusio* (Holmgren), *rufatum* (Bridgman), *scotiae*

(Bridgman), *stigmatellae* Horstmann, *tamariscator* Aubert.

2. **Diadegma latungulum subgroup:** Ovipositor sheaths 1.4–1.6 times as long as the first tergite of the gaster, ovipositor straight (as in Fig. 15). Claws conspicuously pectinate (possible autapomorphy), the subapical teeth nearly as long as the apical one (Fig. 6). Parasitoids of *Mompha* species (Momphidae). One species: *latungulum* (Thomson).

3. **Diadegma consumptor subgroup:** Ovipositor sheaths 1.1–2.0 times as long as the first tergite of the gaster, ovipositor straight (possible synapomorphy) (Fig. 15). Claws inconspicuously pectinate (Fig. 7), the subapical teeth less than half as long as the apical one. Parasitoids of Psychidae (as far as known: possible synapomorphy). Species: *consumptor* (Gravenhorst), *ledicola* Horstmann, *longicaudatum* Horstmann, *rectificator* Aubert.

4. **Diadegma flexum subgroup:** Ovipositor sheaths 1.7–2.0 times as long as the first tergite of the gaster, ovipositor conspicuously upcurved near the tip (possible synapomorphy) (Figs 13, 14). Claws inconspicuously pectinate (as in Fig. 7), the subapical teeth less than half as long as the apical one. Hosts unknown. Species: *flexum* Horstmann, *pulicator* Aubert.

## PRESENTATION OF RECORDS

All specimens (or parts of series) listed have been determined by KH. Hosts are given the names currently believed to be valid, with synonymy (as labelled) also given. Foodplants are cited only when they have appeared on the data label. While each individual rearing is regarded as a record, the summary we give also includes (in brackets) the number of independent collections listed—i.e. differing in either host, foodplant or place. Place name, country abbreviation, and depository (or depositories) for the specimens are given for each independent collection:

the numbers of specimens recorded against each host/foodplant category are divided according to depository so that each specimen remains traceable, but otherwise they are bulked together.

Abbreviations used are: [for countries] A = Austria; BG = Bulgaria; BY = Belarus; CH = Switzerland; D = Germany; DEN = Denmark; F = France; FIN = Finland; GB = Great Britain; GR = Greece; H = Hungary; I = Italy; IRL = Ireland; M = Moldavia; N = Norway; NL = Netherlands; P = Portugal; PL = Poland; R = Russia; S = Sweden; Y = former Yugoslavia, and [for depositories] Aeschlimann = private collection, Montpellier; Aubert = Aubert collection in Musée Zoologique, Lausanne; Bauer = private collection, Großschwarzenlohe/Nürnberg; Bridgman = Bridgman collection in Castle Museum, Norwich; Budapest = Természettudományi Múzeum Allattára; Eberswalde = Deutsches Entomologisches Institut; Haeselbarth = Haeselbarth collection in Zoologische Staatssammlung, München; Hilpert = Hilpert collection in Landessammlungen für Naturkunde, Karlsruhe; Hinz = Hinz collection in Zoologische Staatssammlung, München; Horstmann = private collection, Würzburg; Huemer = private collection, Innsbruck; Jordan = private collection, Soyhières/Delémont; Jussila = private collection, Turku; Kolarov = private collection, Sofia; Leiden = Nationaal Natuurhistorisch Museum; London = Natural History Museum; Lund = Zoologiska Institution; München = Zoologische Staatssammlung; NMS = National Museums of Scotland, Edinburgh (includes Shaw collection); Rill = Rill collection in Zoologisches Museum, Kiel; St. Petersburg = Zoological Institute, Academy of Sciences; Sawoniewicz = private collection, Warszawa; Šedivý = private collection, Praha; Stockholm = Naturhistoriska Riksmuseet; Strobl = Strobl collection in Benediktinerabtei, Admont; Torino = Museo Regionale di Scienze Naturali; Wroclaw = Muzeum Przyrodnicze.

Knowledge of voltinism and phenology are important in understanding host range, and we have expressed this largely from material in NMS, most of which comes from GB. We use the term "bivoltine" to indicate at least two generations, though recognising that in practice more than one "summer" (= non-diapause) generation is likely to arise under favourable conditions in species that exhibit such a generation. It is also possible that some species will show more obligate differences in voltinism in different parts of their range. Campopleginae is not one of the subfamilies of Ichneumonidae known to include species that overwinter as adults in temperate climates and we presume that the only options open to the species we are dealing with are to overwinter as a cocooned stage or as a young larva in a host that overwinters partly grown. This is also consistent with the general view of Campopleginae as being pro-ovigenic and having a relatively short adult life. It is not certain for any of these parasitoids at what stage in its larval life the host is attacked, but it seems likely to happen relatively early in most or perhaps all cases. Many of the hosts involved change their mode of feeding part of the way through their larval life and, when relevant, attention is drawn to this in the commentary. Information on host biology has been directly observed or taken from Emmet (1988, 1991).

A table of the number of rearings included in this paper from each host genus is also given (Table 1). As the Lepidoptera in general have been extensively sampled, this indicates the tightness of the host groups involved overall. The table also records the *Diadegma* species reared from each host genus. This allows host utilization patterns to be overviewed, and it also reveals the cases in which more than one *Diadegma* species is associated with a host genus.

## KEY

Specimens of the *Diadegma nanus* group are small or very small, and have very few distinctive characters. Males usually cannot be determined, and the determination of females is likely to be uncertain in many cases, especially if only one specimen is available for examination. The specimens must be very carefully mounted, with all parts of the body clearly visible (especially the pleurae, the propodeum and the gaster from above and from one side), and with the apical tergites of the gaster and the ovipositor in their normal positions. The latter is often not the case in material collected or preserved in liquid, and the determination of those specimens may be particularly difficult or impossible. The key to species given here was difficult to construct and may prove difficult to use unless reliably determined

material is also available for comparison. In particular this is necessary to guard against misidentifying specimens of additional (= undescribed) species, which may be fairly numerous. For this reason four segregates that probably represent undescribed species are included in the key (and their rearing data are listed after the other species).

Among the most important characters are the colour of the hind tibiae and the ovipositor length. The colour of the hind tibiae refers to the outer aspect (the inner side is usually red or reddish brown) which is whitish or yellowish red basally and medially, and usually brownish or black subbasally and apically. The ovipositor length is expressed as an index, being the ratio of the visible length of the ovipositor sheaths (seen from the side) to the length of the first tergite of the gaster (measured along the dorsal surface).

KEY TO FEMALES OF THE *DIADEGMA NANUS* SPECIES GROUP IN WESTERN EUROPE

1. Ovipositor not or hardly surpassing tip of gaster, ovipositor index 0.3. (Areolet open (as in Fig. 2). Area superomedia 1.0–1.3 times as long as wide, constricted caudally and usually closed by a wrinkle (Fig. 8)) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
   – Ovipositor surpassing tip of gaster, ovipositor index at least 0.4. (Other characters variable) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2. Scape ventrally, front and middle coxae whitish to whitish yellow. Hind femora for the greater part light red. Third tergite of the gaster to a varying extent yellowish red . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *crassum* (Bridgman)
   – Scape, front and middle coxae, hind femora and gaster usually totally dark brown or black. Sometimes tips of coxae and small lateral spots on third tergite of gaster yellowish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *pusio* (Holmgren)
3. Hind femora dark brown or black **and** ovipositor index 0.5–0.8 (*D. crataegi* and *D. exareolator* with ovipositor index 0.9–1.0 sometimes have dark hind femora and may run here, but *D. crataegi* differs by the area superomedia 1.3–1.5 times as long as wide, and *D. exareolator* differs by the combination of an open areolet and the hind tibiae whitish basally and medially) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
   – Hind femora yellowish red to reddish brown, sometimes darkened basally and apically, **and/or** ovipositor longer . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
4. Area superomedia 1.7 times as wide as long, extended caudally, grading into area petiolaris with almost no boundary (Fig. 9). Areolet very oblique, closed by a faint vein (Fig. 1). Second tergite of gaster as long as wide. (Ovipositor index 0.6) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *scotiae* (Bridgman)
   – Area superomedia at most 1.3 times as wide as long, usually with parallel sides or somewhat constricted caudally (Fig. 10). Areolet open or closed. Second tergite of gaster at least 1.1 times as long as wide . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5. Areolet closed by a faint vein. Area superomedia usually somewhat wider than long. Ovipositor index 0.5–0.7. (Hind tibiae whitish to whitish yellow medially) ............ 6

– Areolet open (Fig. 2). Area superomedia as long as wide or somewhat longer than wide (Fig. 10). Ovipositor index 0.7–0.8 ......................................................... 7

6. Postpetiole about 0.9 times as long as wide. Second tergite of gaster 1.0–1.1 times as long as wide. Scape and coxae dark brown or black .................... *laricinellum* (Strobl)

– Postpetiole about 1.1 times as long as wide. Second tergite of gaster 1.5 times as long as wide. Scape ventrally, front coxae and middle coxae apically conspicuously yellow ....
................................................................................. *tamariscator* (Aubert)

7. Hind tibiae whitish medially ........................................................ species 1

– Hind tibiae yellowish brown medially ................................................... 8

8. Mesopleura with fine and irregular wrinkles dorsally and medially. Postpectal carina incised centrally .................................................... *callisto* Horstmann

– Mesopleura coriaceous dorsally and medially. Postpectal carina straight or somewhat bent centrally .................................................... *elishae* (Bridgman)

9. Ovipositor index 0.4–0.6. (Flagellum filiform, scarcely wider medially than subapically. Hind tibiae whitish to whitish yellow basally and medially, yellowish brown to medium brown subbasally and apically) ......................................................... 10

– Ovipositor index at least 0.6 (*D. brevivalve* with an index of 0.6–0.7 has the flagellum fusiform and the hind tibiae yellowish red basally and medially and not darkened subbasally) ................................................................................. 11

10. Ovipositor index 0.4. Front and middle coxae whitish yellow. Gaster to a varying extent reddish or reddish brown. Areolet closed by a very faint vein or open ..............
................................................................................. *micrurum* (Thomson)

– Ovipositor index 0.5–0.6. Coxae and gaster black, at most tips of front coxae whitish yellow. Areolet open ......................................................... *melanium* (Thomson)

11. Ovipositor index 0.6–0.7. Hind tibiae yellowish red, with only a narrow light brown ring apically. Flagellum fusiform, 1.3 times as wide medially as subapically. (Areolet closed)
................................................................................. *brevivalve* (Thomson)

– Ovipositor index at least 0.8. Hind tibiae usually darkened subbasally and apically, though sometimes inconspicuously. Flagellum often filiform ................................. 12

12. Ovipositor index 0.8–1.0 **and** hind tibiae yellowish to yellowish red basally and medially, yellowish brown to light brown subbasally and apically, with little contrast. Front and middle coxae for the greater part or totally whitish yellow ........................... 13

– Ovipositor index at least 1.2 **and/or** hind tibiae whitish to whitish yellow basally and medially, medium brown to black subbasally and apically, with much contrast. Front and middle coxae often black ............................................................... 14

13. Area petiolaris with fine but conspicuous transverse wrinkles. Areolet usually closed. Ovipositor index 0.8–0.9. Base of flagellum often somewhat yellowish brown ventrally
................................................................................. *anurum* (Thomson)

– Area petiolaris coriaceous. Areolet open. Ovipositor index 0.9–1.0. Base of flagellum dark brown .................................................... *lithocolletis* Horstmann

14. Ovipositor index 0.8–1.1. (Hind tibiae whitish to whitish yellow basally and medially, medium to dark brown or black subbasally and apically, with much contrast) ........ 15

– Ovipositor index at least 1.1 (*D. ledicola* with an index of 1.1–1.2 has the hind tibiae with less contrast) ......................................................................... 20

15. Areolet open. (Ovipositor index 0.9–1.0. Hind tibiae whitish basally and medially, brownish black to black subbasally and apically) ........................ *exareolator* Aubert

– Areolet closed (except as an aberration) .............................................. 16

16. Scape ventrally and front and middle coxae usually conspicuously whitish yellow, or middle coxae for the greater part black. (Area superomedia 0.9–1.1 times as long as wide. Ovipositor index 0.8–0.9. Hind tibiae whitish to whitish yellow basally and medially, brownish black to black subbasally and apically) .............. *stigmatellae* Horstmann

- Scape and coxae dark brown or black, at most tips of front coxae whitish . . . . . . . . . . . 17
17. Hind tibiae medium brown subbasally, dark brown apically. Area superomedia 1.0–1.1 times as long as wide. (Ovipositor index 0.9–1.1) . . . . . . . . . . . . . . . *holopygum* (Thomson)
 - Hind tibiae brownish black to black subbasally as well as apically. Area superomedia 1.1–1.5 times as long as wide . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18
18. Area superomedia 1.3–1.5 times as long as wide. Ovipositor index 0.9–1.0. Body length 3–4 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *crataegi* Horstmann
 - Area superomedia 1.1–1.2 times as long as wide. Ovipositor index 0.8–0.9. Body length 4–5 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 19
19. Hind legs very slender, hind femora 5.4–5.7 times as long as wide . . . . . . . . . . . species 2
 - Hind femora 4.6–4.9 times as long as wide . . . . . . . . . . . . . . . . . . . . . . . . . . . . species 3
20. Claws conspicuously pectinate, the subapical teeth of hind claws nearly as long as the apical one (Fig. 6). Second tergite of gaster 0.8 times as long as wide. (Ovipositor index 1.4–1.6) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *latungulum* (Thomson)
 - Claws not so strongly pectinate, subapical teeth conspicuously shorter than the apical one (Fig. 7). Second tergite of gaster at least as long as wide . . . . . . . . . . . . . . . . . . . . . . . 21
21. Ovipositor index 1.1–1.5 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22
 - Ovipositor index 1.7–2.0 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 27
22. Hind tibiae light red, with a yellow spot basally, scarcely darkened subbasally and apically. Third tergite of gaster for the greater part or totally light red. (Ovipositor index 1.3–1.4) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *rufatum* (Bridgman)
 - Hind tibiae with more contrast. Third tergite of gaster for the greater part or totally black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 23
23. Hind tibiae yellowish to light red basally and medially, light to medium brown subbasally, medium to dark brown apically, with less contrast . . . . . . . . . . . . . . . . . . . . . . . . 24
 - Hind tibiae whitish basally and medially, medium brown to black subbasally and apically, with much contrast . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 25
24. Second tergite of gaster 1.1–1.3 times as long as wide. Ovipositor index 1.1–1.2. Scape ventrally, front and middle coxae usually for the greater part or totally yellowish to light red . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *ledicola* Horstmann
 - Second tergite of gaster 0.9–1.0 times as long as wide. Ovipositor index 1.2–1.5. Scape, front and middle coxae usually for the greater part or totally black . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *consumptor* (Gravenhorst)
25. Body length 2–3 mm. Hind tibiae dark brown to black subbasally. (Area petiolaris with conspicuous transverse wrinkles. Ovipositor index 1.2–1.3) . . . . . . . . . *nanus* (Gravenhorst)
 - Body length 4–5 mm. Hind tibiae medium brown subbasally . . . . . . . . . . . . . . . . . . . . 26
26. Area petiolaris with conspicuous transverse wrinkles. (Ovipositor index 1.2–1.5) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *duplicatum* Horstmann
 - Area petiolaris coriaceous, without transverse wrinkles. (Ovipositor index 1.2) . . . species 1
27. Ovipositor conspicuously upcurved near tip (Figs 13, 14) . . . . . . . . . . . . . . . . . . . . . . . 28
 - Ovipositor straight over its total length (Fig. 15) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 29
28. Body length 4–5 mm. Areolet large, touching radius (or nearly so) (Fig. 3). Ovipositor very conspicuously upcurved near tip (Fig. 13). (Ovipositor index 1.7–2.0) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *flexum* Horstmann
 - Body length 3.3 mm. Areolet very small, very oblique (Fig. 4). Ovipositor less conspicuously upcurved near tip (Fig. 14). (Ovipositor index 1.8) . . . . . . . . . . . . . *pulicator* Aubert
29. Areolet oblique, with second recurrent vein distal to middle (Fig. 5). Area superomedia somewhat wider than long (Fig. 11). (Ovipositor index 1.7–2.0) . . . . . . . *longicaudatum* Aubert
 - Areolet regular, with second recurrent vein in middle. Area superomedia 1.2 times as long as wide (Fig. 12). (Ovipositor index 1.7) . . . . . . . . . . . . . . . . . . . . . *rectificator* Aubert
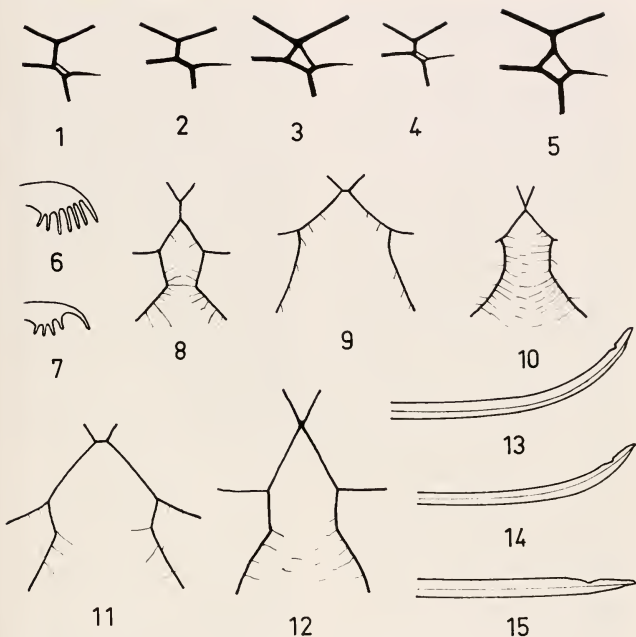
Figs. 1–5. Areolet of fore wing. Fig. 1: *Diadegma scotiae* (Bridgman); Fig. 2: *D. elishae* (Bridgman); Fig. 3: *D. flexum* Horstmann; Fig. 4: *D. pulicator* Aubert; Fig. 5: *D. longicaudatum* Horstmann. Figs 6–7. Claw of hind leg. Fig. 6: *D. latungulum* (Thomson); Fig. 7: *D. longicaudatum* Horstmann. Figs 8–12. Area superomedia of propodeum. Fig. 8: *D. pusio* (Holmgren); Fig. 9: *D. scotiae* (Bridgman); Fig. 10: *D. elishae* (Bridgman); Fig. 11: *D. longicaudatum* Horstmann; Fig. 12: *D. rectificator* Aubert. Figs 13–15. Ovipositor tip. Fig. 13: *D. flexum* Horstmann; Fig. 14: *D. pulicator* Aubert; Fig. 15: *D. longicaudatum* Horstmann.

## REARING AND DISTRIBUTION RECORDS, ANALYSES OF HOST RANGE AND TAXONOMIC REMARKS

### *Diadegma anurum* (Thomson)

*Tischeria ekebladella* (Bjerkander) (Tischeriidae) on *Quercus robur*: 2 ♀ Methven Wood/ Perths./GB (NMS), 2 ♀ Wytham Wood/ Oxon/GB (Horstmann, NMS), 25 ♀ Kiel/D (Horstmann, Jordan).

29 (3 independent) records: one host species. Univoltine in Britain, like its host which is a leaf miner throughout its preimaginal life. *D. anurum* overwinters in the host's pupation disc in the mine following leaf fall, in which it makes its own cocoon. Only females have been seen and it is probably thelytokous.

*Distribution.*—Reared: D, GB. Non-reared:

D (Haeselbarth, Hilpert, Horstmann), M (St. Petersburg), PL (Sawoniewicz), S (Lund).

### *Diadegma brevivalve* (Thomson)

*Epermenia illigerella* (Hübner) (Epermeniidae): 2 ♀, 2 ♂ Eberswalde/D (Eberswalde, Horstmann), 1 ♀ Goslar/D (München).

5 (2 independent) records: one host species (feeding on Umbelliferae). Scholz (1996) has recently shown that two taxa have been confused under the host name *illigerella*, and it is possible that these records might be referable to *Epermenia falciformis* (Haworth). In Britain the *Epermenia* formerly referred to *E. illigerella* appear all to belong to *E. falciformis* (Godfray & Sterling 1996). This species is bivoltine, feeding on *Angelica* or *Aegopodium*, the first generation in spun leaflets and the second by mining a branch stem into the umbel, and the winter may be passed as an egg. It is not clear whether or how the life history of *E. illigerella* differs, or which of the possible host species occur in the areas where *D. brevivalve* has been found. *D. brevivalve* is probably a highly specialised parasitoid, but the available rearing data are insufficiently clear to suggest voltinism or how the winter is passed.
Distribution.—Reared: D. Non-reared: D (Horstmann), R (St Petersburg), S (Lund).

### *Diadegma callisto* Horstmann

*Callisto coffeella* (Zetterstedt) (Gracillariidae) on *Salix silesiaca*: 3 ♀, 7 ♂ Tatry/PL (Horstmann, Sawoniewicz).

10 (1 independent) records: one host species. Apparently highly host specialised. The host at first feeds in a mine, and subsequently in a folded leaf. It is (in Britain) univoltine and overwinters in the cocoon stage. The available rearing data for *D. callisto* are not precise enough to be indicative of voltinism or the overwintering stage.
Distribution.—Reared: PL.

### *Diadegma consumptor* (Gravenhorst)

No host record.
Aubert (1971: 38 f.) described a subspecies *alpestrator* Aubert from the Alps, which agrees with the lectotype of *D. consumptor* in structure, proportions and general colour pattern, but differs from it by its darker colour (scape, legs). However, very little is known about the distribution and variability of *D. consumptor*. The lectotype (from Genoa), which is both aged and damaged, is the only specimen so far attributed to the nominate subspecies, and at least one intermediate has been seen from within the distributional area of the supposed subspecies *alpestrator*. It is our view that recognition of two subspecies is unwarranted and *alpestrator* Aubert is here formally reunited with the nominate subspecies (**syn. nov.**).
Distribution.—Non-reared: A (Horstmann), CH (Lund), F (Aubert), I (Haeselbarth, Horstmann, Wroclaw).

### *Diadegma crassum* (Bridgman)

*Ectoedemia argyropeza* (Zeller) (Nepticulidae): 1 ♂ Innsbruck/A (München).
*Bucculatrix bechsteinella* (Bechstein & Scharfenberg) (syn. *crataegi* Zeller) (Bucculatricidae) on *Crataegus* sp.: 2 ♀ Pitt Down/Winchester/Hants./GB (NMS).
*Bucculatrix cidarella* Zeller on *Alnus glutinosa*: 1 ♀, 3 ♂ Bremen/D (Horstmann, München), 1 ♀ Puszcza Borecka/Gizycko/PL (Sawoniewicz), 7 ♀, 5 ♂ Emer Bog/Hants./GB (Horstmann, NMS); on unrecorded plant: 1 ♂ Abbots Wood/Sussex/GB (Bridgman), 1 ♀ Trelasker/Cornwall/GB (NMS).
*Bucculatrix demaryella* (Duponchel) on *Betula pubescens*: 2 ♀ Soldany/Wegorzewo/PL (Sawoniewicz); on unrecorded plant: 6 ♀ Wateringbury/Kent/GB (NMS), 1 ♀ Horsham/Sussex/GB (Bridgman), 1 ♂ Hawks Wood/Cornwall/GB (NMS).
*Bucculatrix frangutella* (Goeze) (syn. *alnella* (Villers)) on *Frangula alnus*: 3 ♀ Wageningen/NL (NMS); on *Rhamnus catharticus*: 1 ♀ Chippenham Fen/Cambs./GB (NMS).
*Bucculatrix thoracella* (Thunberg) on *Tilia* sp.: 1 ♂ Bristol/GB (NMS).

*Bucculatrix ulmella* Zeller on *Quercus robur*: 4 ♀, 3 ♂ Botley Wood/Hants./GB (NMS).

*Bucculatrix* sp. on *Betula* sp.: 1 ♀ Hambergen/Osterholz-Scharmbeck/D, 1 ♀ Schierbrok/Delmenhorst/D (München).

*Calybites phasianipennella* (Hübner) (Gracillariidae) on *Polygonum hydropiper*: 1 ♀ Oyter Moor/Bremen/D (München).

47 (18 independent) records: 45 (96%) are from *Bucculatrix* (6 species). While the other two should be regarded with considerable suspicion (the final instar larvae of *Bucculatrix* species are notorious for straying widely from their foodplant before constructing their cocoons, making their accidental inclusion in other samples particularly likely to happen), the fact that both of these supposed hosts start out as miners could also be taken to indicate some plasticity at the periphery of the host range. All but one (ex *B. thoracella*) of the British specimens seen have overwintered in the host cocoon and, from its core host range of *Bucculatrix* species, *D. crassum* appears to be a univoltine parasitoid restricted to arboreal hosts that overwinter in the cocoon stage. Of the *Bucculatrix* species listed, only *B. ulmella* is normally bivoltine in Britain. The host range of *D. crassum* contrasts with that of *D. pusio*, also a parasitoid of *Bucculatrix*, and the two species show colour differences (see key) that are consistent and without intermediates, even in series from the same locality and host (*B. ulmella* at Botley Wood and *B. demaryella* at Wateringbury; also *B. frangutella* at separate localities).

*Distribution.*—Reared: A, D, GB, NL, PL. Non-reared: D (Haeselbarth, Hilpert), PL (Sawoniewicz).

### Diadegma crataegi Horstmann

*Parornix anglicella* (Stainton) (Gracillariidae) on *Crataegus monogyna*: 3 ♀ Medmenham/Bucks./GB, Wageningen/NL (NMS).

*Parornix betulae* (Stainton) on *Betula* sp.: 1 ♀ Adderstonelee Moss/Roxb./GB (NMS).

*Parornix torquillella* (Zeller) on *Prunus spinosa*: 1 ♀ Wester Frisk/Fife/GB (NMS).

*Parornix* sp. on *Prunus spinosa* or *Crataegus monogyna*: 1 ♀ Warton Crag/Lancs./GB (NMS).

*Phyllonorycter blancardella* (Fabricius) (Gracillariidae) on *Malus* sp.: 1 ♀ Doddiscombsleigh/Devon/GB (NMS).

*Phyllonorycter corylifoliella* (Hübner) on *Crataegus monogyna*: 1 ♀ Reading/Berks./GB (NMS).

*Phyllonorycter oxyacanthae* (Frey) on *Crataegus monogyna*: 4 ♀, 3 ♂ Lymm/Ches./GB (Horstmann, NMS, London), 1 ♀ Leigh Woods/Avon/GB (Horstmann).

*Phyllonorycter* sp. on *Quercus robur*: 1 ♀ Abbots Moss/Ches./GB (NMS).

17 (10 independent) records: 7 host species, all in two genera of relatively small Gracillariidae mining trees and bushes (? especially *Rosaceae*) as young larvae. *Phyllonorycter* species continue to mine throughout their larval life and also pupate in the mine, while *Parornix* species make one or more leaf folds following a rather small *Phyllonorycter*-like mine, and finally pupate in a separate purpose-made site. Most (possibly all) of the rearings listed are from bivoltine hosts, and the rearing data suggest that their generations are attacked by successive generations of the parasitoid. All overwinter in the pupal stage: despite this, *D. crataegi* from these gracillariids collected in late summer or autumn seem always to have emerged as adults in autumn or early winter of the same year. This leaves its means of passing the winter unclear (presuming it cannot do so as an adult). Some aspect of the husbandry may have consistently led to unnaturally early emergence of the adults (i.e. instead of overwintering as a cocooned stage), or it is possible that there may be an overwintering generation in some other host that we have not yet found. Similar uncertainties arise for *D. duplicatum* and *D. stigmatellae*.

*Distribution.*—Reared: GB, NL.

### Diadegma duplicatum Horstmann

*Caloptilia stigmatella* (Fabricius) (Gracillariidae) on *Populus tremula*: 2 ♀, 2 ♂ Hell Coppice/Bucks./GB, MonkWood/Worcs./GB, Loch

Fada/Isle of Coll/GB (NMS), 3 ♂ Waulkmill Bay/Orkney/GB (Horstmann, NMS); on *Salix alba*: 1 ♀ Bad Eilsen/Hameln/D (München); on *Salix aurita*: 1 ♀ Loch Fada/Isle of Coll/GB (NMS); on *Salix caprea*: 1 ♀ Broadmoor/Berks./GB (NMS); on *Salix cinerea* agg.: 5 ♀, 1 ♂ Oyter Moor/Bremen/D (Horstmann, München), 2 ♀ Southleigh/Devon/GB (Horstmann, NMS); on *Salix repens*: 1 ♀ Wedel/Hamburg/D (Haeselbarth), 3 ♀ Holme Chase/Devon/GB (NMS); on *Salix viminalis*: 1 ♀ Troisdorf/Köln/D (München), 1 ♀, 1 ♂ Woolhampton/Berks./GB (Horstmann, NMS); on *Salix* sp.: 1 ♀ Ettrick/Selkirks./GB (NMS); (cocoon collected on *Alnus glutinosa* growing near *Salix* sp.): 1 ♀ Caerlaverock Castle/Dumfries/GB (NMS); (labelled as from *Alnus* sp.): 5 ♀ Bremen/D (Horstmann, München).

*Lyonetia pulverulentella* Zeller (syn. *frigidariella* Herrich-Schäffer) (Lyonetiidae): 3 ♀ Edsåsen/Undersåker/Jämtland/S (Lund).

35 (17 independent) records: 32 (91%) from a single host species, that is predominantly univoltine in Britain and overwinters as an adult. *C. stigmatella* normally feeds on Salicaceae, though it has also occasionally been recorded on both *Betula* and *Alnus*. We accept the above host determinations of *C. stigmatella* from *Alnus* on the grounds that both the cocoon (in which the parasitoid's cocoon is formed) and the adult of *C. stigmatella* differ markedly from the common *Alnus*-feeding species, *Caloptilia elongella*. *Caloptilia* species are leaf miners when small, and it seems significant that the only host recorded above (3 individuals, but only one independent record) that is not *C. stigmatella* is, although in a different family, also a miner on Salicaceae: whether this resulted from a misidentification of possibly similar mines, as that of *C. stigmatella* is abnormally linear and not unlike a *Lyonetia* mine at first, or demonstrates a niche-specialised extending host range of an otherwise highly monophagous species is unclear. The available rearing data from *C. stigmatella* also leave the question of how *D. duplicatum* overwinters unanswered, as

all cocoons have emerged in the year they were made. Although it seems to be a univoltine parasitoid tied to a univoltine host, there is thus a possibility that we have not yet recognised the host or adults of the overwintering generation of what is really a bivoltine parasitoid (see also comments under *D. crataegi* and *D. stigmatellae*).

*D. duplicatum* differs from *D. holopygum* only in the length of the ovipositor (ovipositor index 0.9–1.1 in *holopygum*, 1.2–1.5 in *duplicatum*). But because their host ranges seem to be appreciably different, and because the ovipositor length does not vary (beyond the limits given above) within series from the same locality and host, they are treated as separate species. They cannot be regarded as seasonal forms of the same taxon, as both can be adult in early autumn.

*Distribution.*—Reared: D, GB, S. Non-reared: BG (Kolarov).

### *Diadegma elishae* (Bridgman)

*Parnornix alpicola* (Wocke) (Gracillariidae) on *Dryas octopetala*: 1 ♀ Lüner See/Vorarlberg/A (Huemer).

*Parornix devoniella* (Stainton) (syn. *avellanella* (Stainton)) on *Corylus avellana*: 2 ♀, 1 ♂ Kiel/D (Horstmann).

*Parornix scoticella* (Stainton) on *Sorbus aria*: 1 ♀, 1 ♂ Hambleden/Bucks./GB (NMS); on *Sorbus aucuparia*: 1 ♀ Alderley Edge/Ches./GB (Horstmann), 1 ♀ Pitlochry/Perths./GB (NMS).

*Parornix torquillella* (Zeller) on *Prunus spinosa*: 2 ♀, 1 ♂ Cappercleuch/Peebles./GB, Crackington/Cornwall/GB (NMS).

*Parornix* sp. on *Prunus spinosa*: 1 ♀, 2 ♂ West Wycombe/Bucks./GB (Horstmann, NMS); on *Prunus spinosa* or *Crataegus* sp.: 1 ♀ Faringdon/Oxon/GB (NMS).

*Phyllonorycter nicellii* (Stainton) (Gracillariidae) on *Corylus avellana*: 1 ♀ Kiel/D (Horstmann).

(The types, 2 ♀, 2 ♂ (Bridgman), were reared from "either *Ornix* [= *Parornix*] *scoticella* or *Nepticula aucuparia* [sic] [= *Stigmella nylandriella* (Tengström)]" from an unnamed British locality but, although subsequent rearing records (of both *D.*

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*elishae* and bona fide parasitoids of Nepticulidae) would very strongly suggest the former, we have not included these specimens in the analysis).

16 (10 independent) records: 15 (94%) from one genus (4 or more species). The remaining record is of a host that makes a mine which we know from direct personal experience is extremely easily confused with the fold of *Parornix devoniella* and, although *Phyllonorycter* is closely related to *Parornix*, it is hard to be confident that the host determination is correct. Thus *D. elishae* appears to be a specialist parasitoid of the genus *Parornix*, and it is of interest that while the great majority of *Parornix* species feed on trees and bushes, there is also a record of *D. elishae* from one of the few that feeds on low plants (*Dryas*), though it may be significant that in its habitat *Dryas* is often as tall as any co-occurring vegetation. The 9 GB specimens are all from Rosaceae, and appear to reflect at least a strong leaning towards hosts on that plant family in GB, if not in the rest of Europe. The winter is passed in the cocoon stage by both parasitoid and hosts. The rearing data suggest that *D. elishae* may be partly bivoltine, but clear evidence is lacking.
*Distribution.*—Reared: A, D, GB. Non-reared: A (Horstmann), PL (Sawoniewicz), R (St. Petersburg).

### Diadegma exareolator Aubert

*Bedellia somnulentella* (Zeller) (Lyonetiidae) on *Calystegia sepium*: 7 ♀, 3 ♂ Chartres/Eure-et-Loir/F (Horstmann, NMS); on *Calystegia soldanella*: 2 ♀, 2 ♂ Kennack Sands/Cornwall/GB (NMS); on *Convolvulus arvensis*: 1 ♀ Darbres/Ardèche/F (NMS), 1 ♀, 2 ♂ Budapest/H (Budapest); on *Calystegia* or *Convolvulus*: 4 ♀, 6 ♂ Gwithian/Cornwall/GB, Hayling Island/Hants./GB, Horton/Glower/GB, Tillingham/Essex/GB (NMS); on unrecorded plant: 2 ♀, 1 ♂ Malta (NMS). *Aspilapteryx tringipennella* (Zeller) (Gracillariidae) on *Plantago lanceolata*: 1 ♀, 2 ♂ Aviemore/Inverness./GB (NMS), 2 ♀, 2 ♂ Tantallon/E. Lothian/GB (Horstmann,

NMS); on unrecorded plant: 1 ♀ Portland/Dorset/GB (NMS), 3 ♂ Burren/Co. Clare/IRL (London).
*Tebenna micalis* (Mann) (Choreutidae) on *Pulicaria dysenterica*: 1 ♀ Noss Mayo/Devon/GB (NMS).
*Digitivalva pulicariae* (Klimesch) (Yponomeutidae): 3 ♀, 3 ♂ Hale/Cornwall/GB (London).
*Paraswammerdamia lutarea* (Haworth) (Yponomeutidae): 2 ♀, 2 ♂ Munster/Lüneburg/D (London).
*Plutella xylostella* (Linnaeus) (Yponomeutidae) on *Brassica rapa*: 2 ♀, 2 ♂ Kiel/D (Hinz, Horstmann).

57 (17 independent) records: although 31 (54%) are from a single species (*Bedellia somnulentella*), the remaining records cover a further 3 families and include highly migratory hosts. Rearing data indicate that the parasitoid is bivoltine, and cocoons appear to produce adults always in the year they are formed. All the hosts recorded above except *Paraswammerdamia lutarea* feed on low vegetation and two (*Tebenna micalis*, *Plutella xylostella*) feed by windowing beneath a web rather than by mining, as far as is known even when very young. *D. exareolator* clearly has a strong association with *Bedellia somnulentella* but we regard it as a species with a well diversified host range. The available rearing data suggest that *Aspilapteryx tringipennella*, which mines through the winter, regularly provides the means for *D. exareolator* to get through in a growing host, and that *Paraswammerdamia lutarea* is another host usable by the overwintering generation.
*Distribution.*—Reared: D, F, GB, H, IRL, Malta. Non-reared: BG (Kolarov), F (Aubert), P (NMS).

### Diadegma flexum Horstmann

No host record.
*Distribution.*—Non-reared: BG (Kolarov), D (Haeselbarth, Hinz, Horstmann), I (Bauer, Haeselbarth).

### Diadegma holopygum (Thomson)

*Tischeria marginea* (Haworth) (Tischeriidae) on *Rubus plicatus*: 1 ♀ Czestochowa/PL (Sawo-

niewicz); on *Rubus caesius*: 1 ♀ Wloclawek/PL (Sawoniewicz).

*Bucculatrix artemisiella* Herrich-Schäffer (syn. *artemisiae* auctt.) (Bucculatricidae) on *Artemisia campestris*: 3 ♀, 1 ♂ Torun/PL (Sawoniewicz).

*Bucculatrix gnaphaliella* (Treitschke) on *Helichrysum arenarium*: 1 ♀ Nienawiszcz/Poznan/PL (Sawoniewicz).

*Lyonetia clerkella* (Linnaeus) (Lyonetiidae) on *Malus domestica*: 1 ♀, 1 ♂ Edinburgh/GB (NMS); on *Prunus avium*: 1 ♀ Feldkirch/Vorarlberg/A (Huemer); on unrecorded plant: 1 ♀, 1 ♂ Asker/Oslo/N (Šedivý).

*Lyonetia pulverulentella* Zeller (syn. *frigidariella* Herrich-Schäffer) on *Salix pentandra*: 2 ♀, 1 ♂ Puszcza Borecka/Gizycko/PL, Rezerwat Spytkowo/Gizycko/PL (Sawoniewicz).

*Aspilapteryx tringipennella* (Zeller) (Gracillariidae) on *Plantago lanceolata*: 2 ♀, 2 ♂ Ascot/Berks./GB (NMS).

*Calybites auroguttella* (Stephens) (Gracillariidae) on *Hypericum perforatum*: 2 ♀ Ipsden/Oxon/GB (NMS), 2 ♀, 2 ♂ Farnham Royal/Surrey/GB (London).

*Calybites phasianipennella* (Hübner) on *Polygonum hydropiper*: 5 ♀, 1 ♂ Oyter Moor/Bremen/D (Horstmann, München), 1 ♀ Oldenbüttel/Bremen/D (München), 1 ♀, 1 ♂ Torun/PL (Sawoniewicz); on *Polygonum mite*: 1 ♀, 2 ♂ Czystochleb/Torun/PL, Gizycko/PL (Sawoniewicz); on *Rumex acetosa*: 9 ♀, 4 ♂ Ascot/Berks./GB (Horstmann, NMS), 2 ♀, 4 ♂ St. Jean du Gard/Gard/F (NMS); on *Rumex* sp.: 3 ♀, 2 ♂ Whitbarow Moss/Cum./GB (NMS).

*Paronix finitimella* (Zeller) (Gracillariidae) on *Prunus cerasifera*: 1 ♀ Gizycko/PL (Sawoniewicz).

*Phyllonorycter maestingella* (Müller) (syn. *faginella* (Zeller)) (Gracillariidae) on *Fagus sylvatica*: 2 ♀ Köln/D (München).

*Phyllonorycter sylvella* (Haworth) on *Acer campestre*: 1 ♀ Poznan/PL (Sawoniewicz).

*Coleophora fuscocuprella* Herrich-Schäffer (Coleophoridae) on *Corylus avellana*: 1 ♀ Ruhede/Skovlund/DEN (NMS).

*Coleophora violacea* (Haworth) on *Betula* sp.: 1 ♀ Havant Thicket/Hants./GB (NMS).

*Mompha locupletella* (Denis & Schiffermüller) (Momphidae) on *Epilobium montanum*: 1 ♀ Kinkajmy/Bartoszyce/PL (Sawoniewicz), 2 ♀, 1 ♂ Sparkwell/Devon/GB (Horstmann,

NMS); on *Epilobium obscurum*: 2 ♀ Emer Bog/Hants./GB (NMS); on *Epilobium* sp.: 2 ♀, 4 ♂ Ballyonneely/Galway/IRL (NMS), 1 ♀, 2 ♂ Puszcza Borecka/Gizycko/PL (Sawoniewicz).

*Millieria dolosalis* (Heydenreich) (syn. *dolosana* auctt.) (Choreutidae) on *Aristolochia clematitis*: 1 ♀, 1 ♂ St. Jean du Gard/Gard/F (NMS); on *Aristolochia pistolochia*: 9 ♀, 7 ♂ Darbres/Ardèche/F (Horstmann, NMS).

100 (32 independent) records: although 50 (50%) are from Gracillariidae, and especially *Calybites*, 4 genera in that family are involved and overall the records span 7 families of Lepidoptera (15 species). Although a few records are from hosts on trees and bushes, most are from hosts feeding in the field layer, and a particular association with that sector of the overall habitat probably accounts for the lack of records from *Caloptilia* (which feed entirely on trees and shrubs) among the records for Gracillariidae. Cocoons of *D. holopygum* resulting in late summer or autumn always seem to emerge the same year, but the available rearing data suggest that *Aspilapteryx tringipennella* and *Mompha locupletella*, both of which mine through the winter, provide the regular means for this bivoltine parasitoid to go through in a growing host. The possible role of *Coleophora fuscocuprella* and *C. violacea* in this respect is interesting: each is one of relatively few arboreal *Coleophora* species that attains full growth in the autumn but does not pupate until spring, and the single *D. holopygum* reared from *C. violacea* emerged in spring from a host case collected the previous autumn. The emergence date for the specimen from *C. fuscocuprella* is uncertain.

Distribution.—Reared: A, D, DEN, F, GB, IRL, N, PL. Non-reared: BG (Kolarov), I (Haeselbarth), PL (Horstmann), R (St. Petersburg), S (Lund).

## *Diadegma laricinellum* (Strobl)

*Coleophora laricella* (Hübner) (Coleophoridae) on *Larix decidua*: 1 ♀, 2 ♂ Farnham Royal/

Surrey/GB (London): 1 ♂ Fortingall/
Perths./GB (NMS), 1 ♀, 1 ♂ Schleswig/D
(Horstmann), 1 ♀, 1 ♂ Admont/Steiermark/A
(Strobl), 1 ♀ Zernez/Engadin/CH (Horst-
mann), 2 ♀, 2 ♂ Trimmis/Graubünden/CH,
Scheid/Graubünden/CH, 1 ♀ Val Aurina/
Südtirol/I (Aeschlimann).

14 (8 independent) records: one host spe-
cies. The host starts its larval life as a nee-
dle miner without a case. It hibernates
partly grown and is univoltine. The para-
sitoid is presumably also univoltine and is
carried through the winter in the partly
grown host, emergence taking place from
the host case in early/mid summer.
*Distribution.*—Reared: A, CH, D, GB, I.
Non-reared: R (St. Petersburg).

## Diadegma latungulum (Thomson)

*Mompha conturbatella* (Hübner) (Momphidae) on
   *Epilobium angustifolium*: 6 ♀, 5 ♂ Broughton
   Down/Hants./GB, Lullingstone/Kent/GB,
   Silverwells/Berwicks./GB (NMS); on unre-
   corded plant: 1 ♀ Tjörnarp/Kristianstad/S
   (Lund).
*Mompha epilobiella* (Denis & Schiffermüller) (syn.
   *fulvescens* (Haworth)) on *Epilobium hirsutum*:
   36 ♀, 20 ♂ Bromley/Kent/GB, Catfield/
   Norf./GB, Chichester/Sussex/GB, Fecken-
   ham Wild Moor/Worcs./GB, Horning/
   Norf./GB, Horseheath/Cambs./GB, Leck-
   ford/Hants./GB, Northwood Hill/Kent/GB,
   Solihull/Warwicks./GB, The Flits/Here-
   fords./GB, Darbres/Ardèche/F (NMS), 2 ♀, 1
   ♂ Rezerwat Laz Piwnicki/Torun/PL (Sawon-
   iewicz); on *Epilobium* sp.: 2 ♀ Goslar/D, Bad
   Eilsen/Hameln/D (München), 2 ♀, 2 ♂
   Kiel/D (Horstmann, Rill), 1 ♂ Alperton/
   Middlesex/GB (London).
*Mompha langiella* (Hübner) (syn. *epilobiella* (Roe-
   mer) nec (Denis & Schiffermüller)) on *Circaea
   lutetiana*: 2 ♀ Coombe Martin/Devon/GB
   (NMS).
*Mompha locupletella* (Denis & Schiffermüller) on
   *Epilobium alsinifolium*: 1 ♂ Whitebrook/Mon-
   mouths./GB (NMS); on *Epilobium montanum*:
   1 ♀ Havant Thicket/Hants./GB (NMS); on
   *Epilobium tetragonum*: 3 ♀, 1 ♂ Cadsonbury/
   Cornwall/GB, Plymouth/Devon/GB (NMS),
   1 ♂ Sparkwell/Devon/GB (Horstmann); on

unrecorded plant: 1 ♀, 3 ♂ Cornwall/GB,
   Marwellham Quay/Devon/GB (NMS).
*Mompha nodicolella* Fuchs on *Epilobium angusti-
   folium*: 1 ♀ Camberwell/London/GB (NMS),
   9 ♀, 1 ♂ East Ham/Essex/GB (Horstmann,
   NMS).
*Mompha ochraceella* (Curtis) on *Epilobium hirsu-
   tum*: 3 ♀, 1 ♂ Bromley/Kent/GB, Worces-
   ter/GB, Bulford/Wilts./GB (NMS).
*Mompha propinquella* (Stainton) on *Epilobium te-
   tragonum*: 2 ♂ Colypool/Devon/GB, Plymp-
   ton/Devon/GB (NMS); on *Epilobium* sp.: 3 ♀
   Plympton/Devon/GB, Ryton/Warwicks./GB
   (NMS).
*Mompha subbistrigella* (Haworth) on *Epilobium
   montanum*: 1 ♀ Winchester/Hants./GB (NMS);
   on *Epilobium* sp.: 1 ♀, 2 ♂ Brotheridge/
   Worcs./GB (NMS).
*Mompha* sp. on *Epilobium montanum*: 1 ♀, 2 ♂
   Mühlhausen/Thüringen/D (München).

118 (39 independent) records: all from
*Mompha* (8 species). The distribution of
rearing records from the above *Mompha*
species is an approximate reflection of the
sampling effort, but it is noteworthy that
two other well-sampled but rather small
species, *M. raschkiella* mining *Epilobium an-
gustifolium* and *M. miscella* mining *Helian-
themum*, have consistently failed to pro-
duce *D. latungulum* in GB (Shaw unpub-
lished). The *Mompha* species attacked by
*D. latungulum* use their foodplants in a va-
riety of ways ranging from tightly spin-
ning shoots to mining leaves, and galling
or boring in stems and seedpods. *D. latun-
gulum* is bivoltine and its cocoons invari-
ably emerge in the year of formation.
Some of the host species overwinter as
adults and others as partly fed larvae:
while *D. latungulum* is often an abundant
parasitoid of summer larvae of the former
category, its presence at a site appears to
depend on the co-occurrence of *Mompha*
species that overwinter as partly grown
larvae thereby providing the means for it
to overwinter.

We have examined the male syntype of
*Pectinella latungula* (Thomson) var. *deleta*
Morley and it appears to belong to *D. la-*

*tungulum,* as Fitton (1976: 342) has already supposed.

*Distribution.*—Reared: D, GB, PL, S. Non-reared: BG (Kolarov), D (Bauer, Haeselbarth, Hinz, Horstmann), F (Lund), FIN (Jussila), GB (London), Y (Sawoniewicz).

### Diadegma ledicola Horstmann

*Diplodoma herminata* (Geoffroy) (Psychidae): 1 ♀ Monk Wood/Worcs./GB (NMS).

*Oreopsyche matthesi* Bourgogne (Psychidae): 1 ♀, 1 ♂ Montalegre/Vila Real/P (Aubert).

*Proutia betulina* (Zeller) (Psychidae): 2 ♀, 2 ♂ Hatert/Nijmegen/NL (Horstmann, München), 1 ♀ Groesbeek/NL, 1 ♀ Bremen/D (München).

*Psyche casta* (Pallas): 4 ♀, 1 ♂ Orpington/Kent/GB, Avon Gorge/Bristol/GB, Painswick/Glos./GB, South Stack/Anglesey/GB (NMS).

Psychidae Gen. sp. on *Ledum palustre*: 1 ♀, 1 ♂ Heidmoor/Segeberg/D (Horstmann), 1 ♀ Salemer Moor/Lauenburg/Elbe/D (Hinz).

17 (11 independent) records: all from Psychidae (4 or more species). The parasitoids have emerged from the host cases in the summer in which they were collected: as the known hosts are essentially synchronous, univoltine and overwinter partly grown it is probable that the parasitoid is also univoltine and overwinters in the young host larva.

*Distribution.*—Reared: D, GB, NL, P. Non-reared: BG (Hinz), BY (St. Petersburg), D (Hinz), F (Aeschlimann), M (St. Petersburg), P (Aubert).

### Diadegma lithocolletis Horstmann

*Bucculatrix nigricomella* Zeller (Bucculatricidae) on *Chrysanthemum leucanthemum*: 1 ♀ Dunajek/Olecko/PL (Sawoniewicz).

*Acrocercops imperialella* (Zeller) (Gracillariidae): 1 ♀ Wicken Fen/Cambs./GB (NMS).

*Callisto denticulella* (Thunberg) (Gracillariidae) on *Malus domestica*: 1 ♀, 2 ♂ Gizycko/PL (Sawoniewicz).

*Phyllonorycter emberizaepenella* (Bouché) (Gracillariidae) on *Lonicera periclymenum*: 5 ♀, 2 ♂ Balmaha/Stirlings./GB, Endrick Mouth/Dunbartons./GB, Kilmelford/Argyll/GB, Meth-

ven/Perths./GB (NMS), 2 ♂ Presmennan/E. Lothian/GB (Horstmann, NMS), 3 ♀ Bremen/D (Hinz, Horstmann); on *Lonicera tatarica*: 1 ♀ Torun/PL (Sawoniewicz); on *Lonicera xylosteum*: 1 ♂ Gizycko/PL (Sawoniewicz); on *Lonicera* sp.: 2 ♀, 4 ♂ Hulshorst/Gelder Land/NL. (NMS), 3 ♀ Wollah/Bremen/D (München); on unrecorded plant: 2 ♂ Hamburg/D (Haeselbarth), 2 ♂ Österlöv/Kristianstad/S (Lund), 1 ♂ Rotenburg/Bremen/D (München), 1 ♀ Reher Kratt/Itzehoe/D (Horstmann).

*Phyllonorycter ulmifoliella* (Hübner) on *Betula* sp.: 1 ♀ Harpstedt/Delmenhorst/D (München).

*Perittia herrichiella* (Herrich-Schäffer) (Elachistidae) on *Lonicera xylosteum*: 2 ♀ Blankenburg/Thüringen/D (Torino), 1 ♀, 3 ♂ Czerwony Dwor/Olecko/PL, Leszczowek/Suwalki/PL, Ojców/Kraków/PL (Sawoniewicz), 2 ♀, 1 ♂ Villars-Colmars/Alpes de Haute Provence/F (NMS).

44 (23 independent) records: although 38 (86%) are from just two species of leaf miners on *Lonicera* (*Phyllonorycter emberizaepennella* and *Perittia herrichiella*) these two are in different families and the full host list spans 5 genera in 3 families, on a range of field layer plants as well as trees. *D. lithocolletis* overwinters as a cocooned stage (the numerous specimens from *Ph. emberizaepennella* have all done so, within the exceptionally tough overwintering cocoons of the host: indeed, this peculiarity of the host may be an important determinant of host range within the genus *Phyllonorycter*). It is unclear whether *D. lithocolletis* is univoltine or bivoltine in the northern part of its range, but the fairly rapid emergence of cocoons from *Pe. herrichiella* in the same summer that they were formed suggests bivoltinism in S. Europe. *D. lithocolletis* exhibits an interesting host range with an undeniably strong association with certain miners on *Lonicera*, but with evidence of both selection (*Phyllonorycter trifasciella* (Haworth), also mining *Lonicera*, is a common and well-sampled host that has not so far yielded this parasitoid) and a host family extension even there, and enough records out-

side that core to indicate considerable plasticity and recruitment of a broader host spectrum.

*Distribution.*—Reared: D, F, GB, NL, PL, S. Non-reared: I (München).

### *Diadegma longicaudatum* Horstmann

*Bijugis bombycella* (Denis & Schiffermüller) var. *silvicolella* Sieder (Psychidae) : 1 ♀ Hochobir/ Kärnten/A (München).
*Sterrhopterix fusca* (Haworth) (syn. *hirsutella* (Hübner)) (Psychidae): 2 ♀, 1 ♂ Braunschweig/D (Horstmann, München).

4 (2 independent) records: all from Psychidae (2 species). The available rearing data do not clearly indicate how *D. longicaudatum* overwinters, but field collection dates of adults suggest that it may be bivoltine.

Originally, *D. longicaudatum* Horstmann was described (Horstmann 1969: 445) from specimens with a longer ovipositor (index 1.9–2.0), and *D. germanicum* Horstmann subsequently (Horstmann 1973: 145) from specimens with a shorter ovipositor (index 1.7–1.8). In other respects the two taxa are similar. Subsequently intermediate forms have been found, even in series from the same locality, and therefore the two taxa are here synonymized (**syn. nov.**). Aubert (1976: 205) synonymized *D. germanicum* with *D. rectificator* Aubert (were this to be correct, *D. longicaudatum* would be the valid name of the species). But the differences given by Horstmann (1973: 145; see key) remain constant in all the material so far studied and therefore *D. rectificator* is still treated as a species separate from *D. longicaudatum*.

*Distribution.*—Reared: A, D. Non-reared: A (Haeselbarth, Horstmann), BG (Kolarov), D (Bauer, Haeselbarth, Hinz, Horstmann), F (Aubert, Horstmann, Leiden), H (Horstmann), PL (Sawoniewicz), R (St. Petersburg).

### *Diadegma melanium* (Thomson)

*Bucculatrix noltei* Petry (Bucculatricidae) on *Artemisia vulgaris*: 1 ♀, 7 ♂ Smykovo/Ostroda/ PL, Torun/PL (Sawoniewicz).

8 (2 independent) records: one host species. *D. melanium* is a rarely encountered species but it seems probable that it is a regular parasitoid of *B. noltei* (note, however, that this host does not occur throughout the distribution of *D. melanium*). The host is univoltine, feeds in late summer and overwinters in its cocoon. With a single exception collected in June, adults of *D. melanium* have been collected and reared only in July, and it seems likely also to be univoltine.

*Distribution.*—Reared: PL. Non-reared: D (Haeselbarth, Horstmann, München), GB (Bridgman), S (Lund).

### *Diadegma micrurum* (Thomson)

No host record.
*Distribution.*—Non-reared: Nord/F (Lund), R (St. Petersburg).

### *Diadegma nanus* (Gravenhorst)

*Coleophora juncicolella* Stainton (Coleophoridae) on *Calluna vulgaris*: 3 ♀ Muir of Dinnet/ Aberdeens./GB (Horstmann, NMS).

3 (1 independent) records: one host species. The host is univoltine and overwinters partly grown, no doubt carrying the parasitoid through. *C. juncicolella* is not rare but it is local to heathland and moorland habitats and rather seldom reared. It seems probable that *D. nanus* will be found to be a specialised and regular parasitoid of it, though to date *D. nanus* has been regarded as a rare species.

*Distribution.*—Reared: GB. Non-reared: D (Horstmann), S (Lund).

### *Diadegma pulicator* Aubert

No host record.
*Distribution.*—Non-reared: Alpes de Haute Provence/F (Aubert).

### Diadegma pusio (Holmgren)

*Bucculatrix absinthii* Gärtner (Bucculatricidae) on *Artemisia absinthium*: 1 ♀ Räplinge/Öland/S (NMS).

*Bucculatrix capreella* Krogerus on *Achillea millefolium*: 5 ♀, 1 ♂ Aviemore/Inverness./GB, Invercauld/Aberdeens./GB (NMS).

*Bucculatrix cidarella* Zeller: 1 ♀, 1 ♂ Bexley/Kent/GB (London), 1 ♀ locality unknown (Bridgman).

*Bucculatrix demaryella* (Duponchel) on *Castanea sativa*: 2 ♀, 1 ♂ Wateringbury/Kent/GB (NMS).

*Bucculatrix frangutella* (Goeze) on *Rhamnus catharticus*: 1 ♀ Leckford/Hants./GB (NMS).

*Bucclatrix laciniatella* Bernander on *Artemisia laciniata*: 2 ♀, 1 ♂ Möckelmosen/Öland/S (NMS).

*Bucculatrix nigricomella* Zeller on *Leucanthemum vulgare*: 1 ♀, 2 ♂ Blackford/Edinburgh/GB (Horstmann, NMS), 1 ♂ Whitstable/Kent/GB (NMS).

*Bucculatrix noltei* Petry on *Artemisia vulgaris*: 1 ♀ Torun/PL (Sawoniewicz); on unrecorded plant: 2 ♀, 2 ♂ Büchen/Lauenburg/Elbe/D (Horstmann, Rill).

*Bucculatrix ulmella* Zeller on *Quercus robur*: 3 ♀ Botley Wood/Hants./GB, Colchester/Essex/GB, Wimbledon Common/London/GB (NMS).

28 (15 independent) records: all from *Bucculatrix* (9 species). The rearing data indicate that *D. pusio* is a bivoltine taxon specialist, using as summer hosts *Bucculatrix* species that are univoltine or bivoltine on plants in the field layer but in either case that do not overwinter in the cocoon stage, and then for its overwintering generation attacking arboreal *Bucculatrix* species that do overwinter in the cocoon stage in the robust cocoons of which it also overwinters. (Contrast the host range of the apparently univoltine *D. crassum*, which has been reared only from the latter host group.)

Distribution.—Reared: D, GB, PL, S. Non-reared: A (Haeselbarth), GR (Lund), I (Haeselbarth), PL (Sawoniewicz), S (Stockholm).

### Diadegma rectificator Aubert

No host record.
Distribution.—Non-reared: P (Aubert).

### Diadegma rufatum (Bridgman)

*Prochoreutis myllerana* (Fabricius) (Choreutidae) on *Scutellaria galericulata*: 4 ♀, 1 ♂ Oxford/GB (Horstmann, NMS), 2 ♂ Port Appin/Argyll/GB, Stover Park/Devon/GB (NMS); on *Scutellaria* sp.: 1 ♀ Bad Eilsen/Hameln/D (München); on unrecorded plant: 1 ♂ Woodbastwick/Norf./GB (NMS), 1 ♀ Kullen/Malmöhus/S (Lund).

*Prochoreutis ?myllerana* (as *Choreutes* [sic] *scintillulana* [sic]): 3 ♀, 3 ♂, unlocalised GB (Bridgman).

*Prochoreutis sehestediana* (Fabricius) on *Scutellaria galericulata*: 8 ♀, 8 ♂ Ashurst/Hants./GB, Barton Turf/Norf./GB, Catfield/Norf./GB (NMS); on *Scutellaria minor*: 1 ♀, 1 ♂ Plymouth/Devon/GB (NMS).

*Prochoreutis myllerana* or *P. sehestediana* on *Scutellaria galericulata*: 18 ♀, 12 ♂ Bexley/Kent/GB, Endrick Mouth/Stirlings./GB, Loch Tay/Perths./GB, Strumpshaw/Norf./GB (NMS).

64 (15 independent) records: all from the two species of *Prochoreutis* that occur in the region and feed on *Scutellaria*. *D. rufatum* is a highly specialised species and, like many parasitoids characteristic of wet habitats, is appreciably redder in colouration than most of its congeners. All of the many cocoons we have had alive have emerged in the year they were formed and, although the means by which *Prochoreutis* species (both of which are bivoltine) pass the winter is unclear, the rearing data suggest that *D. rufatum* is also a bivoltine species that overwinters in partly grown hosts.

Distribution.—Reared: D, GB, S. Non-reared: BY (St. Petersburg), D (Hilpert, Horstmann), PL (Sawoniewicz), S (Jussila, Lund).

### Diadegma scotiae (Bridgman)

*Phaulernis fulviguttella* (Zeller) (Epermeniidae) on *Angelica sylvestris*: 1 ♀, 2 ♂ Glen Lyon/Perths./GB, Possil/Glasgow/GB (NMS), 3

♀, 2 ♂ Utsjoki/Kevo/FIN (Horstmann, Jussila); (as "*Heydenia auromaculella*") on unrecorded plant: 1 ♀, 5 ♂ Shetland/GB (Bridgman).

14 (4 independent) records: one host species. The host is univoltine, feeding in autumn among spun seeds and overwintering as a pupa. The two specimens of *D. scotiae* (from Glen Lyon) seen that are preserved with their cocoons emerged in August from the pupae (parasitoid cocoon spun within the host's pupal cuticle) of hosts collected as larvae the previous autumn. This use of host pupal cuticle is a regular practice of only a very small minority of Campoplegine, but it is seen in several genera. The specimens labelled as reared from "*Heydenia auromaculella*" are presumed to be from *P. fulviguttella* on the grounds that *Heydenia* Hofmann, 1868 (preocc.) was applied in Epermeniidae and the name *auromaculella* appears to be interpretable within British Epermeniidae only as a lapsus for *auromaculata* Frey, which is a synonym of *fulvigutella*. *D. scotiae* is a northern species and it is clear that it is univoltine.

*Distribution.*—Reared: FIN, GB. Nonreared: R (St. Petersburg).

## Diadegma stigmatellae Horstmann

*Caloptilia alchimiella* (Scopoli) (Gracillariidae) on *Quercus robur*: 2 ♀ Innerleithen/Peebles./GB, Kerfield/Peebles./GB (NMS).

*Caloptilia betulicola* (Hering) on *Betula*: 1 ♀ Chat Moss/Manchester/GB (NMS).

*Caloptilia cuculipennella* (Hübner) on *Ligustrum vulgare*: 8 ♀, 11 ♂ Branscombe/Devon/GB (Horstmann, NMS), 1 ♀, 1 ♂ Portland/Dorset/GB (NMS).

*Caloptilia falconipennella* (Hübner) on *Alnus* sp.: 2 ♀ Bexley/Kent/GB, Medmenham/Bucks./GB (NMS).

*Caloptilia robustella* Jäckh on *Quercus robur*: 1 ♀ Reading/Berks./GB (NMS).

*Caloptilia stigmatella* (Fabricius) on *Populus alba*: 1 ♀, 2 ♂ Ainsdale/Lancs./GB (NMS); on *Populus nigra*: 1 ♀ Hampstead Heath/London/GB (NMS); on *Populus tremula*: 3♀ Milton Hide/Sussex/GB (NMS); on *Salix ci-*

*nerea* agg.: 2 ♀, 4 ♂ Branscombe/Devon/GB, Southleigh/Devon/GB (NMS), 7 ♀, 5 ♂ Otmoor/Oxon/GB, Woodley/Berks./GB (Horstmann, NMS); on unrecorded plant: 2 ♀, 1 ♂ locality unknown (Bridgman); (labelled as from *Alnus* sp.): 3 ♀, 1 ♂ Bremen/D (Horstmann, München).

*Caloptilia syringella* (Fabricius): 2 ♀ Folkestone/Kent/GB (NMS).

*Caloptilia* sp. on *Quercus* sp.: 1 ♀ Coventry/Warwicks./GB (NMS).

*Parornix anglicella* (Stainton) (Gracillariidae) on *Crataegus monogyna*: 7 ♀, 4 ♂ Balgaverie/Ayrshire/GB, Bawsinch/Edinburgh/GB, Blackford Hill/Edinburgh/GB, Catfield/Norf./GB, Reading/Berks./GB, Spott/E. Lothian/GB (NMS).

*Parornix finitimella* (Zeller) on *Prunus spinosa*: 3 ♂ Noss Mayo/Devon/GB, Lower Earley/Berks./GB (NMS).

*Parornix torquillella* (Zeller) on *Prunus spinosa*: 20 ♀, 15 ♂ Balmaha/Stirlings./GB, Benane Head/Bute/GB, Blackford Hill/Edinburgh/GB, Chilbotton/Hants./GB, Clovenfords/Selkirks./GB, Endrick Mouth/Stirlings./GB, Morston/Norf./GB, Southleigh/Devon/GB, Tregroes/Cards./GB (NMS), 4 ♀, 6 ♂ Saffron Walden/Essex/GB (Horstmann, NMS).

*Parornix* sp. on *Prunus spinosa*: 4 ♀, 4 ♂ Hampstead Heath/London/GB, West Wycombe/Bucks./GB, Woodchester Park/Glos./GB (NMS).

129 (40 independent) records: all from two genera (10 species) of relatively large Gracillariidae that are at first leaf miners on trees and bushes and then fold leaves, finally pupating in a purpose-made site away from where they fed. We accept the record from *C. stigmatella* on *Alnus* on the grounds already outlined in the commentary for *Diadegma duplicatum*. The host group, broadly, has two generations in the summer both of which are attacked by *D. stigmatellae*, apparently successively. However, although some of the hosts (*Parornix* species, in particular) overwinter as pupae, cocooned stages of *D. stigmatellae* have appeared to be incapable of diapausing and adults have always emerged in the year cocoons are formed, even if emergence is late into the autumn or early win-

ter. Although we suspect that this may be a consequence of husbandry, we cannot discount the possibility that we may not have yet recognised the adults or hosts of the overwintering generation of this parasitoid, despite its being a widespread and abundant species in GB (see also remarks under *D. crataegi* and *D. duplicatum*).

*Distribution.*—Reared: D, GB. Non-reared: D (Horstmann), F (Leiden).

### *Diadegma tamariscator* (Aubert)

No host record.

*Distribution.*—Non-reared: Corsica/F (Aubert). The specimen of uncertain status from Rhodes/GR (Lund) commented upon by Aubert (1989: 58) has also been examined, but its identity remains uncertain.

The following four series may each represent an undescribed species, but more material is needed to be certain of their status.

### *Diadegma* species 1

*Bucculatrix capreella* Krogerus (Bucculatricidae) on *Achillea millefolium*: 1 ♀ Granish Moor/Aviemore/Inverness./GB (NMS).

The host is univoltine and overwinters as an adult, but the parasitoid adult emerged in late July, soon after making its cocoon. This suggests that the parasitoid is not entirely specialised to this particular host.

### *Diadegma* species 2

*Caloptilia robustella* Jäckh (Gracillariidae) on *Quercus robor*: 3 ♀, 1 ♂ Redgrave Fen/S.Lopham/Norfolk/GB (NMS).

The host is bivoltine and overwinters as a pupa. The parasitoids overwintered in their cocoons in the host cocoons and this taxon appears to be bivoltine. It is conceivable that it is specialised to this host.

### *Diadegma* species 3

*Elachista argentella* (Clerck) (Elachistidae) on grasses: 2 ♀ Linkim Shore/Berwicks./GB (NMS).

The host is univoltine, and passes the winter as a partly fed larva. The rearing data suggest that the parasitoid is also univoltine, and that it overwinters as a larva in the host larva. It is conceivable that it is specialised to this host.

### *Diadegma* species 4

*Coleophora gryphipennella* (Hübner) (Coleophoridae) on *Rosa* sp.: 2 ♀ Inverkeithing/Fife/GB (NMS).

The univoltine host overwinters as a partly fed larva, and the rearing data suggest that the parasitoid is similarly univoltine, overwintering as a larva inside its host. It is conceivable that it is specialised to this host.

### DISCUSSION

The wide spectrum of host range characteristics revealed here for a group of closely related parasitoids warrants some discussion. There are, in fact, a number of threads that have a bearing on the complex processes in evolutionary ecology that must inevitably relate to speciation. To avoid the objection that the subgroups of the *D. nanus* group we have recognised are of uncertain relationship to one another, we will restrict comment to situations that pertain within the *D. nanus* subgroup, and clearly indicate the subgroup of any other species we mention.

It has been hypothesised (Shaw 1994) that in koinobiont parasitoids one way that new species first arise is as extreme specialists, and (for those that do not conserve and refine their extreme specialisation, as some certainly do) their host ranges may then tend to expand by a process of eventual (and incremental) recruitment of not only taxonomically related but also ecologically or physically similar hosts as they are encountered within a parasitoid's searching environment. This broadening of host range was regarded as providing the conditions that would promote the next speciation process, involving behav-

ioural specialisation on a fraction of that host range by a nascent species in response to sufficiently strong ecological opportunity and isolating mechanisms. General predictions of this hypothesis include the following. (1) While some parasitoids will be "taxon specialists" with host ranges that (at one extreme) may remain limited to a single species or (at the other extreme) may have broadened to involve many species in a given taxonomic group, there will also be parasitoids with host ranges that have broadened from some level of taxon specialisation so as also to encompass "ecologically" (including behaviourally or morphologically) similar but taxonomically unrelated hosts. (2) If it is particularly from species with broadened host ranges (whether remaining taxon specialists or not) that there is a tendency for nascent species to diverge through extreme specialisation in response to changing ecological opportunities, initially monophagous "young" species should arise that are most closely related to "old" species having wider host ranges. (3) Depending on the extent to which any subsequent tendency for the host ranges of the "young" species has had time and opportunity to occur (but presuming that it has been less manifest than in the "old" species), an overall pattern of very varied breadth of host range in closely related species would be expected, with no particular leaning towards close relationships between those having the narrowest (or the broadest) host ranges, but rather a tendency for species with broad host ranges to be most closely related to ("young") extreme specialists, with perhaps adjacent or shared hosts.

Unfortunately there are considerable difficulties in testing this hypothesis with appropriate rigour, as it would demand not only a very robust (and complete) phylogenetic reconstruction of the group of parasitoids in question, but also a clear knowledge of the host ranges and ecological circumstances pertaining at the time

the hypothesised speciation events took place. In more practical terms, there are probably insurmountable problems in trying to recognise and assign polarity to phylogenetically informative morphological character states separating genuine sister species that are so close and have diverged so recently that their current ecological attributes remain informative about conditions surrounding their divergence. Whether molecular techniques would offer better prospects is untested. At any rate, unfortunately we can be certain that currently we are not in a position to reconstruct the phylogeny of this group of *Diadegma* with any confidence: not only is there no definitive demonstration of monophyly in our interpretation of the *D. nanus* group, or even of any of its subgroups, but also the morphological features by which the species can be separated are very slight and reflect character states that are almost certainly highly labile and unpolarisable. On top of this there is little doubt that we know only a proportion of the extant species (quite apart from the prospect of there being extinct sister species), and we lack host range data for several of those that we do know. Nevertheless, the hypothesis connecting host range and speciation in koinobionts provides a framework against which to examine the pattern of host ranges seen in this group of *Diadegma* species, and if we are able to suggest close relationships between some species pairs it may inform, if not strictly test, the hypothesis.

There are seven described species (*anurum, brevivalve, callisto, laricinellum, melanium, nanus, scotiae*) known from only a single host species, five of them having been reared on more than one independent occasion. Another (*duplicatum*) probably falls into this category, allowing for the strong possibility that the singly independent anomalous host records may be the result of host misidentification. These may be absolute specialists: generally, most con-

geners and/or related genera of the known host have been sufficiently well sampled for us to be confident that the parasitoid certainly does not occur widely on them. Nine species (*crassum, crataegi, elishae, pusio, rufatum, stigmatellae; latungulum* of the *latungulum* subgroup; *ledicola* and *longicaudatum* of the *consumptor* subgroup) are also taxon specialists, albeit (to a variable extent) with wider host ranges: no recruitment of hosts seems to have occurred beyond a narrow range of taxonomically related hosts. In another three species (*exareolator, holopygum, lithocolletis*), however, host ranges are taxonomically much broader, and include hosts from several families—though not all hosts in those families are used. In these cases the host range has clearer ecological and possibly physical parameters than taxonomic ones, and it is suggested that these are the species which have incrementally broadened their host range by recruitment from disparate taxonomic groups, perhaps over long timescales but certainly from an initially narrow base.

In practice some of the absolute specialists may not be clearly differentiated as a category from the slightly more broadly based taxon specialists, if the host of the former kind has few close relatives within the parasitoid's searching environment available to be recruited. It may be significant, however, that the taxonomically most isolated species seem to be either absolute specialists (*brevivalve, scotiae*) or taxon specialists (*rufatum, latungulum* of the *latungulum* subgroup), as this might imply that these species, that have failed to appreciably broaden their host ranges, are "old specialists" which have not given rise to recognisable sister species in the relatively recent past. The trend seen here is consistent with the speciation hypothesis outlined by Shaw (1994), and it is also seen in *Aleiodes*. Moreover, as relatively isolated taxa within defined groups are easier to recognise than genuine sister species, examining other koinobiont groups

to see whether the most isolated species tend to be relatively taxon-specialised may provide the clearest test of the generality of this hypothesised link between host range expansion and subsequent speciation: if there is little evident trend it may suggest that this speciation mechanism is at best of minor importance in comparison with others. It is important, though, to apply the test the right way round—not to test whether taxon specialists tend to be abnormally isolated, as the hypothesised "young specialists" are expected not to be. One study that lends some support to this hypothesis is Gauld & Janzen's (1994) phylogenetic analysis of Costa Rican species of the campoplegine genus *Cryptophion*. Although they envisaged somewhat different evolutionary scenarios, they concluded that the most basal (i.e. the most isolated) species are taxon specialists, and that host range expansion has been an important force in the evolutionary biology of the group.

Some of the other specialists in our study (*anurum, callisto, duplicatum, laricinellum, melanium, nanus*) belong to a central core of very closely related species that include those with the widest host range (*exareolator, holopygum, lithocolletis*) and, although sister species relationships cannot be suggested with confidence, this is also compatible with the speciation hypothesis, in which "young specialists" arise through speciation following host range diversification. Some putative pairs of "young specialists"/parent species from within this core group that would fit the hypothesis rather well are *anurum/lithocolletis* (possible synapomorphies: areolation of propodeum, colour of legs, ovipositor length, body size), *duplicatum/holopygum* (practically indistinguishable in all characters except length of ovipositor—see species entry for *D. duplicatum*) and *callisto/elishae* (practically indistinguishable in all characters except minor details of thorax—see key), but as already explained we are unable to claim that the

species tentatively paired are really the most closely related on objectively formulated grounds.

There are also some simpler influences on host range that can be clearly seen. In temperate climates the overwintering strategy of parasitoids is a key feature of their biology and the need to get through the winter often has a strong and evident bearing on host associations. In *Diadegma* species the two options for overwintering appear to be as a cocooned stage or as an early instar larva in a partially fed overwintering host larva. Collectively the host group of the species treated in this paper includes host species that overwinter in these two stages, but also hosts that overwinter in stages (egg, adult) in which these particular parasitoids are not carried.

In so far as they have been reared, the *Diadegma* species dealt with in this paper all kill the host as a prepupa (or pupa in the case of *scotiae*) and pupate within the host's pupation site. Their dependence on their hosts for pupation site selection (and the extent of host cocoon construction) is reflected by the overwintering strategy of the parasitoids: the only ones that definitely overwinter in the cocoon stage parasitise hosts that also overwinter in that stage in toughly constructed and/or cryptic sites (if *duplicatum* normally overwinters in the cocoon it represents an exception to this generalisation, though the cocoon of its host *Caloptilia* species, which overwinters as an adult, is as tough as those of the few *Caloptilia* species that overwinter in cocoons). This appears to reflect the need for a safe haven for this overwintering strategy, as the species that attack univoltine hosts which overwinter as eggs or adults are generally bivoltine species that overwinter in association with a different set of hosts, either in a protected cocoon (e.g. *pusio*) or as a young larva (e.g. *exareolator, holopygum*). From the viewpoint of the hosts, overwintering as non-susceptible stages and pupating

ephemerally in relatively exposed situations might be interpreted as a defensive strategy, as specialisation on such hosts is clearly difficult for parasitoids having the biology of *Diadegma*.

The hosts of the overwintering generation assume a high importance in the realised host range of some species (e.g. *exareolator, holopygum*; and *latungulum* of the *latungulum* subgroup), and these hosts may in fact be the more fundamental in the evolutionary ecology of the parasitoids, implying that host range expansion into summer hosts may have been a secondary process from an initially narrower univoltine base. Some of the data seem to be compatible with this: for example, there is what appears to be a closely related pair of species (*pusio* and *crassum*, which are practically indistinguishable except for colour: possible synapomorphies in areolation of propodeum, wing venation, ovipositor length) that attack essentially the same range of hosts in the overwintering generation, but only one is bivoltine and has summer hosts. While a fission into bivoltine and univoltine populations may have promoted a speciation, this has not resulted in a full separation of host range, perhaps because the summer hosts did not by themselves provide a possible route to speciation. If this speculation is correct in relation to the *pusio* (bivoltine)/*crassum* (univoltine) pair, it may be that a nascent species (*pusio*) has arisen as a direct result of a broadening of host range, not in this case by budding off as an extreme specialist. However, it is also possible that an ancestral bivoltine "old taxon specialist" having recruited a wide range of *Bucculatrix* species as hosts provided a base from which a univoltine species (*crassum*) budded off, with a suite of univoltine overwintering hosts already in place (conceivably promoted by a temporary or spatial scarcity of the summer hosts).

A difference in phenology resulting from changes in host range that restricts gene flow could often be important in the

speciation processes affecting temperate koinobionts, but the suggested mechanisms through which *pusio* and *crassum* might have separated, from "old taxon specialist" ancestry, appear not to be the most usual. It may be more significant that the putative "young specialist"/parent species pairs already discussed (*anurum*/*lithocolletis*, *duplicatum*/*holopygum* and *callisto*/*elishae*) involve apparently univoltine specialists and bivoltine parent species with a diversified host range; a pattern that is also discernible in the genus *Aleiodes* (Shaw 1994 and unpublished), in which there is some experimental evidence that a phenological difference of this kind may indeed be driving an incipient speciation.

Given the importance of understanding how the winter is passed it is unsatisfactory that for some species for which we have otherwise strong host range information (*crataegi*, *duplicatum*, *stigmatellae*) we cannot rule out the possibility that there is an overwintering generation on a completely different host group that we have not yet discovered. The latter three species all attack Gracillariidae and it is perhaps more likely that the methods used to rear the captive hosts (which either cannot or do not easily change their feeding site) in deteriorating autumn tree leaves is what has led to an abnormal emergence of the adults in the late autumn and early winter instead of the cocooned stage overwintering, in which case there would be no "missing" generation. More investigation is needed to settle this point, and also the remote possibility that these *Diadegma* species overwinter in the adult stage, but for now it seems parsimonious to suppose that the anomaly is just an artefact.

Host size is another factor that will almost certainly influence host range, though this influence is not necessarily easy to evaluate. There are four species (*crataegi*, *elishae*, *lithocolletis*, *stigmatellae*) that regularly use what appears to be a largely non-overlapping range of arboreal Gracillariidae (i.e. not counting the specialists *callisto* and *duplicatum*). Notwithstanding the complication that these gracillariids have very differently structured parasitoid complexes as a consequence of host feeding biology (Askew & Shaw 1986), the four *Diadegma* species appear each to use quite discrete size ranges of host (*Parornix* and *Callisto* being on the whole intermediate in size between the larger *Caloptilia* and the smaller *Phyllonorycter*), and it is possible that the apparent partitioning within the overall host resource is essentially a matter of the parasitoids' being able to use hosts of only a particular, and rather narrow, size range. Against this, however, is the wide size range of the hosts of *D. exareolator*. The failure of *D. latungulum* (*D. latungulum* subgroup) to use the smallest *Epilobium*-feeding *Mompha*, *M. raschkiella*, in Britain may be for reasons other than its size, as the parasitoid complex of *M. raschkiella* is surprisingly different from that of its congeners in several other respects (Shaw unpublished).

The *D. nanus* subgroup has a very clear association with hosts that mine (at least in their early instars). This is perhaps most clearly seen from the usage of host families such as Epermeniidae and Choreutidae (Table 1), in which several common and well-sampled species that do not have mining larvae are not attacked. These include the epermeniid *Epermenia chaerophyllella* (Goeze) (cf. Shaw & Aeschlimann 1994), and the choreutids *Choreutis pariana* (Clerck) (cf. Shaw 1984) and *Anthophila fabriciana* (Linnaeus) (Shaw unpublished). An interesting question arises from the probably complete failure (presuming the single record to be erroneous) of the *D. nanus* group to have colonised potential host groups such as Nepticulidae. The generally small size of Nepticulidae (which is not only an extensive group of leaf miners but also a very thoroughly sampled one, cf. Askew & Shaw 1986, Askew 1994) does

Table 1. Overall host range of the *Diadegma nanus* group, given as the total number of records for each host genus recorded (with family totals in brackets). The parasitoid species concerned are listed in descending order in which they contribute to the number of records for the particular host genus.

| Host genus | Number of records | *Diadegma* species |
|---|---|---|
| **Nepticulidae (1)** | | |
| *Ectoedemia* | 1 | *crassum* |
| **Tischeriidae (31)** | | |
| *Tischeria* | 31 | *anurum, holopygum* |
| **Psychidae (21)** | | |
| *Bijugis* | 1 | *longicaudatum* |
| *Diplodoma* | 1 | *ledicola* |
| *Oreopsyche* | 2 | *ledicola* |
| *Proutia* | 6 | *ledicola* |
| *Psyche* | 5 | *ledicola* |
| *Sterrhopterix* | 3 | *longicaudatum* |
| Genus indet. | 3 | *ledicola* |
| **Lyonetiidae (42)** | | |
| *Bedellia* | 31 | *exareolator* |
| *Lyonetia* | 11 | *holopygum, duplicatum* |
| **Bucculatricidae (88)** | | |
| *Bucculatrix* | 88 | *crassum, pusio, melanium, holopygum, lithocolletis, species 1* |
| **Gracillariidae (304)** | | |
| *Acrocercops* | 1 | *lithocolletis* |
| *Aspilapteryx* | 15 | *exareolator, holopygum* |
| *Callisto* | 13 | *callisto, lithocolletis* |
| *Caloptilia* | 98 | *stigmatellae, duplicatum, species 2* |
| *Calybites* | 43 | *holopygum, crassum* |
| *Parornix* | 89 | *stigmatellae, elishae, crataegi, holopygum* |
| *Phyllonorycter* | 45 | *lithocolletis, crataegi, holopygum, elishae* |
| **Choreutidae (83)** | | |
| *Millieria* | 18 | *holopygum* |
| *Prochoreutis* | 64 | *rufatum* |
| *Tebenna* | 1 | *exareolator* |
| **Yponomeutidae (14)** | | |
| *Paraswammerdamia* | 4 | *exareolator* |
| *Plutella* | 4 | *exareolator* |
| *Digitivalva* | 6 | *exareolator* |
| **Epermeniidae (19)** | | |
| *Epermenia* | 5 | *brevivalve* |
| *Phaulernis* | 14 | *scotiae* |

Table 1. Continued.

| Host genus | Number of records | *Diadegma* species |
|---|---|---|
| **Coleophoridae (21)** | | |
| *Coleophora* | 21 | *laricinellum, nanus, holopygum, species 4* |
| **Elachistidae (11)** | | |
| *Perittia* | 9 | *lithocolletis* |
| *Elachista* | 2 | *species 3* |
| **Momphidae (133)** | | |
| *Mompha* | 133 | *latungulum, holopygum* |

not seem to be the answer, as there are several comparably small species of host (in the genera *Bucculatrix* and *Lyonetia* in particular) that are used by a number of these *Diadegma* species. The monotrysian family Nepticulidae is, however, a very inpenetrable host group: the only ichneumonoid koinobionts that seem able to exploit it are the several subfamilies of Braconidae that are essentially specialists on that host group (cf. Shaw & Huddleston 1991), but it is not known whether the failure of others to do so is for reasons of competitive exclusion or physiological incompatibility. Dacnonypha (Eriocraniidae) and the monotrysian families Incurvariidae and Heliozelidae, that have been well sampled in the area, also seem free of attack, and it would be hard to interpret the failure to colonise these leaf mining hosts as a result of competitive displacement by more specialised ichneumonoids. It is worth noting, however, that there are some monotrysian hosts of the *D. nanus* group (Tischeriidae), though otherwise hosts are in the Ditrysia. The main underrepresented lower ditrysian groups would appear to be Coleophoridae and Elachistidae, both of which have been well sampled and are known to suffer heavy parasitism from other parasitoid groups.

## ACKNOWLEDGMENTS

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# Generic Relationships Within the Tribes Cratocentrini and Phasgonophorini (Hymenoptera: Chalcididae)

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*Abstract.*—According to most recent classification, the subfamily Chalcidinae is divided into four tribes: Brachymeriini, Chalcidini, Cratocentrini, and Phasgonophorini. It has been suggested that the tribes Phasgonophorini and Cratocentrini are sister groups and together they form the sister group to a monophyletic group consisting of Brachymeriini and Chalcidini. A cladistic study was conducted to test the relationship between Cratocentrini and Phasgonophorini and to establish the generic relationships, using all known taxa in each tribe. *Brachymeria, Chalcis,* and *Dirhinus* were used as outgroups. Parsimony analysis using the branch and bound search option of PAUP (Ver. 3.1.1), resulted in 14 minimum length trees. None of the trees could be rooted to make Cratocentrini and Phasgonophorini sister groups. Reanalysis of data after successive weighting of characters resulted in a single most parsimonious tree that is identical to one of the original 14 trees. This tree was selected as the preferred hypothesis. These results corroborate the relationships for tribes in Chalcidinae suggested from my previous analysis of chalcidid phylogeny. In addition this study established the generic relationships within Cratocentrini and Phasgonophorini for the first time. The results suggest that *Megachalcis* and *Trigonurella* are the basal lineages of tribes the Cratocentrini and Phasgonophorini, respectively. Because these two genera were not used to represent the tribes in my previous cladistictic analysis, the effect of taxon sampling on my chalcidid phylogeny was tested by including these two taxa in the analysis. This analysis showed no effect of taxon sampling on previous phylogenetic analysis. Since this analysis used a separate set of characters than the family level phylogeny analysis, the two data sets were combined and resulting data matrix of 41 taxa and 65 characters were analyzed. This analysis resulted in 14 minimum length trees and successive weighting gave 10 minimum length trees one step longer than any of the 14 minimum length trees from equally weighted data. There is some disagreement between the phylogenetic hypothesis resulting from this analysis for Chalcididae and results of my previous analysis of family phylogeny. This illustrates the effect of biased taxon and character sampling on the results of phylogenetic analysis.

Cratocentrini and Phasgonophorini (Hymenoptera: Chalcididae) are two morphologically distinct groups within the subfamily Chalcidinae. Host records (available only for few species) indicate that the species of both tribes are parasites of wood boring beetle larvae, an unusual host asssociation in Chalcididae (Boucek 1988). They are among the largest chalcidids, varying from 4 to 20 mm. in length. Cratocentrini are distinctive among chalcidids in having an elongated ovipositor

which is extended beyond the short syntergum (Fig. 56). Although the majority of Phasgonophorini also have a long ovipositor, the syntergum has extended concealing the elongated ovipositor sheaths (Figs. 55, 57). Both groups were extensively studied by Steffan (1950a, 1950b, 1956, 1959, and 1973). At present each tribe consists of eight genera, all distributed in the tropical areas of the world.

Steffan (1959) suggested that Cratocentrini and Phasgonophorini evolved from

the same "stem". He hypothesized that their specialized abdomens were convergently evolved as a result of ovipositing into similar types of hosts. Boucek (1988) stated that these two tribes were sister groups and formed a sister clade to Chalcidini + Brachymeriini but he did not provide any character evidence.

My previous study of higher level phylogeny of Chalcididae (Wijesekara 1997) indicated that Cratocentrini and Phasgonophorini are not closely related. Phasgonophorini is the sister group to Brachimeriini, and these two tribes plus Haltichellinae, Dirhininae, and Epitraninae form the sister group to Cratocentrini (Fig. 74). However my study of family phylogeny used only two examplars of Cratocentrini and Phasgonophorini. Both tribes consist of eight genera, and it therefore seemed that a study of generic relationships among all known genera of Cratocentrini and Phasgonophorini would be useful not only to establish generic relationships within the tribes but also to test the opposing hypotheses regarding the relationship between these two tribes.

TAXONOMIC HISTORY

Many taxa included in Cratocentrini and Phasgonophorini were described in the nineteenth century and classified within in different taxonomic groups. Masi (1944) placed them all within the subfamily Brachymeriinae. Both tribes were established by Steffan (1950a, 1950b).

**Phasgonophorini**

Steffan (1950b) established the Phasgonophorini to include *Phasgonophora* Westwood 1832, *Trigonura* Sichel 1865, *Stypiura* Kirby 1883, *Megalocolus* Kirby 1883, and *Stenochalcis* Masi 1929. He also described a new genus, *Parastypiura* within Brachymeriinae. He suggested that the tribe consisted of two groups of genera: the *Phasgonophora* group, with abdominal tergite I larger than the tergite II (*Phasgonophora* and *Trigonura*), and the *Stypiura* group,

with abdominal tergite I reduced and shorter than tergite II (*Megalocolus, Parastypiura, Stypiura,* and *Stenochalcis*). Steffan (1956) implied that his tribes were natural groups and gave many synonyms for species of *Phasgonophora* and *Cratocentrus.* Steffan (1973) also revised the genera *Stypiura* (six species) and *Parastypiura* (three species) of the Neotropical region. Since Steffan's work, two more genera have been added to the tribe: *Kopinata* and *Trigonurella* (Boucek 1988). At present Phasgonophorini consists of eight genera and 57 species.

**Cratocentrini**

The genera *Larradomorpha* Stadelmann 1792, *Marres* Walker 1841, and *Acanthochalcis* Cameron 1884 were originally placed in Leucospidae, and *Cratocentrus* Cameron 1907 was originally placed in Haltichellinae. Masi (1944) subsequently referred these genera to Brachymeriinae. Later, Cratocentrini was established to include these genera plus *Macrochalcis* Masi 1945 (=*Allocentrus* Cameron 1911); and *Megachalcis* Cameron 1903 (Steffan 1950b). The tribe was revised by Steffan (1959), who added four new genera, *Spatocentrus, Philocentrus, Acrocentrus,* and *Vespomorpha.* Narendran (1984) synonymized *Allocentrus* with *Megachalcis,* and Boucek (1992) synonymized *Larradomorpha* with *Marres.* At present the tribe consists of eight genera and 23 species.

MATERIAL AND METHODS

*Specimens.*—This study was carried out using the collection at the United States National Museum of Natural History, Washington D. C. Additional specimens were borrowed from the following institutions: The Natural History Museum, London; University of Calicut, Kerala, India; South African Museum, Cape Town, South Africa; Plant Protection Research Institute, Pretoria, South Africa; and Museum National de Histoire Naturelle, Paris, France.

*Taxa Used and Character Selection.*—All valid genera of Cratocentrini and Phasgonophorini were included in this study (Appendix 1). In addition, representatives of other major clades of Chalcididae identified in my earlier family level study (Wijesekara 1997) were also included. These taxa served as outgroups for assessing relationships within the tribes Cratocentrini and Phasgonophorini. A representative of Brachymeriini was included because Cratocentrini + Phasgonophorini have been included in Brachymeriinae and Brachymeriini grouped with Phasgonophorini in my previous analysis. Since my previous analysis of family phylogeny indicated that Brachymeriini plus Phasgonophorini form the sister group to a clade consisting of Haltichellinae, Dirhininae and Epitraninae, I also included *Dirhinus* as an outgroup to represent this sister clade. The tree was rooted by including a representative of Chalcidini (*Chalcis*), which the previous analysis suggested to be the most basal lineage in the family.

Comparative morphology was studied for as many species as possible for each genus (See list of Cratocentrini and Phasgonophorini species studied, Appendix 1). Characters that varied among the genera were selected for the analysis. Characters that proved to be synapomorphies for the relevant tribes in my previous study were also included. The generic autapomorphies were not included in the analysis.

*Character Analysis.*—Cladistic analysis was performed using "Phylogenetic Analysis Using Parsimony" (PAUP), version 3.1.1 (Swofford 1993). The branch and bound search option, which guarantees finding all shortest possible trees, was used. All the multistate characters were treated as unordered (non-additive; Fitch 1971). Although there are many criteria that can be used to order characters I prefer not to assume the ordering of the states in multistate characters prior to cladistic analysis (Wijesekara 1997). ACCTRAN optimization, which favors secondary loss

(reversals) of characters over parallel evolution of characters (convergence), was used to optimize the character states. Sixteen ingroup taxa and three outgroup taxa were coded for 40 characters. The character optimization was studied using MacClade version 3.0 (Maddison and Maddison 1992).

*Stability Analysis.*—There are different measures of tree stability for phylogenetic hypotheses. These include the branch lengths (Bremer 1994), Bremer support (decay index), and bootstrap values. Bootstrapping (Felsenstein 1985) and Bremer support (Farris *et al.* 1994) provide a better measure of tree stability than the branch length (Bremer 1994).

The degree of character support for various nodes of the phylogenetic tree was evaluated using bootstrap analysis (Felsenstein 1985) and rescaled branch support (decay) index (Bremer 1988, 1994). AutoDecay version 3.0 (Eriksson 1995) was used to calculate the decay indices.

*Abbreviations Used in Figures 1–65.*— DAS: dorsal axillary surface, FRD: foraminal depression, FRN: frenum, HC: hind coxa, HF: hind femur, HS: horizontally directed spur, HT: hind tibia, HTS: hind tibial spur, LBR: labrum, LS: lateral sulcus, LM: lamella, MAN: mandible, MEP: mesosternal process, MES: mesepisternum, MNS: mesonotal spiracle, MS: malar sulcus, MV: marginal vein, OCE: ocellus, OS: outer spur, PET: petiole, PMV: postmarginal vein, PRE: prepectus, PRM: posterior pronotal margin, PRN: pronotum, PRO: propodeum, SCA: supraclypeal area, SCR: scrobe, SMV: submarginal vein, STV: stigmal vein, TD: tarsal depression, TEG: tegula, TOR: torulus, TR: trocanter, TV: tergite V, TVII: tergite VII, VER: vertex.

## RESULTS AND DISCUSSION

### Characters Selected

Forty morphological characters were scored for a total of 19 taxa (Table 1). Eight

Table 1. Data matrix for Phasgonophorini and Cratocentrini.

| Taxon | Characters | | | |
|---|---|---|---|---|
| | 1234567890 | 1111111112<br>1234567890 | 2222222223<br>1234567890 | 3333333334<br>1234567890 |
| Chalcis | 0011011000 | 0000000000 | 0001000100 | 2000010000 |
| Brachymeria | 0021013000 | 0000102000 | 0010102001 | 0010010000 |
| Dirhinus | 0001110000 | 0101101000 | 1010110100 | 0000010000 |
| Acanthochalcis | 1221112001 | 1101010001 | 2101020112 | 1110002030 |
| Megachalcis | 1221112000 | 1121010101 | 2100020112 | 1110012000 |
| Cratocentrus | 1221112020 | 1102010011 | 2111020112 | 1110002030 |
| Marres | 1221112000 | 1102010110 | 2101010112 | 1110002030 |
| Vespomorpha | 1221112000 | 1102010010 | 2101010112 | 1110002040 |
| Spatocentrus | 1221112001 | 1102010110 | 2111010112 | 1110012010 |
| Philocentrus | 1221112001 | 1102010010 | 2111020112 | 1110012020 |
| Acrocentrus | 1221112020 | 1102010011 | 2111010112 | 1110012010 |
| Phasgonophora | 2000000011 | 1111102010 | 3200100000 | 0111011000 |
| Trigonura | 2000000001 | 1111102010 | 3200100000 | 0111011000 |
| Trigonurella | 2100013000 | 1111102000 | 3210100000 | 0010010000 |
| Stypiura | 2010001110 | 1102102010 | 3200101000 | 0020111101 |
| Megalocolus | 2000001110 | 1102102010 | 3200101000 | 0010211101 |
| Stenochalcis | 2100011110 | 1101102000 | 3200101000 | 0020213100 |
| Kopinata | 2100001100 | 1101102010 | 3200101000 | 0010111001 |
| Parastypiura | 2000001111 | 1101102010 | 3200101000 | 0011011001 |

of the characters were also used in the previous analysis of family phylogeny. Those characters are indicated by an asterisk (*) following the character number. The characters are described below and measures of fit for each character are given in table 2.

*Characteristics of the Head:*

1. Size of the labrum.
   0. Large, as broad as base of mandible (Fig. 1).
   1. Half as long as base of mandible (Fig. 2).
   2. Less than half as broad as base of mandible (Fig. 3).

Both tribes have the typical chalcidid condition of an exposed and contiguous labrum. Phasgonophorini has a small labrum whereas Cratocentrini has a relatively larger labrum, intermediate in size between Brachymeriini and Phasgonophorini. Although the structure of the labrum has been used previously for phylogenetic inference within Chalcidoidea (Darling 1988), the size of the labrum has not.

2. Supraclypeal area.
   0. Without a modified bridge with same sculpture as rest of the face (Fig. 3).
   1. Modified to form a bridge, i.e., with different sculpture than rest of the face (Fig. 4).
   2. Toruli located at the anterior margin of the clypeus and the supraclypeal area is reduced (Fig. 2).

In Phasgonophorini the antennal toruli are located away from the clypeal margin. The area between the clypeal margin and antennal toruli is sometimes modified forming a bridge of different sculpture between the scrobal base and clypeus. In most species there is a slight indication of this bridge-like structure, but the area is more or less continuous with the rest of the face having same sculpture. In some other groups this is distinctly differentiated. Cratocentrini differs in having the toruli located at the clypeal margin and hence having very reduced supraclypeal area.

3. Malar region.
   0. Without a sulcus or carina (Fig. 3).
   1. A sulcus present (Fig. 5).
   2. A carina present (Fig. 6).
In most chalcidids the malar region has a distinct sulcus running from the ventral margin of the eye to base of the mandible. The sulcus is absent from most Phasgonophorini, present as a sulcus in *Stypiura* and *Chalcis*, and indicated as a carina in Brachymeriini. In Cratocentrini it is traceable and carina-like as in Brachymeriini.

4. Face.
   0. Distinctly convex (Fig. 7).
   1. Concave or flat (Fig. 8).
Most chalcidids have an almost concave face because of the very large scrobal depression extending from eye margin to eye margin. In most Chalcidinae the scrobes are smaller and the face is flat or slightly convex. In Phasgonophorini the face is distinctly convex because it bulges forward from the vertex and eye margin.

5*. Location of the antennal toruli.
   0. Above the level of the antennal toruli margin (Fig. 4).
   1. Below the level of lower eye margin (Fig. 9).
Cratocentrini consistently have the antennal toruli located just below the level of the lower eye margin. Most Phasgonophorini have the toruli located above the eye margin while a few species have the toruli located just below the lower eye margin.

6. Antenna.
   0. Slender and long with funicle segments longer than broad (Fig. 60).
   1. Stout and short with only first funicle segment longer than broad (Fig. 61).
Slender and long antenna are characteristic of most Phasgonophorini. The funicular segments are elongated and of the same width although slightly decreasing in length towards the apex. By contrast, species with stout antenna have the first

funicle segment slender and long and the other segments distinctly shorter and progressively widening towards the apex. Stout and short antenna are characteristic of most Cratocentrini, Brachymeriini and Dirhininae.

7. Antennal scrobe.
   0. More than 2× as long as broad near toruli and parallel sided (Fig. 7).
   1. Less than 2× as long as broad near toruli and almost pear-shaped with a blunt lateral margin (Fig. 4).
   2. More than 2× as long as broad near toruli and pear-shaped with sharp, flange-like lateral margin (Fig. 9).
   3. More than 2× as long as broad near toruli and pear-shaped with a sharp, smooth lateral margin (Fig. 8).

Antennal scrobes are generally well defined in Chalcididae. In Cratocentrini, Phasgonophorini, and Brachymeriini they are deeper than in other chalcidids. This is probably due to forward growth of the frons. The scrobes are longer in Cratocentrini because the toruli are located closer to the clypeal margin below the level of the lower eye margin.

In some Phasgonophorini the antennal toruli are located above the lower eye margin and the scrobal cavity is shorter. In those species the frons, lateral to the margin of the scrobal cavity, is inflected slightly into the cavity giving it a triangular or pear-shaped appearance (Fig. 4). In Phasgonophorini the scrobe cavity is not margined sharply but in *Brachymeria* and Cratocentrini it is sharply margined. The condition in *Brachymeria* is distinctly different from that of Cratocentrini. The sharp margin of *Brachymeria* is smooth and shiny and resembles the condition in Phasgonophorini. The scrobal margin of Cratocentrini is more flange-like and the toruli are located relatively further apart than in Brachymeriini or Phasgonophorini (Fig. 9).
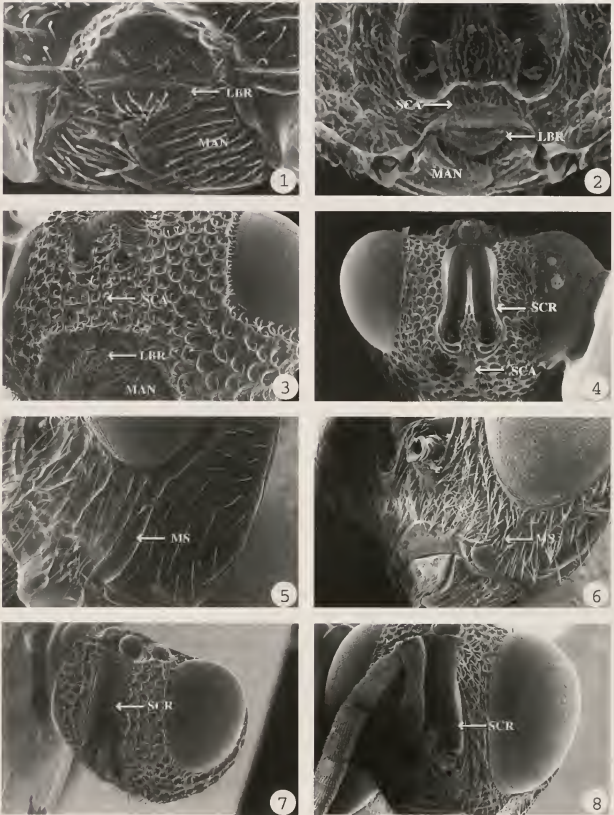
Figs. 1–8.  1–3. Lower front view of face. 1. *Chalcis* sp. 2. *Cratocentrus* sp. 3. *Phasgonophora sulcata*. 4. *Stypiura* sp., front view of face. 5–6. Malar sulcus. 5. *Chalcis* sp. 6. *Brachymeria* sp. 7–8. Face. 7. *Phasgonophora sulcata*. 8. *Brachymeria* sp.

Table 2. Character diagnostics.

| Character | Minimum steps | Tree steps | Maximum steps | CI | HI | RI | RC |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 2 | 11 | 1.000 | 0.000 | 1.000 | 1.000 |
| 2 | 2 | 4 | 11 | 0.500 | 0.500 | 0.778 | 0.389 |
| 3 | 2 | 4 | 10 | 0.500 | 0.500 | 0.750 | 0.375 |
| 4 | 1 | 1 | 8 | 1.000 | 0.000 | 1.000 | 1.000 |
| 5 | 1 | 2 | 9 | 0.500 | 0.500 | 0.875 | 0.438 |
| 6 | 1 | 2 | 6 | 0.500 | 0.500 | 0.800 | 0.400 |
| 7 | 3 | 5 | 11 | 0.600 | 0.400 | 0.750 | 0.450 |
| 8 | 1 | 1 | 5 | 1.000 | 0.000 | 1.000 | 1.000 |
| 9 | 2 | 4 | 7 | 0.500 | 0.500 | 0.600 | 0.300 |
| 10 | 1 | 5 | 6 | 0.200 | 0.800 | 0.200 | 0.040 |
| 11 | 1 | 2 | 3 | 0.500 | 0.500 | 0.500 | 0.250 |
| 12 | 1 | 2 | 2 | 0.500 | 0.500 | 0.000 | 0.000 |
| 13 | 2 | 2 | 3 | 1.000 | 0.000 | 1.000 | 1.000 |
| 14 | 2 | 4 | 9 | 0.500 | 0.500 | 0.714 | 0.357 |
| 15 | 1 | 1 | 9 | 1.000 | 0.000 | 1.000 | 1.000 |
| 16 | 1 | 1 | 8 | 1.000 | 0.000 | 1.000 | 1.000 |
| 17 | 2 | 2 | 10 | 1.000 | 0.000 | 1.000 | 1.000 |
| 18 | 1 | 3 | 3 | 0.333 | 0.667 | 0.000 | 0.000 |
| 19 | 1 | 3 | 7 | 0.333 | 0.667 | 0.667 | 0.222 |
| 20 | 1 | 3 | 4 | 0.333 | 0.667 | 0.333 | 0.111 |
| 21 | 3 | 3 | 11 | 1.000 | 0.000 | 1.000 | 1.000 |
| 22 | 2 | 2 | 11 | 1.000 | 0.000 | 1.000 | 1.000 |
| 23 | 1 | 4 | 7 | 0.250 | 0.750 | 0.500 | 0.125 |
| 24 | 1 | 2 | 8 | 0.500 | 0.500 | 0.857 | 0.429 |
| 25 | 1 | 1 | 9 | 1.000 | 0.000 | 1.000 | 1.000 |
| 26 | 2 | 3 | 9 | 0.667 | 0.333 | 0.857 | 0.571 |
| 27 | 2 | 2 | 6 | 1.000 | 0.000 | 1.000 | 1.000 |
| 28 | 1 | 1 | 9 | 1.000 | 0.000 | 1.000 | 1.000 |
| 29 | 1 | 1 | 8 | 1.000 | 0.000 | 1.000 | 1.000 |
| 30 | 2 | 2 | 9 | 1.000 | 0.000 | 1.000 | 1.000 |
| 31 | 2 | 2 | 9 | 1.000 | 0.000 | 1.000 | 1.000 |
| 32 | 1 | 2 | 9 | 0.500 | 0.500 | 0.875 | 0.438 |
| 33 | 2 | 3 | 4 | 0.667 | 0.333 | 0.500 | 0.333 |
| 34 | 1 | 2 | 3 | 0.500 | 0.500 | 0.500 | 0.250 |
| 35 | 2 | 3 | 4 | 0.667 | 0.333 | 0.500 | 0.333 |
| 36 | 1 | 2 | 4 | 0.500 | 0.500 | 0.667 | 0.333 |
| 37 | 3 | 3 | 11 | 1.000 | 0.000 | 1.000 | 1.000 |
| 38 | 1 | 1 | 3 | 1.000 | 0.000 | 1.000 | 1.000 |
| 39 | 4 | 4 | 6 | 1.000 | 0.000 | 1.000 | 1.000 |
| 40 | 1 | 2 | 4 | 0.500 | 0.500 | 0.667 | 0.333 |

8. Ocellar triangle.

    0. Not raised above vertex (Fig. 10).

    1. Raised above vertex (Fig. 11).

Most chalcidids have two lateral ocelli located further apart from each other than from the front ocellus and the ocellar triangle is not raised above the level of the vertex. In some Phasgonophorini the ocelli are located close together so that they are equidistant from each other and the ocellar triangle is raised above the vertex.

9. Vertex within ocellar triangle.

    0. Normal, not modified (Fig. 10).

    1. Raised medially between the lateral ocelli (Fig. 11).

    2. Raised lateral to the lateral ocelli (Fig. 12).

In general all three ocelli lie in a triangle on the vertex, with the lateral ocelli lying closer to the posterior margin of the vertex. In some Phasgonophorini the area within the triangle is distinctly raised above the the surrounding area resulting in the posterior margin of the vertex rising between the lateral ocelli (Fig. 13). In Cratocentrini the area within the ocellar triangle is sharply raised closer to the lateral ocelli giving the appearance of two sharp spines (Fig. 12).

10. Carina behind lateral ocelli.

    0. Absent.

    1. Present (Fig. 13).

In some Cratocentrini and Phasgonophorini the vertex is separated from the occiput by a short transverse carina just behind the lateral ocelli in the mid dorsal area of the head.

11. Foraminal cavity/depression.

    0. Continuous around occipital foramen (Fig. 14).

    1. Dorsally interrupted (Fig. 13).

Delvare (1992) used this character for within tribe relationships of Chalcidini and considered that the continuous foraminal depression, not delimited by carina or sharp edge, is the ancestral condition for the tribe. The species of Chalcidini that show no evidence of a depression are considered derived. All the genera of the two tribes studied show a distinct foraminal depression.

*Characteristics of the mesosoma:*

12. Width of the pronotum.

    0. Pronotal width at least 2.5× the median length (Fig. 10).
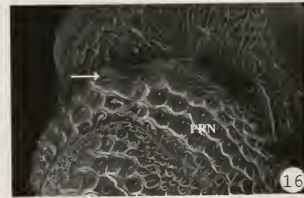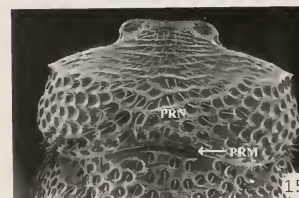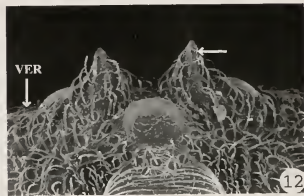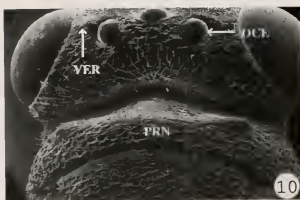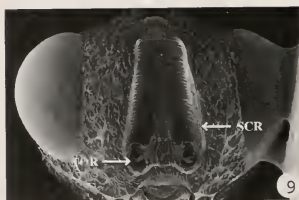
Figs. 9–16. 9. *Cratocentrus* sp., front view of face. 10. *Brachymeria* sp., dorsal view of head and pronotum. 11–12. Ocellar triangle. 11. *Stypiura* sp. 12. *Cratocentrus* sp. 13–14. Head, posterior view. 13. *Phasgonophora sulcata*. 14. *Brachymeria* sp. 15–16. Pronotum (arrows indicate the raised area). 15. *Cratocentrus* sp. 16. *Megachalcis* sp.

1. Pronotal width less than 2.5× the median length (Fig. 15).

Both Phasgonophorini and Cratocentrini have a relatively broad pronotum. In Brachymeriini and Chalcidini the pronotum is distinctly short anterio-posteriorly.

13. Pronotal surface.
    0. Flat (Fig. 15).
    1. Raised lateral to the median line (Fig. 16).
    2. Raised as bump near each posterior lateral margin (Fig. 17).

The plesiomorphic state of the dorsal pronotal surface of Chalcididae is flat without any raised areas. Some groups of Phasgonophorini have the pronotum raised on both sides of the median line resulting in a shallow median furrow on the pronotum (Fig. 16). A bump-like raised area at each lateral corner of the pronotum is another modification shown by some genera of Cratocentrini (Fig. 17). These bumps are very distinct in *Megachalcis*. They are located away from the median line closer to the posterior margin of the pronotum, between the lateral margin and median line.

14. Posterior margin of the pronotum.
    0. Broadly concave (Fig. 10).
    1. Medially triangular (Fig. 18).
    2. Medially rounded (Fig. 15).

The shape of the posterior margin of the pronotum of chalcidids varies from broadly concave to emarginate. The most commonly observed condition is a broadly concave posterior margin. This character is probably correlated to the degree to which the head can be directed backwards. In most Phasgonophorini the curvature is so acute that it appears medially triangular and in most Cratocentrini the posterior margin is more rounded (Fig. 15).

15*. Externally visible region of the prepectus
    0. Relatively large and elongated, plate-like (Fig. 19).

1. Reduced to a very thin or knob-like sclerite (Fig. 20).

The chalcidid prepectus is a semi-annular, transverse sclerite. Delvare (1992) found the median process of the prepectus to be phylogenetically informative to resolve Chalcidini relationships. However within Cratocentrini and Phasgonophorini the median process does not vary. Instead the lateral arm of the prepectus near the tegula and the pronotal/mesonotal juncture has twisted to form a small plate-like sclerite that supports the mesothoracic spiracle and separates the mesopleural margin from the mesonotal margin. The size of this exposed plate-like area of the prepectus varies within Chalcididae. In Cratocentrini and Chalcidini the plate-like area is reduced to an extent that it is difficult to observe externally. The reduced state is autapomorphic for Cratocentrini and Chalcidini within Chalcididae. In Phasgonophorini, Brachymeriini, and Haltichellini the plate is distinct externally.

16*. Mesothoracic spiracle.
    0. Covered by postero-lateral margin of pronotum (Fig. 19).
    1. Exposed (Fig. 20).

In most Hymenoptera the pronotal lobe covers the mesothoracic spiracle completely (Gibson 1985). Chalcididae except Cratocentrini have the mesothoracic spiracle covered by the posterior lateral margin of the pronotum.

17*. Relative size and shape of the tegula.
    0. Linear, scond axillary sclerite covered (Fig. 20).
    1. Both ventrally and posteriorly expanded, oval shape, second axillary sclerite of the wing completely covered.
    2. Ventrally expanded, second axillary sclerite of the wing exposed (Fig. 19).

In Chalcidini and Cratocentrini the tegula is not modified, it is pear shaped and extends from the anterio-lateral margin of pronotum to posterio-lateral mar-
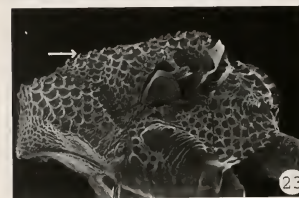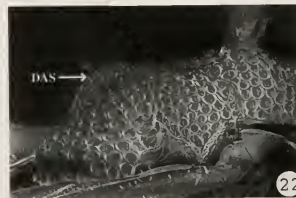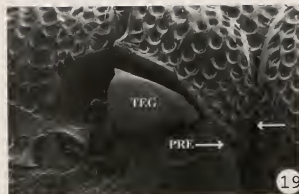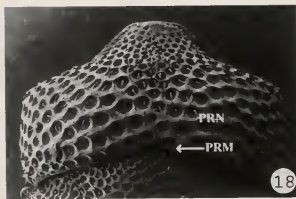
Figs. 17–24. 17–18. Pronotum (arrows indicate raised areas). 17. *Trigonura* sp. 18. *Phasgonophora sulcata.* 19–20. Mesothorax lateral view. 19. *Phasgonophora sulcata.* 20. *Cratocentrus* sp. 21–22. Axillae and scutellum. 21. *Phasgonophora sulcata,* 22. *Megachalcis* sp., 23. *Phasgonophora sulcata,* lateral view of the thorax (arrow indicate the sculpture). 24. *Chalcis* sp., mesepisternum.

gin. In Phasgonophorini and Barachymer-iini the tegula is ventrally expanded giving a triangular appearance.

18. Dorsal axillar surface
    0. Flat (Fig. 21).
    1. Raised (Fig. 22).
The axillar carina divides the axilla into two regions, the lateral axillar surface and the dorsal axillar surface (Gibson 1985). Usually the dorsal axillar surface is flat and level with the scutum and scutellum. However in some Cratocentrini this surface is distinctly raised.

19. Sculpture of the mesosoma
    0. Not scabrous.
    1. Scabrous (Fig. 23).
It is difficult to define the surface sculpture of most chalcidoids. Within Chalcididae, Cratocentrini and Phasgono-phorini have a sculpture much coarser than other chalcidids. Boucek (1992) referred to the sculpture of *Stypiura* as "rasp-like" and the sculpture of *Parastypiura* as "sharp transverse rugae". I divided the type of sculpture into two main groups: rasp-like and non rasp-like. The non rasp-like condition consists of many different sculptures that can not be grouped into distinct categories. Rasp-like sculpture consists of rough sharp projections or wrinkles and can be classified as scabrous (Harris 1979).

20. Mesepisternum
    0. Not projected between forecoxa (Figs. 24, 25).
    1. Projected medially between forecoxa (Fig. 26).
The mesepisternal region of Chalcididae is divided into two parts by a transverse carina. This carina delimits a smooth and angulate anterior mesepisternum from a horizontally sculptured ventral area anterior to the mid coxal foramen. Delvare (1992) called this sculptured ventral area the mesosternal shelf. The smooth area anterior to the carina has sometimes been referred to as the epicne-mium and the carina as the epicnemial carina (Delvare 1992; Gibson 1985). The smooth epicnemial area supports the forecoxa. In some Cratocentrini the mesosternal shelf is anteriorly projected between the forecoxa (Fig. 26). The condition in other Chalcididae varies but the mesepisternum does not distinctly project as in some cratocentrines.

21*. Propodeum
    0. Angulate in relation to scutellum (Fig. 27).
    1. Horizontal in relation to the scutellum.
    2. Medially depressed and vertical with lateral projections (Fig. 28).
    3. Horizontal anteriorly and sloping steeply posteriorly (Fig. 29).
Characteristics of the propodeum have been used in classification of Chalcididae (Boucek & Delvare 1992). In most studies, however, the arrangement of carinae on the propodeum has been given more importance than the overall structure. These patterns of carina are autapomorphic and do not indicate relationships among the genera. Within Chalcididae the propodeum of Cratocentrini is unique, being medially short (depressed) and vertical between the lateral angulate projections (Fig. 28). In many Phasgonophorini species the propodeum has the anterior ⅓–⅔ horizontal and steeply sloping posteriorly. A steeply sloping posterior portion of the propodeum is a unique feature of the tribe. However there are variations within the tribe. For example, in *Steno-chalcis* the propodeum is almost parallel to the scutellum although closer examination shows that more than ⅔ of the anterior propodeum is parallel to the scutellum and the posterior ⅓ is steeply sloping as in other Phasgonophorini. The posteriorly sloping propodeum is not very prominent in *Trigonurella* where the propodeum seems angulate. Comparative study shows that it is a variation of the sloping
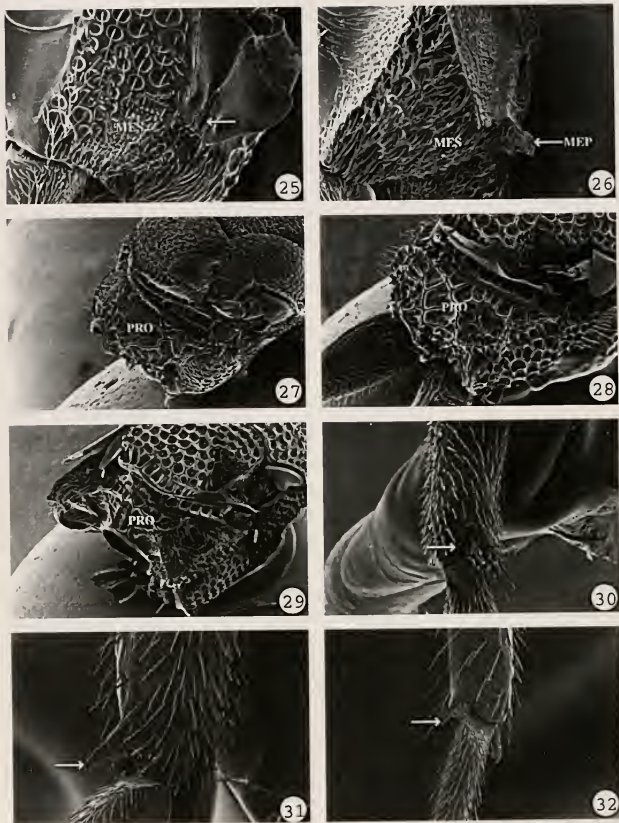
Figs. 25–32.  25–26. Mesepisternum. 25. *Phasgonophora sulcata*. 26. *Cratocentrus* sp. 27–29. Propodeum. 27. *Brachymeria* sp. 28. *Phasgonophora sulcata*. 29. *Cratocentrus* sp. 30–32. Foretibiae apex (apex indicated by arrow). 30. *Brachymeria* sp. 31. *Cratocentrus* sp. 32. *Phasgonophora sulcata*.

propodeum and not similar to the angulate state in other chalcidids.

*Characters of the Legs:*

22*. Apical margin of the foretibia.
   0. Without horizontally directed stout spur or elongation (Fig. 30).
   1. With horizontally directed stout spur (Fig. 31).
   2. Without horizontally directed spur but distinctly expanded giving the appearance of a spur (Fig. 32).

In Cratocentrini there is a distinct short outward directed spur at the apex of the foretibia. This is in addition to the usually long, modified spur that forms the antennal brush (strigil). Other chalcidids do not possess such a spur but in Phasgonophorini the apex of the foretibia has expanded outwards, giving the appearance of a horizontal spur.

23. Shape of the hindcoxa.
   0. Elongate, more than 2× as long as broad (Fig. 33).
   1. Not elongate, 2× as long as broad or less (Fig. 34).

A greatly swollen hind coxa is characteristic of all species of Chalcididae. The hindcoxa of many chalcidoids is swollen proximally and are pear-shaped or club-shaped. However the shape and size of the hindcoxa varies among different groups within the Chalcididae. Brachymeriini and Haltichellinae usually have a short pear-shaped hindcoxa whereas Chalcidini have a long club-shaped hindcoxa. Although many taxa of Cratocentrini and Phasgonophorini have long club-shaped hindcoxa as in other chalcidines, a few taxa in both groups exhibit the pear-shaped hindcoxa.

24. Inner basal tooth of the hindfemur.
   0. Absent (Fig. 35).
   1. Present (Fig. 36).

On the hindleg near the articulation of the trochanter and femur in Chalcididae, where the arched tibia fits into the dentate margin of the femur, some species possess a distinct tooth, which originates from the inner side of the femur. This tooth makes a furrow or notch into which the hind tibia can be folded. This character has been used for identification of the genera of Cratocentrini (Boucek 1988), but it has not been used for determining phylogenetic relations. The inner tooth is present in many cratocentrines but is not found among the phasgonophorines.

25. Length of the hindtibia.
   0. Short, not reaching the trochanter (Fig. 37).
   1. Long, touching the trochanter (Fig. 38).

The hindtibia is arched and fits into the toothed margin of the femur in almost all Chalcididae although the degree of curvature of the tibia varies among groups. The curvature of the tibia has been used as a character in chalcidid taxonomy, the length of the hind tibia has never been used. Usually, in the folded position, the hindtibia touches the trochanter near its point of articulation to the femur but in some groups the tibia is distinctly shorter and terminates before reaching the trochanter. This feature occurs only in chalcidids with a diagonally truncated hind tibial apex. Haltichellinae have a perpendicularly truncated hindtibial apex, but the tibia is not distinctly arched.

26. Tarsal depression of hind tibia.
   0. As long as first tarsal segment (Fig. 39).
   1. As long as first two or three tarsal segments combined (Fig. 40).
   2. Longer than first three tarsal segments combined (Fig. 41).

The tarsal depression refers to the dorsal area of the hindtibia, which accommodates the tarsus when folded. In Chalcididae a distinct tarsal depression is not frequently observed except in a few groups. Groups that possess a distinct tarsal depression include Epitraninae and Cratocentrini. Within the groups that
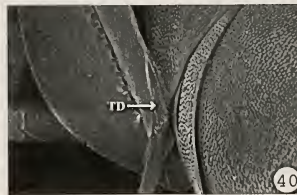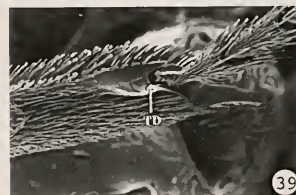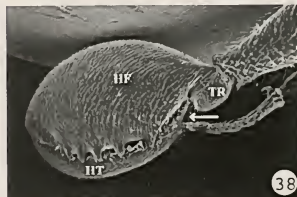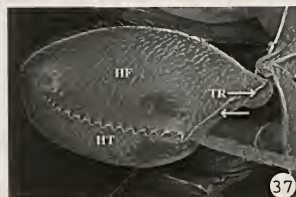
Figs. 33–40. 33–34. Hind coxa and femur. 33. *Cratocentrus* sp. 34. *Megachalcis* sp. 35. *Phasgonophora sulcata*, inner surface of hind femur. 36–38. Hind femur and tibia. 36. *Cratocentrus* sp. (inner surface). 37. *Trigonura* sp. 38. *Cratocentrus* sp. (outer surface). 39–40. Tarsal depression. 39. *Stypiura* sp. 40. *Vespomorpha* sp.

show a tarsal depression the length of this depression may vary. I divided this variation into the above three states.

27. Hind tibial spurs.
    0. Absent.
    1. Single stout spur present (Fig. 42).
    2. Single weak spur present (Fig. 43).

The number of hind tibial spurs has been used to characterize various family groups and genera of Chalcididae (Boucek 1992). The subfamily Chalcidinae characteristically has only a single hind tibial spur or none. Boucek (1992) stated that Cratocentrini and Phasgonophorini do not possess hind tibial spurs. My studies revealed that many phasgonophorine genera have a single hind tibial spur that is very reduced in size (Fig. 42). Chalcidini and Brachymeriini also have a single hind tibial spur, but it is well developed and appears flexible and weak relative to the stout spur found in Phasgonophorini.

28*. Apex of the hindtibia.
    0. Diagonally truncate, ventral corner at acute angle but not produced into a spine (Fig. 37).
    1. Diagonally truncated, elongated into a spine (Fig. 38).

The tip of the hindtibia of Chalcididae shows three different states: truncated at a right angle, diagonally truncated and elongate into a long spine, or diagonally truncated but not elongate into a spine. In Chalcidini, Cratocentrini, Dirhininae, and Epitraninae the hindtibial apex is elongate into a spine. In all Brachymeriini and Phasgonophorini it is diagonally truncated but not elongated into a spine.

*Characteristics of the Wings:*

29*. Patch of elongate setae on the anterior ventral margin of the forewing.
    0. Absent.
    1. Present (Fig. 44).

Species of Cratocentrini have a patch of posteriorly directed elongate setae on the ventral surface of the forewing near the distal end of the costal cell. This is an autapomorphy for the tribe.

30. Hamuli.
    0. Proximal hamulus straight, not curved like others, and separated slightly (less than its own length) from the others (Fig. 45).
    1. Proximal hamulus straight and distinctly separated (at least by a distance equal to its own length) from the others (Fig. 46).
    2. Three hamuli morphologically similar and located equidistant from each other (Fig. 47).

The hamuli are structures on the anterior margin of the hindwing used for wing coupling. Most chalcidids have three hamuli on each hindwing, although the number varies, especially in Epitraninae. The proximal hamulus is not curved as the others and could not function for coupling. The two hamuli distal to the body do the coupling of wings and the one proximal to the body probably has more of a sensory function. Since it is not curved it looks different from the other hamuli. It is also separated slightly from the two distal hamuli. However in Cratocentrini the proximal hamulus is not differentiated from the other two. It is curved and located equidistant from the distal hamuli. In *Brachymeria* the straight proximal hamulus is separated distinctly from the distal pair (Fig. 46); this is autapomorphic for the genus.

31. Length of postmarginal vein.
    0. Shorter than marginal vein (Fig. 62).
    1. Longer than marginal vein (Fig. 63).
    2. As long as marginal vein (Fig. 64).

Wing venation has been used by many chalcidoid taxonomists to define and identify genera (Boucek 1988; Delvare 1992). Grissell (1995) unsuccessfully attempted to quantify wing venation based on vein length ratios, and Heydon (1989) hypothesized that primitive pteromalids
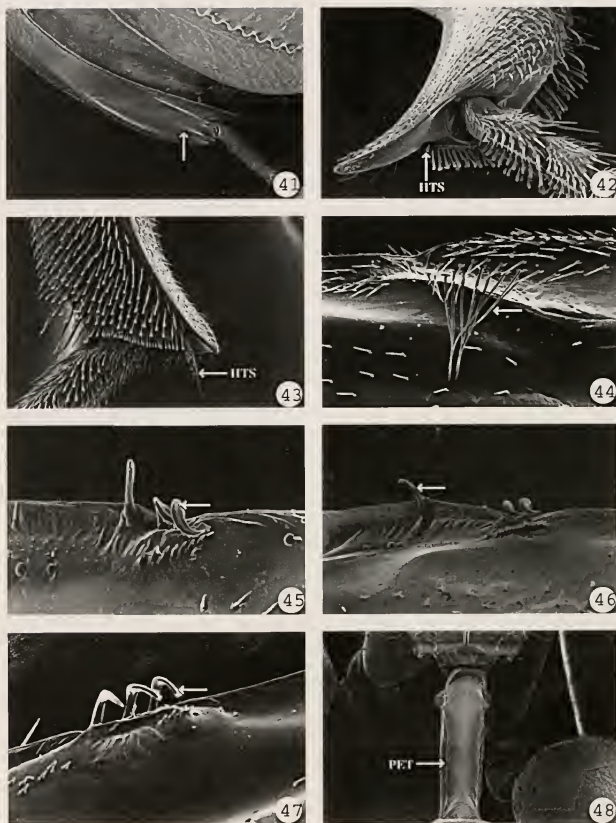
Figs. 41–48.  41. *Cratocentrus* sp., tarsal depression. 42–43. Hind tibial spur. 42. *Stypiura* sp. 43. *Brachymeria* sp. 44. *Cratocentrus* sp., anterior ventral margin of the forewing. 45–47. Hamuli. 45. *Phasgonophora sulcata*. 46. *Brachymeria* sp. 47. *Cratocentrus* sp. 48. *Chalcis* sp., petiole.

have a postmarginal vein longer than the marginal vein. However the length of the postmarginal vein varies within chalcidids. The shorter postmarginal (than marginal) characteristic of Phasgonophorini and Brachymeriini is almost equal in length to the stigmal vein in Phasgonophorini and longer than the stigmal vein in Brachymeriini. Cratocentrini and *Chalcis* have a longer postmarginal vein, much longer than the stigmal vein and as long as or longer than the marginal vein.

32. Length of marginal vein relative to stigmal vein.

    0. More than four times the length of stigmal vein (Fig. 62).

    1. Less than four times the length of stigmal vein (Fig. 63).

Cratocentrini have a distinctly shorter marginal vein than most other chalcidids. In most chalcidids the marginal vein is more than four times the length of the stigmal vein.

*Characteristics of the Metasoma:*

33. Petiole length.

    0. Longer than wide (Fig. 48).

    1. Transverse, not visible in dorsal view (short) (Fig. 49).

    2. Half as long as wide; visible in dorsal view (Fig. 50).

The attachment of the petiole to the metasoma is characteristic of different groups of chalcidids but the size of the body of the petiole varies within groups. In many groups, the petiole varies from transverse to distinctly long and slender, although in some groups (e.g. Cratocentrini) it is constant in size. The surface of the petiole is sometimes differently sculptured in various groups, and this may be phylogenetically informative at the species level. In Cratocentrini, the petiole is transverse and not visible in dorsal view, whereas in phasgonophorini the petiole varies from transverse and not visible in dorsal view (usual condition) to half as

long as wide and visible in dorsal view (rarely).

34. Lateral sulcus of first metasomal tergum.

    0. Absent (Fig. 51).

    1. Present (52).

In *Phasgonophora*, the anterior dorsal area of the first tergum is raised into a transverse crest followed by longitudinal carinae (Fig. 52). These carinae are laterally delimited by a sulcus, which originates near the petiole and runs along the dorsolateral margin of tergum one, ending before the posterior margin of the tergum. A similar sulcus is present in some other Phasgonophorini. The transverse crest is autapomorphic for *Phasgonophora*.

35. First and second metasomal terga of females.

    0. Independent (Fig. 52).

    1. Fused, line of fusion distinct (Fig 51).

    2. Fused, no trace of line of fusion (Fig. 53).

The structure of the basal terga varies in chalcidids. Some species of Phasgonophorini have the first two basal tergites fused, without a trace of the line of fusion, so that only six terga are visible. In other Phasgonophorini, the two terga may be independent, the second tergite anteriorly telescoped into the first or united with the fusion line apparent, so that it is possible to count seven metasomal segments. Steffan (1959) suggested that the enlargement of the first tergites of Phasgonophorini gives rigidity for the abdomen for drilling in wood and attacking xylophagous beetle larvae.

36. Fifth metasomal tergum of the female.

    0. As long as the first tergum (Fig. 53).

    1. Distinctly shorter than the first tergum (Fig. 52).

In many chalcidids the tergum 1 is subequal in length to the preceding terga but in a few chalcidids the tergum 5 is longer and covers a major part of the metasoma. In Cratocentrini tergites 2–4 are almost hidden under tergum 1 and the ter-
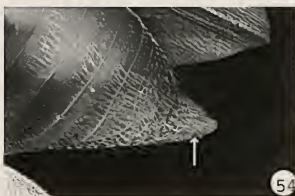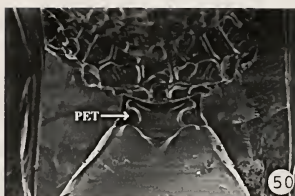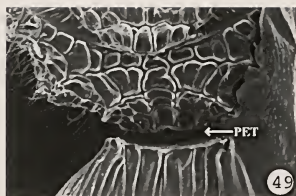
Figs. 49–56.　49–50. Petioles. 49. *Phasgonophora sulcata*. 50. *Stypiura* sp. 51–53. Metasoma. 51. *Stypiura* sp. 52. *Phasgonophora sulcata*. 53. *Cratocentrus* sp. 54–56. VIIth abdominal tergite and ovipositor (arrows indicate the VIIth tergum). 54. *Trigonurella* sp. 55. *Phasgonophora sulcata*. 56. *Cratocentrus* sp.

gum 5 is almost as long as the tergum 1 (Fig. 53). Reduction of terga 2–4 gives rigidity to the abdomen of Cratocentrini for drilling in wood (Steffan 1959).

37. Lengths of the seventh metasomal tergum and elongation ovipositor sheaths.
   0. Not elongate, completely covering the short ovipositor sheath (Fig. 54).
   1. Elongate, completely covering the long ovipositor sheaths (Fig. 55).
   2. Short, not covering the elongate ovipositor sheaths (Fig. 56).
   3. Slightly elongate, covering the ovipositor sheaths (Fig. 65).

Cratocentrini are unique in having distinctly elongate ovipositor sheaths that are exposed beyond the apex of the metasoma (Fig. 56). It is also characteristic of most Phasgonophorini to have elongated ovipositor sheaths but in this case they are not exposed, and instead the seventh metasomal tergite has also been elongated to cover the sheaths. Elongation of the seventh metasomal segment (which is correlated with the elongation of ovipositor) can be observed in some species of *Brachymeria* and also in Haltichellinae. However, these two conditions are not homologous. In the case of Haltichellinae and *Brachymeria*, the tergite is produced beyond the location of cerci. Hence the cerci are located closer to the anterior margin of the eighth tergite.

In Phasgonophorini, the anterior part of the tergite is produced. This is evident by the position of cerci. In Phasgonophorini the cerci are located closer to the posterior margin of the seventh metasomal tergite. The seventh tergite in *Trigonurella* is short, completely covering the ovipositor sheath as in the majority of *Brachymeria*. In the *Stenochalcis* the seventh tergite is intermediate between *Brachymeria* and many Phasgonophorini. However the state in *Stenochalcis* is homologous to other Phasgonophorini because the cerci are located closer to the posterior margin of tergite seven.

38. Density of the setae on seventh tergite.
   0. Uniformly distributed (Fig. 57).
   1. Densely distributed beyond cerci (Fig. 58).

This is a character that varies within the tribe Phasgonophorini. In some species the surface area beyond the cerci is distinctly different from the anterior part of the seventh tergite. The difference seems to be in the density of hairs, the posterior region having more dense hairs (Fig. 58).

39. Tufts of silvery setae on metasomal tergites (Fig. 53).
   0. Absent.
   1. One pair of lateral tufts on tergite five.
   2. Two pairs of lateral tufts on tergite five and six.
   3. Single continuous tuft on tergite five.
   4. Silvery hairs evenly distributed on all tergites.

Silvery setae on metasomal tergites are characteristic of Cratocentrini. I have identified four different patterns. *Acanthochalcis* and *Cratocentrus* have two pairs of lateral tufts on their fifth metasomal tergite whereas *Acrocentrus* and *Spatocentrus* have a single pair. Steffan (1959) suggested that these silvery setae patterns provide good characters for identification of Cratocentrini.

40. Posterior end of ovipositor sheath.
   0. Straight (Figs. 55, 56).
   1. Curved downwards (Fig. 59).

Both Phasgonophorini and Cratocentrini have distinctly elongate ovipositor sheaths. Cratocentrini have completely exposed sheaths because the last metasomal tergite is short and in Phasgonophorini most of the sheath is covered by the elongate seventh tergite. In general the sheaths are straight but in some groups of Phasgonophorini the sheaths are distinctly curved downward.
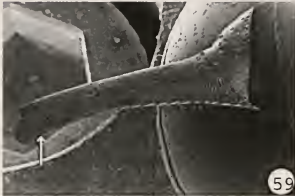
Figs. 57–59. 57–58. VII$^{th}$ tergum. 57. *Phasgonophora sulcata*. 58. *Stypiura* sp. (arrow indicate are of different sculpture). 59. *Stypiura* sp., VII$^{th}$ tergum and ovipositor (arrow indicates the ovipositor).

## Phylogenetic Analysis

The branch and bound search option of PAUP yielded 14 most parsimonious completely resolved trees of length 98, consistency index of 0.646, and retention index of 0.843. The strict consensus tree (Fig. 66) shows that the 14 trees were a result of only three areas of conflict. The first conflict (**I** in Fig. 66) involves the placement of one outgroup (*Dirhinus*), whereas the second and third conflicts (**II & III** in Fig. 66) involve the Cratocentrini clade. The cladogram with the best character evidence was selected by using successive character weighting (Carpenter 1988). Reanalysis after successive weighting using the retention index and a base weight of 1000 yielded a single most parsimonious tree with a consistency index of 0.826 and retention index of 0.940 (Fig. 67), which is 98 steps long under equally weighted characters.

Selection of outgroup taxa could affect the relationships among the genera within Phasgonophorini and Cratocentrini. To test the effect of my outgroups on relationships among ingroup taxa I ran the analysis deleting one outgroup at a time. The three analyses gave ingroup tree topologies identical to that observed with all three outgroups. This indicates that there is no effect of the selected outgroups on intra-tribal relationships proposed in this study. The outgroups *Brachymeria* and *Dirhinus* form a monophyletic group with Phasgonophorini, to the exclusion of Cratocentrini in all 14 most parsimonious trees. This supports my previous finding that Cratocentrini and Phasgonophorini together do not form a monophyletic group.

## DISCUSSION

The first area of irresolution in the strict consensus (node **I** Fig. 66), accounts for seven of the most parsimonious trees, by alternating the placement of *Dirhinus*. In one set of seven most parsimonious
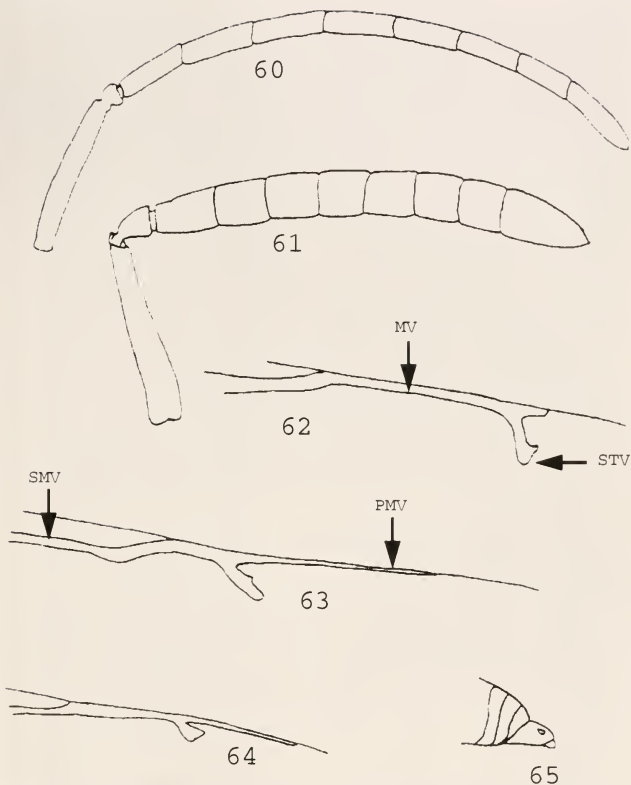
Figs. 60–65. 60–61. Antennae. 60. *Phasgonophora sulcata* 61. *Cratocentrus* sp. 62–65. Forewing venation. 62. *Phasgonophora sulcata*. 63. *Cratocentrus* sp. 64. *Chalcis* sp. 65. *Stenochalcis* sp., VIIth tergum and ovipositor.

trees *Dirhinus* is placed as sister to Phasgonophorini + *Brachymeria* while in the other set of seven trees with an otherwise identical topology, *Dirhinus* is placed as the sister group to Phasgonophorini (Fig. 68, A & B). The second area of conflict (node **II** Fig. 66), which involves the relationship between *Acanthochalcis* and *Megachalcis*, also has two possibilities (Fig. 69, A–F vs. G). The third area (node **III** Fig.
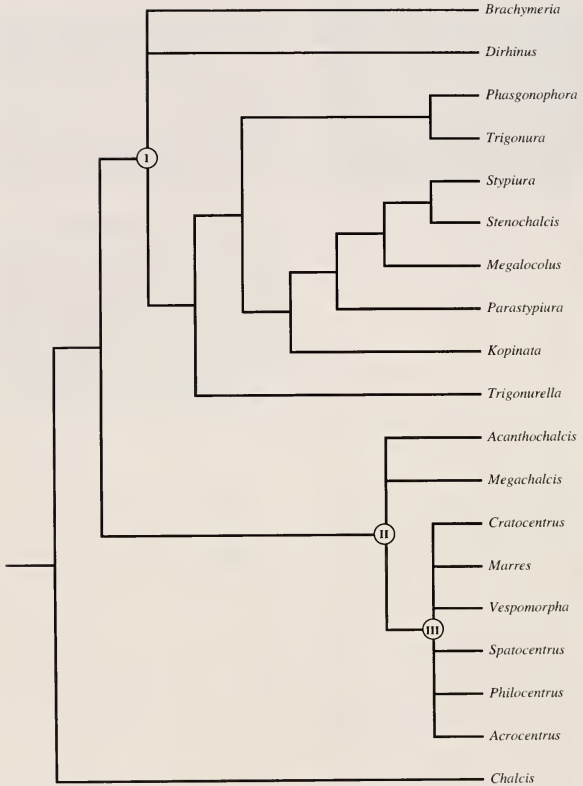
Fig. 66. Strict consensus cladogram of the 14 minimal length trees that resulted from the parsimony analysis of the character data in Table 1 (Length = 98, consistency index = 0.643, retention index = 0.843).

66), involves all the Cratocentrini except *Acanthochalcis* and *Megachalcis*, and has seven posibilities (Fig. 69, A–G). In four of the seven resolutions *Acrocentrus, Philocen-* *trus* and *Spatocentrus* form a clade within Cratocentrini with *Acrocentrus* being the sister group of the other two taxa (*Acrocentrus* clade) (Fig. 69, C–F). In two of

these four resolutions the *Marres* + *Vespomorpha* clade alternates from being the sister group of the *Acrocentrus* clade to being the sister group of a more inclusive *Cratocentrus* + *Acrocentrus* clade (Fig. 69, C & D). In the other two resolutions, (Fig. 69, E & F) a paraphyletic *Marres* and *Vespomorpha* alternate being the sister group to the *Acrocentrus* clade while *Cratocentrus* remains the sister group to them. Both resolutions in which *Marres* or *Vespomorpha* become sister to the *Acrocentrus* clade have a zero length branch and hence are not fully supported by the data (Coddington & Scharff, 1994). Two of the remaining three resolutions (Fig. 69, B & G) have a monophyletic *Spatocentrus* + *Philocentrus* group, with the monophyletic *Cratocentrus* + *Acrocentrus* as the sister group in one resolution (Fig. 69, G) and *Marres* + *Vespomorpha* as the sister group in the other (Fig. 69, B). The third resolution (Fig. 69, A) is identical to the preferred hypothesis (after successive weighting). The characters that unambiguously support the different resolutions are indicated in Fig. 69, A–G.

## Monophyly of Cratocentrini and Phasgonophorini

Monophyly of the tribes Cratocentrini and Phasgonophorini was supported in my previous analysis (Wijesekara 1997) of the higher level phylogeny of Chalcididae. However that analysis used only two taxa from each of these two tribes. The present analysis used all the known genera from both tribes and the results confirm the monophyly of both tribes. Monophyly is supported by twelve unambiguous characters in Cratocentrini and by five unambiguous characters in Phasgonophorini (Fig. 67). This study explicitly supports the monophyly of these tribes using character evidence for the first time. Steffan (1950b) defined Cratocentrini using the following characters: antenna inserted just above the clypeus (Character 5 of this study); forewing with postmarginal vein longer than

short marginal vein (Character 31); metafemur with an inner tooth basally (Character 24); metatibia with long tarsal depression (Character 20); and female metasoma with only four visible terga. The number of visible metasomal terga is correlated with the size of the fifth metasomal terga. I have used the size of the fifth metasomal segment as a character instead of number of visible tergites. This study indicates that, of the characters used by Steffan, only the long tarsal depression supports the monophyly of Cratocentrini. New synapomorphies for the group, unambiguous in this study, are: 1) size of the labrum (Character 1, state 1); 2) reduced area between toruli and clypeus (character 2, state 2); 3) dorsally interrupted foraminal cavity (Character 11, state 1); 4) exposed mesonotal spiracal (Character 16, state 1); 5) medially projected mesepisternum (Character 20, state 1); 6) medially depressed propodeum (Character 21, state 2); 7) horizontally directed spur of foretibial margin (Character 22, state 1); 8) distinct tuft of spines on the front ventral margin of the forewing near distal end of the costal cell (Character 29, state1); 9) morphologically similar hamuli (Character 30, state 2); 10) marginal vein less than $4\times$ the length of stigmal vein (Character 32, state 1); and 11) short seventh metasomal tergite (Character 37, state 2).

The tribe Phasgonophorini was defined by the following characters (Steffan, 1950a): face convex (Character 4 in this study); occiput concave; clypeus located away from lower ocular margin (Character 5); pronotum long (Character 12); procoxae modified to receive mandibles; abdominal tergite VII of the female elongated (Character 37); and sculpture of the thorax consisting of large foveoles (Character 19). The concave occiput and modified procoxae are common to most chalcidids and hence I did not use them as characters in this study. Except for the convex face and elongate tergite VII, all other characters are variable among phas-
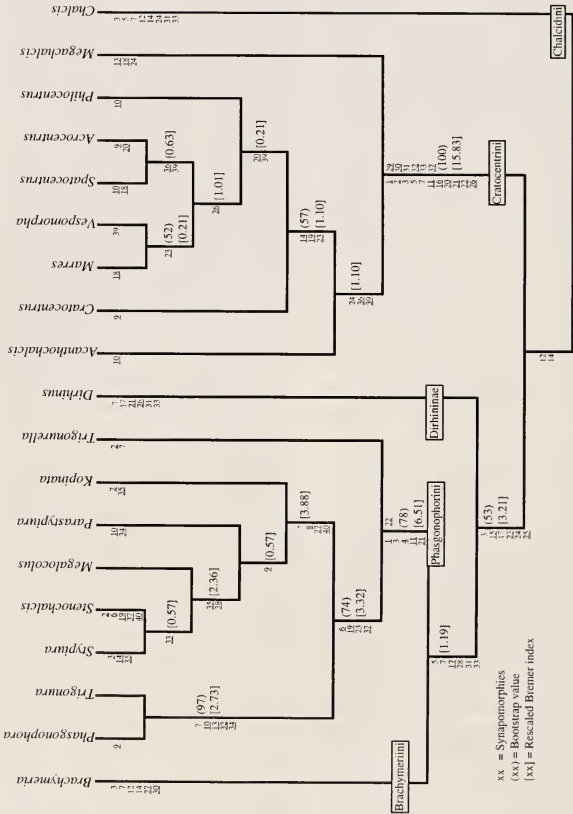
Fig. 67. Preferred most parsimonious tree for the data in Table 1 selected after successive weighting (Length = 98, consistency index = 0.823, retention index = 0.940).

xx = Synapomorphies
(xx) = Bootstrap value
[xx] = Rescaled Bremer index
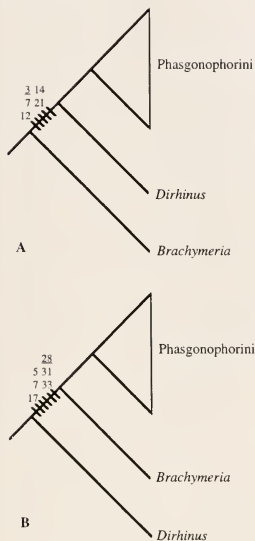
Fig. 68. Two minimal length topologies which resulted from conflict I in strict consensus tree.

gonophorines. The present analysis indicates that only the convex face (Character 4, state 0) can support the monophyly of Phasgonophorini and provide the following new synapomorphies for the tribe: 1) labrum less than half as broad as base of mandible (Character 1, state 2); 2) dorsally interrupted foraminal cavity (Character 11, state 1); 3) posteriorly sloping propodeum (Character 21, state 3); and 4) expanded apical margin of the fore tibia (Character 22, state 2).

Boucek's suggestion that the tribes Phasgonophorini and Cratocentrini are closely related and probably sister groups is not supported by this analysis. The phylogenetic hypothesis suggested for groups

within Chalcididae from my previous analysis supports Brachymeriini as the sister group of Phasgonophorini. The present analysis corroborates this finding. Five synapomorphies support the sister group relationship between Phasgonophorini and Brachymeriini of which one character is unambiguous (Fig. 67): apex of hind tibia diagonally truncated, ventral corner at acute angle but not produced into a spine (Character 28, state 0). Other possible synapomorphies for the clade are: 1) antennal toruli located above the lower eye margin (Character 5, state 0); 2) short and triangular antennal depression with sharp margin (Character 7, state 3); 3) expanded tegulae (Character 17, state 1); and 4) petiole transverse (Character 33, state 1). Cratocentrini is the sister group of a clade that includes Brachymeriini and Phasgonophorini (Fig. 67). My analysis also suggests that Trigonurella is the sister group to the rest of Phasgonophorini and Megachalcis is the sister group to rest of the Cratocentrini.

## Generic Relationships within Cratocentrini and Phasgonophorini

The generic relationships within Phasgonophorini are the same in all 14 most parsimonious cladograms which resulted from this analysis. Steffan (1950b) considered that Phasgonophorini had two distinct groups of genera. First, the Phasgonophora group with metasomal tergum 1 longer than tergum 2, and second, the Stypiura group with metasomal tergum 1 shorter than tergum 2. My analysis also provides support for these two groups. Each group is supported by four synapomorphies. The four unambiguous synapomorphies supporting the Phasgonophora group are: 1) presence of a carina behind lateral ocelli (Character 10, state 1); 2) pronotal surface raised lateral to the median line (Character 13, state 1); 3) marginal vein less than four times the length of stigmal vein (Character 32, state 1); and 4) presence of a lateral sulcus on first ab-

Fig. 69. Seven minimal length topologies which resulted from conflict III in strict consensus tree.

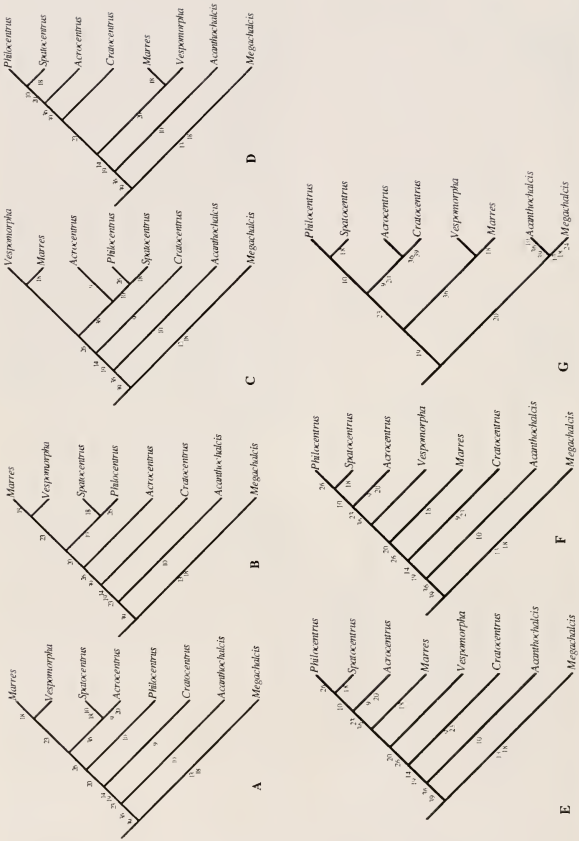dominal tergite (Character 34, state 1). The synapomorphies supporting the *Stypiura* group are: 1) antennal scrobe short and triangular with a blunt margin (Character 7, state 1); 2) ocellar triangle raised above vertex (Character 8, state 1); 3) presence of a single stout spur on hind tibial apex (Character 27, state 1); and 4) downwards curved posterior end of ovipositor sheath (Character 40, state 1) (Fig. 2). Except for character 7, state 1, the others are unambiguous. In addition, this analysis suggests that *Trigonurella* forms a distinct third group within Phasgonophorini (Fig. 67).

Conflicting evidence from the characters evaluated gave seven equally parsimonious resolutions for generic relationships within Cratocentrini (Fig. 69, A–G). I have selected a single hypothesis of generic relationships using successive character weighting which best explains the characters used (Fig. 67). However, most Cratocentrini (except *Acanthochalcis* and *Cratocentrus*) are known from very few specimens. Therefore, we have limited knowledge of character variation within the tribe and the question of the value of some of the selected characters as evidence of phylogenetic affinities remains open.

## Stability of the Phylogeny

Bootstrap analysis and rescaled decay indices indicate substantial support for most of the nodes in the selected phylogeny (Fig. 67). Within Phasgonophorini the two clades that agree with Steffan's groups have more than 50% bootstrap support while the clades within Cratocentrini have little bootstrap support. The rescaled branch support values are shown in Figure 67. The total support index (Bremer 1994) for the selected tree is 0.449.

## Implications of the Tribal Analysis for the Phylogeny of Chalcididae

According to the family-level phylogenetic analysis of Chalcididae (Wijese-kara 1997), neither Cratocentrini + Phasgonophorini nor Brachymeriini + Chalcidini are sister groups. The results of this analysis corroborate the results obtained from the family-level analysis. However, the results of generic level analysis within the tribes indicate that *Megachalcis* and *Trigonurella* are basal taxa within Cratocentrini and Phasgonophorini, respectively. When sampling taxa from a group for inclusion as exemplars in a phylogenetic analysis it is most appropriate to select representatives that are ancestral within the group, as it is more likely that their character states represent the ground plan. In my earlier analysis, I represented Cratocentrini by *Cratocentrus* and *Acanthochalcis*, and Phasgonophorini by *Phasgonophora* and *Megalocolus*. The two apparently most basal groups, *Megachalcis* and *Trigonurella*, were left out. To determine whether my taxon sampling had any effect on family-level phylogeny, I coded *Megachalcis* and *Trigonurella* for the 34 morphological characters used in the family phylogeny and reanalyzed the data. This analysis resulted in the same 42 most parsimonious trees with identical topologies to my previous analysis (Fig. 70) indicating that my results are not affected by taxon sampling.

Sampling of characters as well as sampling of taxa may affect the results of a phylogenetic analysis. The characters used depend on the taxon sample that is selected for the study. The characters that are informative at the lower level of phylogeny may not be suitable to study the relationships at a higher phylogenetic level, hence I have selected one character data set for the study of family phylogeny and a separate data set to study the generic relationships within the tribes (eight characters were common to both data sets). To test the effect of combining the two data sets I scored all the taxa for all the characters (Appendix 2) and reanalyzed the resulting data matrix of 41 taxa and 65 characters (Table 3). The
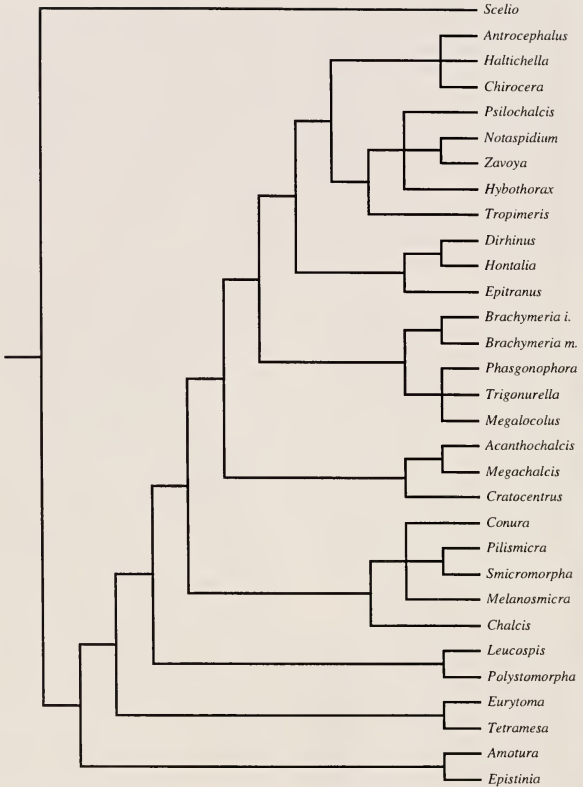
Fig. 70. Phylogeny of Chalcididae. Single most parsimonious tree resulted from successive character weighting after inclusion of basal Phasgonophorini and Cratocentrini taxa (*Trigonurella* and *Megachalcis*) in the taxon sample of the previous study.

Table 3. Data matrix (combined character sets) (polymorphic characters: a = state 0 or 1, b = 0 or 2, c = 0 or 3, d = 1 or 3, e = 1 or 2).

| Taxa | | Characters | | | | | |
|---|---|---|---|---|---|---|---|
| | 123456789 | 1111111111 0123456789 | 2222222222 0123456789 | 3333333333 0123456789 | 4444444444 0123456789 | 5555555555 0123456789 | 666666 012345 |
| *Scelio* | 100210020 | 0071012000 | 100210000a | 0200110000 | 00000???20 | 0000217210 | 00??00 |
| *Leucospis* | 000000020 | 0300111002 | 2112001000 | 0110210000 | 1120010020 | 0000110010 | 002000 |
| *Polystomorpha* | 000000040 | 0300111001 | 2112001000 | 0110210000 | 1100010020 | 0000110010 | 002000 |
| *Eurytoma* | 000000020 | 1401000000 | 2010001000 | 0010200000 | 00000???20 | 00000160a0 | 000000 |
| *Tetramesa* | 000000020 | 0401000000 | 2010001000 | 0010200000 | 00000???20 | 00000160a0 | 0a0000 |
| *Amotura* | 010010020 | 120101?000 | ?010000010 | 0000100000 | 1000000100 | 0000300010 | 000000 |
| *Epistenia* | 010010020 | 020101?000 | ?010000000 | 0010000001 | 1100000?20 | 0000300010 | 003000 |
| *Antrocephalus* | 001110101 | 100b1a?000 | 0011110010 | 01a0000000 | 2100010?00 | 0000c12110 | 01c000 |
| *Haltichella* | 001110101 | 100b1a?000 | 0011110012 | 01a0000000 | 2100010?70 | 0000012110 | 01c000 |
| *Chirocera* | 001110101 | 100211?000 | 0011110012 | 0110000000 | 2100010?70 | 0000112110 | 010000 |
| *Psilochalcis* | 001210101 | 10021a?000 | 0011110012 | 0110200000 | 2100010?70 | 1000212110 | 010000 |
| *Notaspidium* | 001210101 | 110211?000 | 0011110012 | 1110200000 | 2100010?70 | 1000212110 | 010000 |
| *Hybothorax* | 001210101 | 1000102000 | 0011110112 | 0110200000 | 2100010?70 | 1000212110 | 010000 |
| *Zavoya* | 001210101 | 1?0211?010 | ?011110112 | 1400000000 | 2101010??1 | 0000202110 | 110000 |
| *Tropimeris* | 001310101 | 100011?000 | 0011110112 | 0510200000 | 2100010?70 | 1000212110 | 010000 |
| *Brachymeria i.* | 000400101 | 1202113000 | 0011120102 | 0100000000 | 2113110100 | 0110001112 | 011000 |
| *Brachymeria m.* | 000400101 | 1202113000 | 0011120102 | 0100000000 | 2113110100 | 0110001110 | 010000 |
| *Conura* | 100000101 | 1201111000 | 001d001002 | 0200000000 | 212300a000 | 00003030a0 | 010000 |
| *Pilismicra* | 100000101 | 0?01111000 | ?013001000 | 0200200000 | 2113000120 | 0000017010 | 010000 |
| *Melanosmicra* | 100000101 | 12?1111000 | 0013001102 | 0200000000 | 2123001110 | 0000313000 | 010000 |
| *Chalcis* | 100000101 | 1201111000 | 0013001102 | 0200000000 | 2122001000 | 0000303000 | 010000 |
| *Smicromorpha* | 000000101 | 1001110000 | 0013031100 | 0300000000 | 2113000010 | 0000213000 | 000000 |
| *Dirhinus* | 000511101 | 11a0110000 | 0011110100 | 1110100000 | 2122010111 | 0000205060 | 010000 |
| *Hontalia* | 001511101 | 1110110100 | ?011000100 | 1110100010 | 2122000111 | 0000205000 | 012000 |
| *Epitranus* | 001310101 | 11?011?000 | 0011110100 | 1110000000 | 22220001e1 | 0000204000 | 010000 |
| *Acanthochalcis* | 000010111 | 1422112001 | 1013001001 | 2110110001 | 2122001020 | 0021110210 | 002020 |
| *Megachalcis* | 000010111 | 1422112000 | 1013001101 | 2112111001 | 2122000020 | 0021111210 | 010000 |
| *Cratocentrus* | 000010111 | 1422112020 | 1013001001 | 2110210011 | 2122011020 | 0021111110 | 002020 |
| *Marres* | 000010111 | 1422112000 | 1013001101 | 2110211101 | 2122001000 | 0021111?10 | 002030 |
| *Vespomorpha* | 000010111 | 1422112000 | 1013001101 | 2110210101 | 2122001010 | 0021111210 | 002040 |
| *Spatocentrus* | 000010111 | 1422112001 | 1013001101 | 2110211101 | 2122011010 | 0021111110 | 012010 |
| *Philocentrus* | 000010111 | 1422112001 | 1013001001 | 2110210101 | 2122011020 | 0021111?10 | 0??0?0 |
| *Acrocentrus* | 000010111 | 1422112020 | 1013001001 | 2110210111 | 2122011010 | 0021111110 | 012010 |
| *Phasgonophora* | 000010121 | 1200000011 | 1011120101 | 3111100002 | 2112000100 | 0100011111 | 011000 |
| *Trigonura* | 000400121 | 1200000001 | 1011120101 | 3111100102 | 2112000100 | 0100011111 | 010000 |
| *Trigonurella* | 000400121 | 1210013000 | 1011120101 | 3110100002 | 2112010100 | 0100001110 | 010000 |
| *Stypiura* | 000400121 | 1201001110 | 1011120101 | 3110200102 | 2111000100 | 0100001220 | 111101 |
| *Megalocolus* | 000400121 | 1200001110 | 1011120101 | 3110100102 | 2111000100 | 0100001110 | 211101 |
| *Stenochalcis* | 000400121 | 1210011110 | 1011120101 | 3110100002 | 2111000100 | 0100001120 | 213100 |
| *Kopinata* | 000400121 | 1?10001100 | 1011120101 | 3110100102 | 2111000100 | 0100001210 | 111001 |
| *Parastypiura* | 000400121 | 1?00001111 | 1011120101 | 3110100102 | 2111000100 | 0100001111 | 011001 |

polymorphic characters were scored as polymorphic using MacClade. PAUP's heuristic search with 500 random addition sequence replicates options gave 14 most parsimonious trees of length 234, consistency index of 0.491 and retention index of 0.818 (consensus tree Fig. 71).

Filtering trees to remove polytomous trees for which more highly resolved compatible trees exist, yielded 7 most parsimonious trees. Seven different resolutions resulted due to three areas of conflict (Fig. 71, A, B, & C). The first conflict (A) involves the placement of *Smicromor-*

Fig. 71. Strict consensus cladogram of the 14 minimal length trees (Length = 234, consistency index = 0.491, retention index = 0.818) that resulted from the parsimony analysis of the character data in Table 3.

*pha,* the second conflict (B) involves the relationship between *Acanthochalcis* and *Megachalcis,* and the third conflict (C) involves the placement of *Marres* and *Ves-*

*pomorpha.* Successive weighting of the characters using the retention index and 1000 base weight gave 10 most parsimonious trees. Filtering the polytomous

trees yielded four most parsimonious trees (consensus tree Fig. 72). All 10 most parsimonious trees after successive weighting were 235 steps long under equal weighting of characters. Four most parsimonious trees after filtering resulted due to a single area of conflict indicated in the strict consensus tree (A in Fig. 72).

The joint character set favors somewhat different relationships within the family (see comparison in Fig. 73). To obtain the family phylogeny represented in the combined analysis from my previous data set requires two extra steps (tree length 101 instead of 99), and to get the previous family phylogeny from the combined data set requires seven extra steps (tree length 241 instead of 234).

The most obvious change is the shifting of Brachymeriini + Phasgonophorini lineage as the sister group of Haltichellinae instead of Dirhininae + Epitraninae clade. In addition, *Zavoya* becomes sister to the other Haltichellinae and *Smicromorpha* and *Philismicra* groups away from, instead of within, Chalcidini. The sister group relationship between Brachymeriini + Phasgonophorini and Haltichellinae is supported by six synapomorphies of which 3 are unambiguous [characters 29, 45, and 57 (Fig. 72)]. Of these, character 29 is from the family-level study, character 45 is from the tribe-level study and character 47 is common to both studies. None of these characters is unique and unreversed within the clade. In the family level phylogenetic study the sister group relationship between Haltichellinae and Dirhininae + Eipitraninae clade was also supported by six synapomorphies with only a single unambiguous character (Fig. 74). Of these characters, location of the antennal toruli remains a unique and unreversed synapomorphy for both clades while two other characters (Character 3 and Character 25) shows single reversals within the group. The other three characters are much more variable within the

group. Overall the six characters supporting Brachymeriinae + Epitraninae + Haltichellinae are less homoplasious (ci = 0.5, 0.7, 0.3, 0.5, 0.7, and 1.0 for characters 3, 4, 5, 11, 25, and 56 respectively) than the characters supporting the Haltichellinae + Brachymeriini + Phasgonophorini clade in combine analysis (ci = 0.5, 0.5, 0.5, 0.2, 0.2, and 0.4 for characters 16, 29, 42, 45, 48, and 57).

Similarly three synapomorphies (two unambiguous) support the Chalcidini clade including *Smicromorpha* in the family phylogenetic analysis (Fig. 74). The structure of the petiole (Character 56, state 3) is unique for the clade and characters 1 and 31 show a single reversal in *Smicromorpha*. In the combined character analysis, Chalcidini without *Smicromorpha* is supported by four characters (Fig. 72): 1) raised supra clypeal area (Character 1, state 1) and 2) longitudinally oriented spiracle (Character 31, state 2) from the family phylogeny data set; and 3) antennal scrobe shape (Character 16, state 1); and 4) longer postmarginal vein (Character 54, state 1); from the tribal data set. The diagonally truncated hind tibial apex (Character 42, state 1) and fifth metasomal segment (Character 61, state 0) separate *Smicromorpha* from other chalcidines (Fig. 72). The character set which support the Chalcidini + Smicromorphinae in family level study provide less support (ci = 0.5, 0.8, and 1.0 for characters 1, 39, and 56 respectively) than the character set supporting the Chalcidini excluding Smicromorphinae in combine analysis (ci = 1.0, 0.5, 0.8, 0.1, and 0.3 for characters 1, 16, 31, 32, and 34). The abdomen of *Smicromorpha* is highly modified and not comparable to any other chalcidids. Therefore it is highly unlikely that the length of the fifth metasomal segment in *Smicromorpha* can show phylogenetic affinities to other chalcidids. Hence character 61 should not be regarded as evidence for separating *Smicromorpha* from other chalcidines.
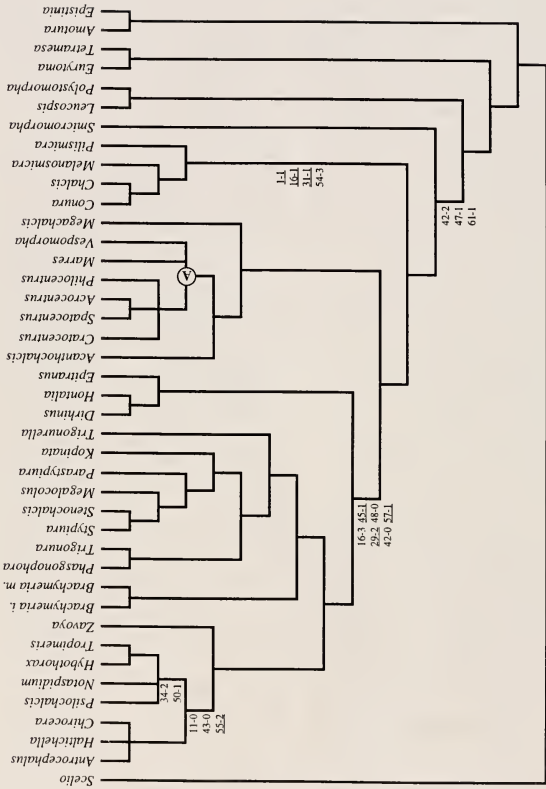
Fig. 72. Strict consensus cladogram of the 10 minimal length trees that resulted from the parsimony analysis of successively weighted data in Table 3 (Length under equal character weights = 235) (numbers on branches refers to character numbers in Appendix 2).
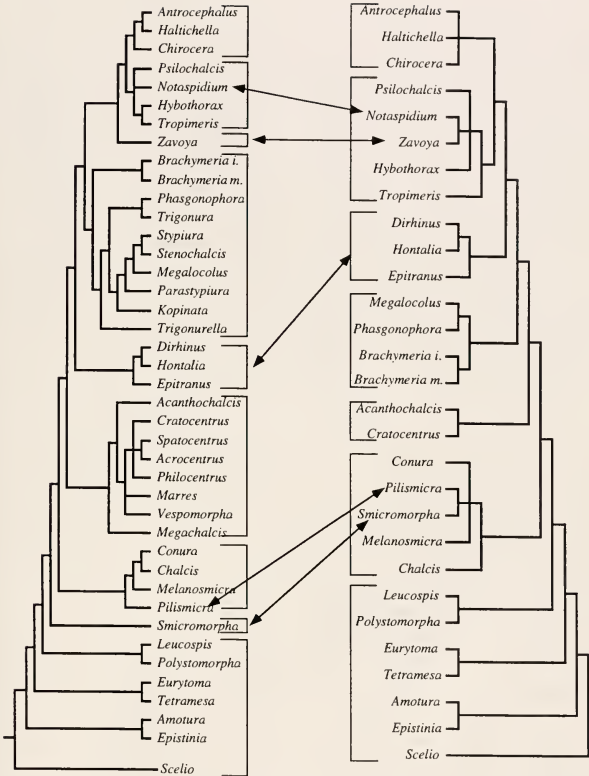
Fig. 73. Comparison of Chalcididae family cladograms resulted from my previous study and from combined character matrix in Table 3. Left. Consensus tree of 10 most parsimonious trees resulting from successive character weighting for combined data matrix. Right. Preferred family phylogeny from the previous study.

The third difference between the family study and the combined character analysis is that in the latter, *Zavoya* is placed as sister to all other Haltichellinae (Figs. 71, 72) instead of as sister to *Notaspidium* within Hybothoracini. (Fig. 74). Two ambiguous characters support the Hybothoracini + Tropimeridini clade (ex-
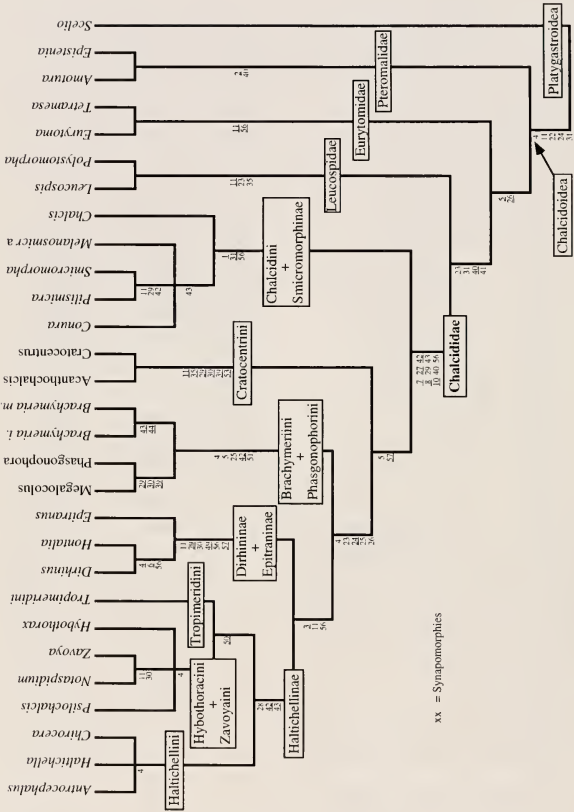
Fig. 74. The preferred family phylogeny of Chalcididae that resulted from my previous study indicating the synapomorphies for clades within the family (numbers on branches correspond to characters in Appendix 2).

xx = Synapomorphies

cluding *Zavoya*) in the combined analysis: the location of the postmarginal vein (Character 50, state 1), and the shape of posterior margin of the pronotum (Character 34, state 2). The sister group relationship between Haltichellini and Hybothoracini (including *Tropimeris*) is supported by three possible synapomorphies: 1) Hypostomal bridge (Character 11, state 3); 2) Presence of two hindtibial spurs (Character 43, state 1); and 3) Shorter marginal vein (Character 55, state 1). Only character 55 provides unambiguous support. Overall the Haltichellini +Hybothoracini including Zavoyini and Tropimeridini in family level analysis has support of less homoplasious characters ($ci = 0.5, 0.6$, and 0.5 for characters 28, 42, 43) than for Haltichellinae + Hybothoracini excluding Zavoyini in combined analysis ($ci = 0.5, 0.4$, and 0.2 for characters 11, 43, and 55).

These results clearly indicate that the characters used for analysis of generic relationships affected the resolution of higher level relationships. This means that the addition of characters which are homoplasious at higher phylogenetic level changed the evolutionary interpretation of characters used for resolving the higher level phylogeny.

It is obvious that combining two character sets that were selected by studying biased taxon samples in relation to one another will produce a data set with biased characters and a biased taxon sample. Therefore, the results of the combined analysis can not be regarded as an appropriate representation of phylogenetic relationships within Chalcididae. Although it is not appropriate to combine two data sets to make a biased data set, this exercise indicates that the family phylogeny I have suggested in my previous study should be subjected to more critical testing by including more taxa from different chalcidid groups to establish a stable phylogenetic hypothesis for the family.

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## APPENDIX 1: TAXA EXAMINED

### Outgroups

1. *Brachymeria* spp.
2. *Chalcis* spp.
3. *Dirhinus* spp.

### Cratocentrini

*Acanthochalcis nigricans* Cameron
*Acanthochalcis unispinosa* Girault
*Acrocentrus erythrothorace* Steffan
*Cratocentrus ruficornis* Cameron
*Cratocentrus pruinosus* Steffan
*Marres dicomas* Walker
*Megachalcis carinata* Steffan
*Megachalcis hirticeps* (Cameron)
*Megachalcis malabarica* Narendran
*Megachalcis timerensis* Boucek
*Philocentrus argenteolus* Steffan
*Spatocentrus arnoldi* Steffan
*Vespomorpha auronitens* Steffan

### Phasgonophorini

*Kopinata partirubra* Boucek
*Megalocolus ducator* (Walker)
*Megalocolus properator* (Walker)
*Megalocolus signator* (Walker)
*Megalocolus tentator* (Walker)
*Parastypiura pulchripennis* (Ashmead)
*Phasgonophora batesii* Boucek
*Phasgonophora gigentia* Ashmead
*Phasgonophora sulcata* Westwood
*Stenochalcis miltoni* (Girault)
*Stypiura candatus* Guerin
*Stypiura conigastra* (Perty)
*Stypiura patesi* (Kirby)
*Stypiura rfiventris* (Sichel)
*Stypiura thoracica* (Schel)
*Trigonura algerti* Burks
*Trigonura bakeri* Masi
*Trigonura californica* Rohwer
*Trigonura dorsalis* Ashmead
*Trigonura elegans* Provancher
*Trigonura euthyrrhini* Dodd
*Trigonura indica* Narendran
*Trigonura insularis* Cresson
*Trigonura javensis* Narendran
*Trigonura leuzouensis* Narendran
*Trigonura pini* Burks
*Trigonura puertoricensis* Wolcott
*Trigonura radiator* Walker
*Trigonura samarensis* Narendran
*Trigonura steffani* Narendran
*Trigonura tarsata* DellaTorre
*Trigonura ulmi* Burks
*Trigonurella achterbergi* Narendran
*Trigonurella elegans* Boucek

## APPENDIX 2: CHARACTER DESCRIPTIONS (COMBINED SET)

The numbers within parentheses indicate the original data set that character came from (1= family level study and 2= tribel level study) and the character number in the original data set respectively.

**Characteristics of the head:**

1. Supraclypeal area (1/1).
    0. Not horizontally raised.
    1. Horizontally raised.
2. Distance between the antennal toruli (1/2).
    0. Distance not more than 2× the diameter of torulus.
    1. Distance more than 2× the diameter of torulus.
3. Orientation of the antennal toruli (1/3).
    0. Lateral and ventral margins of toruli produced forward.
    1. Lateral and ventral margins of toruli not produced and toruli facing forward or upwards.
4. Interantennal projection (1/4).
    0. Not modified; area between toruli continuous with face and appearing raised due to scrobal depressions.
    1. Modified into a round plate with blunt margins.
    2. Modified into a round plate with sharp elevated margins.
    3. Reduced to a thin sheet-like elevation between toruli.
    4. Modified into thick plate which is higher than upper toruli margin.
    5. Absent.
5. Location of the antennal toruli (1/5, 2/5).
    0. Toruli located at or above the level of the lower eye margin.
    1. Toruli located below the level of the lower eye margin.
6. Frons (1/6).
    0. Not produced into horns.
    1. Produced into two strong horns.
7. Labrum habitus (1/7).
    0. Base of the labrum covered by the anterior clypeal margin.
    1. Base of the labrum exposed, not covered by the clypeal margin.
8. Size of the Labrum (2/1).
    0. Large: as broad as base of the mandibles.
    1. Intermediate size: about half as long as base of mandibles.
    2. Small: less than half the length of base of the mandibles.
9. Base of the mandible (1/8).
    0. Covered by the genal margin.
    1. Exposed.
10. Postgenal carina (1/9).
    0. Absent.
    1. Present.
11. Hypostomal bridge and genal bridge (1/10).
    0. Genal bridge absent, hypostomal bridge distinct, hypostomal carina continuous around occipital foramen.
    1. Genal bridge not complete, hypostomal carinae converge below occipital foramen making distinct hypostomal lobes which narrowly unite in the middle.
    2. Post gena converging below the occipital foramen; hypostomal bridge slightly exposed.
    3. Genal bridge absent, hypostomal bridge distinct, and hypostomal carina continuous with a distinct carina around occipital foramen.
    4. Genal bridge completely covering the hypostomal bridge.
12. Median area above clypeus and below antennal toruli (2/2).
    0. Same sculpture as rest of the face; not modified.
    1. Different sculpture; modified to form a bridge between toruli and clypeus.
    2. Absent.
13. Malar sulcus (2/3).
    0. Absent.
    1. Present as a sulcus.
    2. Indicated as a carina.
14. Face (2/4).
    0. Convex distinctly.
    1. Concave or flat.
15. Antennae (2/6).
    0. Slender and long.
    1. Stout and short.
16. Antennal scrobe (2/7).
    0. Long and parallel sided.
    1. Short and almost triangular with blunt margin.
    2. Long and triangular with sharp margin.
    3. Short and triangular with sharp margin.
17. Ocelli triangle (2/8).
    0. Ocelli close to each other and raised above vertex.
    1. Ocelli spread apart and triangle not raised.
18. Vertex within ocellar triangle (2/9).
    0. Normal not modified.
    1. Medially raised between lateral ocelli.
    2. Raised lateral to the lateral ocelli.
19. Carina behind lateral ocelli (2/10).
    0. Absent.
    1. Present.
20. Foraminal cavity/depression (2/11).
    0. Continuous around occipital foramen.
    1. Dorsally interrupted.

**Characteristics of the mesosoma:**

21. Notauli (1/11).
    0. Present.
    1. Absent.
22. Prepectus (1/12).

0. Absent.
1. Present.
23. Externally visible area of the prepectus (1/13, 2/15).
    0. Large and triangular sclerite; ventromedially broad.
    1. Small and distinctly longer than broad; ventromedially narrow, plate like (state 0 in 2/15).
    2. Reduced to a very thin sclerite difficult to see (state 1 in 2/15).
    3. Intermediate size sclerite, as long as broad; ventromedially narrow (state 2 in 1/13).
24. Mesopleural Wing Process (1/15).
    0. At least partly exposed.
    1. Completely covered by tegula.
25. Relative size and shape of the tegula (1/16, 2/17).
    0. Elongated and small, second axilla of the wing joint completely exposed.
    1. Both ventrally and posteriorly expanded, oval shape, second axilla completely covered.
    2. Ventrally expanded, second axilla of the wing exposed (state 1 in 2/17).
    3. Reduced and axilla exposed.
26. Orientation of the area between lower margin of the femoral depression and epicnemial carina in relation to sagittal plane (1/17).
    0. Parallel.
    1. Perpendicular.
27. Parascutal and axillar carinae (1/18).
    0. Converge but extend towards dorsum before meeting each other at transscutal articulation.
    1. Converge to meet each other at transscutal articulation.
28. Axillular carina (1/19).
    0. Absent.
    1. Present.
29. Frenal area of the scutellum (1/20).
    0. Not marked.
    1. Slightly marked.
    2. Distinctly marked by a lamina.
30. Propodeum (1/21, 2/21).
    0. Angulate in relation to scutellum.
    1. Horizontal in relation to scutellum.
    2. Anteriorly horizontal and steeply sloping posteriorly (state 2 in 2/21).
    3. Medially depressed and almost vertical (state 1 in 2/21).
31. Spiracle of the propodeum (1/22).
    0. Small and rounded.
    1. Spiracle elongated and transversely or obliquely oriented.
    2. Longitudinally oriented.
    3. Reduced.
    4. Sunken into propodeum.
    5. Lateral margin modified to a lamina which characteristically extends posteriad.
32. Width of the pronotum (2/12).
    0. Broad.

1. Narrow anterior.
33. Pronotal surface (2/13).
    0. Not raised; normal.
    1. Raised lateral to the median line.
    2. Raised as two bumps near posterior lateral margin.
34. Posterior margin of the pronotum (2/14).
    0. Broadly concave.
    1. Medially acutly emarginate.
    2. Medially abruptly concave.
35. Mesonotal spiracle (1/14, 2/16).
    0. Covered by posterior lateral margin of pronotum.
    1. Exposed.
36. Dorsal axillar surface (2/18).
    0. Flat.
    1. Raised.
37. Sculpture of the mesosoma (2/19).
    0. Not rasp like.
    1. Rasp like.
38. Mesoepisternum (2/20).
    0. Not projected between fore coxa.
    1. Projected medially between fore coxa.
39. Apical margin of the fore tibia (1/23, 2/22).
    0. Without horizontally directed stout spine.
    1. With horizontally directed stout spine .
    2. Without a spur but distinctly expanded similar to spur .
40. Hind coxa (1/24).
    0. Not distinctly enlarged.
    1. Enlarged with flat inner surface.
    2. Enlarged with convex inner surface.
41. Hind femur (1/25).
    0. Normal (not enlarged and toothed).
    1. Enlarged and toothed.
42. Apex of the hind tibia (1/26).
    0. Truncate at right angle.
    1. Diagonally truncated ventral corner at acute angle but not produced into a spine.
    2. Diagonally truncated and elongated into a spine.
    3. Diagonally truncated and outer spur incorporated into a spine.
43. Hind tibial spurs (1/27, 2/27).
    0. Two spurs present.
    1. Single stout spur present.
    2. Spurs absent.
    3. Single weak spur present (state 1 in 2/41).
44. Elongated tooth-like process on hind tibial claws (1/28).
    0. Absent.
    1. Present.
45. Shape of the hind coxa (2/23).
    0. Proximally swollen but not elongated.
    1. Proximally swollen and elongated.
46. Inner tooth of the hind femur (2/24).
    0. Absent.
    1. Present.

47. Length of the arched hind tibia (2/25).
    0. Shorter than trochantus -femoral joint.
    1. Tip of the tibia touching the trochantus-femoral joint.
48. Tarsal depression of hind tibia (2/26).
    0. As long as first tarsal segment.
    1. As long as first two or three tarsal segments together.
    2. Longer than first three tarsal segments together.

**Characteristics of the wings:**

49. Length of marginal vein in relation to submarginal vein (1/30).
    0. Marginal vein short, submarginal vein less than half the length of submarginal vein.
    1. Marginal vein as long as submarginal vein, if shorter submarginal vein not 2× longer than marginal vein.
50. Forewing marginal vein location (1/31).
    0. Located at the anterior margin of the forewing: postmarginal and stigmal veins well developed.
    1. Located away from the anterior margin; post marginal and stigmal veins rudimentary.
51. Vertical nebulous vein on hind wing (1/32).
    0. Absent.
    1. Present.
52. Hamuli (2/30).
    0. Hamulus proximal to body different from others and located slightly away from the rest (less than its own length).
    1. Hamulus proximal to body different and located distinctly away from others (at least by a distance equal to its own length).
    2. Three hamuli morphologically similar and located equidistant from each other.
53. Front ventral margin of the forewing (1/29, 2/29).
    0. Without distinct tuft of spines.
    1. With posteriorly directed tuft of spines near distal end of the coastal cell.
54. Length of postmarginal vein (2/31).
    0. Distinctly shorter than marginal vein.
    1. Longer than marginal vein.
55. Length of marginal vein (2/32).
    0. Longer: more than 4× the length of stigmal vein.
    1. Shorter: less than 4× the length of stigmal vein.

**Characteristics of the metasoma:**

56. Petiole structure (1/33).
    0. Anterior articulation distinct, petiole ventrally membranous.
    1. Both sternum and tergum sclerotized transversely or slightly elongated anterior ventral

margin extended into the propodeum; anterior articulation not separated from the body.
    2. Anterior articulation separate from the body of the petiole ventrally; anterior ventral margin of the body expanded outside the propodeum.
    3. Anterior articulation distinctly separated from the body by a lamella, body variously elongated.
    4. Anterior articulation united with the extended anterior ventral surface of the petiole body; lamella absent.
    5. Anterior articulation separated from body which is distinct dorsally and ventrally and posterior ventral margin not distinctly separated from sternum of gaster.
    6. Anterior articulation distinctly separated from the body only dorsally.
57. Syntergum (1/34)
    0. Convex, seventh and eighth tergites completely fused.
    1. Roof-like, posterior dorsal edge of seventh tergite not fused to eighth tergite.
58. Petiole length (2/33).
    0. Distinctly longer than wide.
    1. Transverse, not visible from dorsal side.
    2. As long as wide; visible from dorsal side.
59. Lateral sulcus of first abdominal tergite (2/34).
    0. Absent.
    1. Present.
60. First and second abdominal tergites of females (2/35).
    0. Independent.
    1. United but line of fusion is distinct.
    2. United with no trace of the line of fusion.
61. Fifth metasomal tergite of the female (2/36).
    0. As long as the first tergites.
    1. Distinctly shorter than the first tergite.
62. Seventh metasomal tergite (2/37).
    0. Short and completely cover the ovipositor sheath.
    1. Elongated and completely cover elongated ovipositor sheaths.
    2. Short and do not cover elongated ovipositor sheaths.
    3. Slightly elongated and cover the ovipositor sheaths.
63. Surface of seventh tergite (2/38).
    0. Differently sculptured beyond cerci.
    1. uniformly sculptured.
64. Tufts of silvery hairs on abdominal tergites (2/39).
    0. Absent.
    1. Two lateral tufts on tergite five.
    2. Four lateral tufts on tergite five and six.
    3. Single continuous tuft on tergite five.
    4. Silvery hairs evenly distributed on tergites.
65. Posterior end of ovipositor sheath (2/40).
    0. Not curved downwards.
    1. Distinctly curved downwards.

# Multi-species Mating Swarms of *Formica* in Southwestern Montana, U.S.A. (Hymenoptera: Formicidae)

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*Abstract.*—In 1995 and 1996 in southwestern Montana, I observed ant mating swarms that each day consisted of at least two of three species of *Formica*: *Formica ciliata* Mayr, *Formica obtusopilosa* Emery, and *Formica subpolita* Mayr. In 1993, *F. ciliata* males also formed swarms above the nest from which they emerged. Although swarming behaviors of males of these species were indistinguishable, the mating posture, the behavior of females during mating, and the duration of mating varied among species. *Formica ciliata* matings averaged five times longer than *F. obtusopilosa* matings and four times longer than *F. subpolita* matings. Predation on alate males at swarms was frequent, with the spider *Dictyna coloradensis* (Dictynidae) probably accounting for most mortality.

The study of ant mating strategies is not only a tool for examining standard aspects of sexual selection theory (e.g. sperm competition), but is critical to an understanding of the social behavior of ants (Bourke and Franks 1995). It is becoming clear that ant mating systems and social systems may have reciprocal influences upon one another. For example, on the one hand, the number of times that a queen mates determines the relatedness among her offspring, which influences the evolution of eusocial behavior (Crozier and Pamilo 1996). On the other hand, intracolonial relatedness (along with possible detriments to inbreeding) determines the cost of mating with another colony member, and thus may influence which mating system reduces the risk of inbreeding (Ross and Keller 1995). Although progress is being made in answering these important questions (e.g. Keller and Passera 1993), we still need to learn much more about the basic form of mating systems in the Formicidae (Hölldobler and Wilson 1990).

Perhaps the most common mating system in ants is for alates to congregate and mate within short-lived swarms (Bourke and Franks 1995). Although swarms often consist of a single species of ant, multi-species swarms have also been reported (Chapman 1954, 1963, Collingwood 1958, Leprince and Francoeur 1986). In a previous paper, I noted that alates of three unidentified species of *Formica* were occasionally present in small numbers within swarms of *Formica subpolita* at one location in southwestern Montana, U.S.A. (O'Neill 1994). Here, I report on *Formica* mating swarms at nearby location which often consisted of mixtures of swarming males and mating pairs of three species, *Formica ciliata*, *F. obtusopilosa*, and *F. subpolita*. I also provide comparative information on the mating behavior of the three species and data on the high level of predation on alates within swarms.

## METHODS

I observed the ants at a site 2 km NW of Logan, Gallatin Co., MT, U.S.A. (45°45'N, 111°35'W) in July of 1993, 1995, and 1996. I visited the site on 18 days, to check for swarms, which were present on 8 days; on five days in 1996, I was present for the entire swarm period. I collected 53 mating pairs for later identification. Females of the three species were easy to

identify in the field, *Formica ciliata* females being completely orange, *F. obtusopilosa* females having orange thoraces, but black heads and abdomens, and *F. subpolita* females being completely shiny black and larger than queens of the other two species. It was much more difficult to identify males in the field. However, once I associated males with females in mating pairs a suite of characters associated with each species and species group (Wheeler and Wheeler 1963) allowed reliable identification of males in the lab; voucher specimens of males and females from mating pairs of all three species have been deposited in the Montana State University Entomology Collection. On six days in 1995 and 1996, I collected alates from spider webs, feeding spiders, or other arthropod predators. All prey were collected within the area encompassed by swarms, during swarming or immediately afterwards.

## RESULTS

*Swarm Location.*—I observed *Formica* mating swarms at two locations. In 1993, a swarm of *F. ciliata* was present on 19 and 20 July just above a large, multi-entrance *F. ciliata* nest on the west side of a grassy ridge among scattered junipers (*Juniperus scopulorum* Sarg.) and yucca (*Yucca glauca* Nutt.). The swarms, which at their peak covered about 2 × 10 m and probably included >200 males, were centered around a patch of yellow sweetclover (*Melilotus officinalis* L.) growing among the nest entrances. Swarms did not form above the nest in 1995 and 1996. Although many alate male and female *F. ciliata* emerged from the colony, they climbed nearby plants and flew away, perhaps to join swarms that I found on a hillside approximately 100 m east of the *F. ciliata* nest. Swarms at this second location were concentrated on the lower half of the hillside, where it was covered by a dense expanse of cheatgrass (*Bromus tectorum* L.) and several clusters of dead and leafless yellow

sweetclover. Swarms were sometimes restricted to several square meters, but at times certainly consisted of over 500 males swarming over an area of ~5 × 50 m (with highly variable density across the swarm). Because I found no *Formica* nests with emerging alates within the swarm area, the alates probably originated elsewhere.

*Species Composition of Swarms.*—Unlike the swarms above the *F. ciliata* nest, those on the hillside always contained males and females of two or three species: *F. ciliata*, *F. obtusopilosa*, and *F. subpolita*. The exact mix of species within swarms was hard to determine because males were difficult to identify and count in the field. However, by identifying females in mating pairs I was able to determine that at least two species were present on each of six days in 1996 (Fig. 1). The relative number of matings observed, however, cannot be used to estimate the relative number of swarming males. Because matings of *F. ciliata* lasted much longer than those of the other two species (see below), the probability of encountering a pair of *F. ciliata* was much higher. It was my impression, however, that *F. subpolita* males were most common, whereas those of *F. obtusopilosa* were least common. This was confirmed by examining males in webs of the spider *Dictyna coloradensis* (see below), which were situated at swarm height and probably captured a representative sample of swarming males. Of the 292 alate males I recovered from *Dictyna* webs, 70.5% were *F. subpolita*, 25.7% were *F. ciliata*, 2.1% were *F. obtusopilosa*, and 1.7% were of one or more other species of *Formica* that apparently joined swarms on occasion. I also found one female each of two unidentified *Formica* perched on plants in the swarm area.

While swarms were in progress, females of the three *Formica* species often perched within 1 m of one another. The overlapping spatial distribution of the females suggests that swarming males of the three
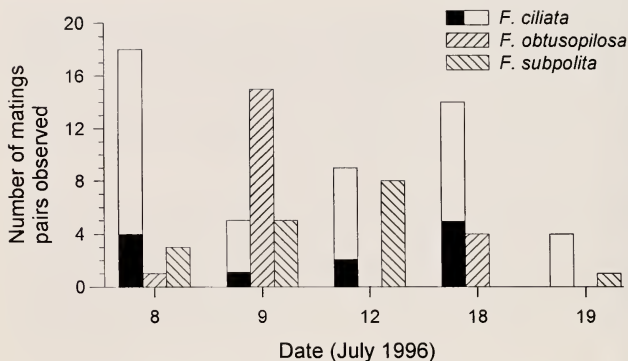
Fig. 1. The number of mating pairs of three species observed at the hillside site on the five days in 1996 when observers were present during the entire swarm period (solid black portions of the *F. ciliata* bars indicate those matings that were the 2nd, 3rd, or 4th for an individual female; no multiple matings were observed for *F. obtusopilosa* on these days, and multiple matings were not recorded for *F. subpolita* in this study).

species also intermingled. Nevertheless, on several days there was a larger scale, though incomplete, segregation of the species at the hillside site. Female *F. ciliata* tended perch in the center and in the northern end of the elongate swarm, while female *F. subpolita* were most abundant at either end of the swarm. The female *F. obtusopilosa* were generally restricted to a small area in the northern half of the swarm. There was also interspecific variation in activity periods. At the hillside site, swarms were active between 0900 and 1130 h on warm, clear days. As judged by the times at which I observed matings in 1996, *F. ciliata* also had a longer daily mating period than the other two species which displayed a more prominent peak of mating activity around 1000 h (Fig. 2).

*Swarming and Mating Behavior.*—Only males actually swarmed, whereas females perched on low vegetation. Swarming behavior of male *F. ciliata* and *F. obtusopilosa* was similar to that previously described

for *F. subpolita* (O'Neill 1994). Males of all three species made slow, irregular flights near the top of the vegetation, generally facing into the wind. Males often restricted their flights to the immediate vicinity of a perched female, eventually landing on the plant and walking along its stems. When a male approached the female, usually after exploring several stems, his body and wings vibrated rapidly, perhaps responding to olfactory cues emanating from the female (Cherix et al. 1993). This behavior near females has also been noted for other species of *Formica* (Kannowski and Johnson 1969, Henderson and Jeanne 1992).

O'Neill (1994) provided descriptions of matings of *F. subpolita*, which typically proceeded as follows. A male mounted a female dorsally, facing the same direction as her, and immediately coupled if she acquiesced. He then released his grip and flipped backwards 180° so that he now faced the opposite direction, venter up. After an average of 27 s (range: 4–63), the
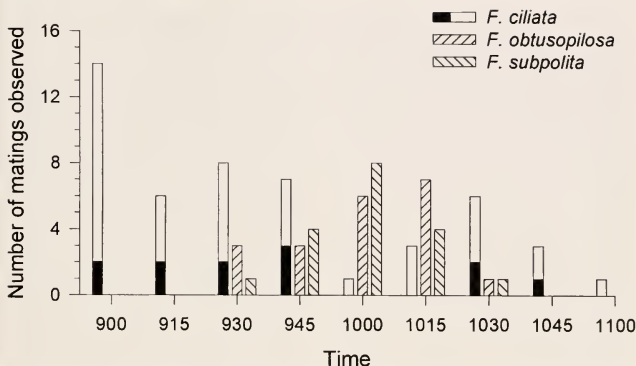
Fig. 2. The frequency distribution of matings observed in 15-min intervals (beginning at the time indicated) on the same five days depicted in Fig. 1 (see Fig. 1 for note on occurrence of multiple matings).

female usually curled her body back and began biting the male, often on the petiole. Nevertheless, mating continued for another 35 s on average, so that complete matings averaged 62 s (range: 28 to 94). Overall, matings of *F. obtusopilosa* were similar to those of *F. subpolita*, although the mean time to biting was just 16.3 s (SE = 2.5; N = 13; range: 2 to 33) and the total duration of mating was 50.6 s (SE = 6.7; N = 13). Biting by females occurred in all 13 *F. obtusopilosa* matings observed from start to finish, whereas it occurred in 88% of *F. subpolita* matings (O'Neill 1994).

Mating by *F. ciliata* was initiated in the same manner as in *F. subpolita* and *F. obtusopilosa*, but it was different in form and duration. After a male *F. ciliata* released his leg grip on the female, he remained arched forward, so that his head was positioned above the female's abdomen. Furthermore, during the prolonged matings, which averaged 260.1 ± 22.0 s (range: 7 to 711 s; N = 54), females rarely reached back to bite males (6% of 54 matings). Thus, the form and duration of mating ap-

pears to be relatively species-specific. However, during *Formica obscuripes* Forel matings, males apparently could adopt either of the postures observed in my study (Talbot 1972).

During mating, one or two other males sometimes arrived and attempted coupling, apparently oblivious to the presence of the copulating male. Twice, a second *F. ciliata* male arrived soon after a mating commenced and disrupted the mating pair. However, neither intruding male was able to mate with the female. These interactions probably resulted when males incidentally homed to the same female, and apparently do not represent fighting for possession of receptive females.

Following mating, females of all three species either left the swarm area by flying upwards or they remained on the same plant awaiting the arrival of another male. Polyandry is a common feature of ant mating systems, especially in the genus *Formica*, where the existence of multiple mating by females has been observed or inferred in 15 of 16 species cited by Cro-

zier and Pamilo (1996). One of these species is *F. subpolita*, whose females mate up to four times each within mating swarms (O'Neill 1994). By continuing to watch females from the time they were first observed *in copula* until they left the area, I also confirmed that polyandry occurs in *F. obtusopilosa* and *F. ciliata*. One female *F. obtusopilosa* was seen to mate three times. Eleven *F. ciliata* females were seen to mate twice, three mated three times, and one mated four times. Not all females were observed continuously, some were collected, and some may have mated prior to my first observation. Thus, multiple mating in these species is probably more common, and each female probably mates more frequently than my observations suggest. The multiple matings by a single *F. ciliata* female typically occurred over a limited portion of the daily swarm period. The mean interval between the termination of one mating and initiation of the next was 5.3 min (SE = 0.9, N = 12), and one *F. ciliata* female mated four times within 31.1 min.

Although females and males of the three species were in close proximity, I found no evidence of cross-species matings among the 53 mating pairs collected and examined. It is possible that males attempted to mate with females of other species, because I observed rejection of "courting" males by females of all three species; unreceptive *Formica* females rejected mating attempts by curling the tips of their abdomens away from mounted males, by walking away, or by dropping off the plant. In all three species, rejections occurred most often just before a female flew away from the swarm, so perhaps the rejections usually signal the end of the receptivity to conspecific males. On several occasions, females remained on their perches after rejecting one male, and soon mated with another. These rejections could represent intraspecific female choice, or females rejecting courting males of other species, but because none of these

rejected males were collected, I could not ascertain their identity.

*Predation on Alates.*—Predations on alates, particularly by spiders and robber flies were common at the hillside site (Table 1). There are three apparent reasons why males made up 98% of the prey. First, males probably far outnumbered females at any given time. Second, because males spent much of the time in flight above the vegetation, they were more susceptible to predation by visually hunting robber flies that intercept airborne prey within swarms (O'Neill 1992). Third, the most common spiders, *D. coloradensis*, built their webs at the tips of plant stems, where single webs captured up to eight males on a single day. Because males flew at the same height as the webs and explored the stems of many plants during a day, they increased their likelihood of contacting a web.

## DISCUSSION

The mating systems of *F. ciliata*, *F. obtusopilosa*, and *F. subpolita* exhibit features in common with many species of ants, including male swarming, a lack of overt fighting among males, and multiple mating by females (Bourke and Franks 1994). Although swarming is common in *Formica*, the locations of swarms relative to the nests from which alates emerge vary both within and between species. Swarming and pairing at variable or unknown distances from nests have been seen for *Formica lugubris* Zett. (Cherix et al. 1993), *Formica obscuripes* Forel (Talbot 1959, 1972), *Formica subnuda* Emery (Chapman 1954, 1963), and *F. subpolita* (O'Neill 1994). Swarming at nests from which the alates emerged has been observed in *Formica dakotensis* Emery (Talbot 1971) and *Formica montana* Emery (Kannowski and Johnson 1969, Henderson and Jeanne 1992). Although many female *Formica pergandei* Emery mate within swarms at their home nests, some apparently disperse prior to mating, presumably to enter swarms else-

Table 1. Arthropods observed capturing or feeding on alate ants at mating swarms. The category "*Formica* spp." includes members of the other three species that were not identified in the field.

| Predator | Prey species and sex | | | |
| --- | --- | --- | --- | --- |
| | *F. ciliata* | *F. obtusopilosa* | *F. subpolita* | *Formica* spp. |
| **ARACHNIDA** | | | | |
| Araneidae | | | | |
| *Metepeira foxi* Gertsch and Ivie | 1 m | — | 1 m | — |
| unidentified araneid | — | — | 15 m | — |
| Dictynidae | | | | |
| *Dictyna coloradensis* Chamberlin | 75 m | 6 m | 206 m, 1 f | 5 m |
| Philodromidae | | | | |
| *Tibellus duttoni* (Hentz) | — | — | 2 m | — |
| Thomisidae | | | | |
| *Misumenops celer* (Hentz) | 1 m | — | — | — |
| **ORTHOPTERA** | | | | |
| Acrididae | | | | |
| *Melanoplus sanguinipes* (Fabricius) | — | — | — | 3 m[1] |
| **HEMIPTERA** | | | | |
| Nabidae | | | | |
| unidentified nymphs | 2 m | — | — | — |
| Reduviidae | | | | |
| unidentified nymphs | 1 m | — | — | — |
| **DIPTERA** | | | | |
| Asilidae | | | | |
| *Efferia staminea* (Williston) | 1 f | — | — | 22 m |
| *Megaphorus willistoni* (Cole) | — | — | 1 f | 19 m |
| *Stenopogon inquinatus* (Loew) | — | — | — | 2 m |
| **HYMENOPTERA** | | | | |
| Sphecidae | | | | |
| *Aphilanthops subfrigidus* | 1 f | — | 3 f | — |

[1] All 5th instars which did not prey on the ants, but rather scavenged them from webs of *D. coloradensis*.

where (Kannowski and Johnson 1969). In southwest Montana, *F. ciliata* swarmed both above nests (in 1993) and within multi-species swarms in a area apparently not harboring any *F. ciliata* nests (in 1995 and 1996). Alates of *F. obtusopilosa* and *F. subpolita* also apparently originated from colonies outside of the swarm area.

There are several potential advantages to be gained by alates that join swarms away from their home nests. First, when colonies produce reproductives of just one sex, the alates from some nests must disperse in order to find mates. For example,

because many *F. montana* colonies produce only male alates, they must disperse and swarm at nests that have produced females (Henderson and Jeanne 1992). Because I saw both male and female alates emerging from the *F. ciliata* colony in 1995 and 1996 when swarms occurred away from the nest, alates of this species appear to have dispersed for other reasons. Second, if extreme inbreeding is detrimental, alates that join multi-colony swarms away from the home nest, will be more likely to mate with non-relatives. Inbreeding would be more likely in monogynous

nests, since many of the alates would be full siblings. Comparative evidence suggests that alate queens from monogynous nests tend to join swarms at a great distance away, but that females from polygynous colonies (which are presumably more genetically diverse) disperse much shorter distances, sometimes mating on or within the nest (Ross and Keller 1995). I cannot directly address this hypothesis as it applies to *F. ciliata*, *F. obtusopilosa*, and *F. subpolita*, because I do not know whether queens within swarms came from monogynous or polygynous colonies. Joining large multi-colony swarms could reduce the risk inbreeding, but when swarms include more than one species, there is the added problem of identifying potential mates of the correct species. This problem could perhaps be solved if the sex pheromones released by females (Cherix et al. 1993) provided species-specificity.

*Formica ciliata*, *F. obtusopilosa*, and *F. subpolita* not only swarm away from their home nests, but gather together in various combinations at the same location on at least two successive years; at a nearby site, *F. subpolita* swarms were observed in the same location on six consecutive years (O'Neill 1994). Multi-species mating swarms also occur in other species of ants, and sometimes involve species of different genera (Chapman 1954, 1963, Collingwood 1958, Leprince and Francoeur 1986). Perhaps different species of ants swarm at the same times and places because alates of each species coincidentally respond to the same habitat cues. However, there may be an advantage to joining high density multispecies swarms if individual alates reduce their risk of predation when predators become temporarily satiated by the glut of food (Hölldobler and Wilson 1990, Bourke and Franks 1995); because at least some colonies would have to join multispecies swarms away from their home nests, this would also promote mating away from nests. Ant mating swarms often provide a flush of prey for a variety

of predators (Whitcomb et al. 1973, Robertson and Villet 1989, O'Neill 1990, 1992, 1994) that may impose a substantial cost on colonies. It is possible that some of the predators at the hillside site became satiated during swarms, thus temporarily reducing the predation risk of the surviving males. O'Neill (1992) found that, during the peak of *F. subpolita* swarms, the great majority of robber flies (primarily *Efferia staminea*) were feeding. When swarms were absent, most of these robber flies were not feeding (although they were actively foraging). However, its seems unlikely that the web building spiders became effectively satiated, because males continued to be trapped in webs throughout a swarm period and full webs were never observed. Finally, it should be noted that the satiation effect might be offset if predators congregated in areas of high prey density, thus actually increasing the risk of predation at swarm sites.

## ACKNOWLEDGMENTS

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# Behavior and Nesting Dynamics of the Neotropical Cavity-nesting Specialist Bee *Megachile assumptionis* Schrottky, with Comparisons to the Nearctic *Megachile brevis* Say (Hymenoptera: Megachilidae)

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*Abstract.*—We describe the behavior and nesting dynamics of the solitary leaf-cutter bee *Megachile assumptionis* Schrottky, which nests exclusively in deserted burrows of the solitary apid bee, *Ptilothrix plumata* Smith. Adults were active between April and September. Males patrolled the nesting sites and flowering bushes searching for females and nectar. Mating occurred both on the soil near the nests and on flowers of *Vernonia rubriramea* (Asteraceae). Females only investigated and selected single-celled deserted nests on trails where *P. plumata* had previously nested. The nest is a vertical burrow in which the walls are lined by the females. The brood cell is linked to the outside by a tunnel filled with leaf fragments. Two caps of masticated leaves close the nest tunnel at different levels and another closes the cell. The nests were supplied with provisions of pollen and nectar and the females laid their eggs on the top of a semisolid provision mass. Adults emerged at different times of the year, which suggests that there are at least two annual generations. Prepupae of *M. assumptionis* can remain dormant in the cells either from October to March or from April to August. The nesting biology of *M. assumptionis* differs from that of the Nearctic *Megachile brevis* Say, particularly in the latter's use of several kinds of cavities and in the comparatively greater abundance and mobility of the individuals.

While the majority of bees are solitary, constructing their nests in bare, drained ground exposed to sunlight (Batra 1984; Martins and Antonini 1994; Martins et al. 1996), the family Megachilidae shows a wide range of nesting types, including species that construct free-standing nests, many that nest in the soil, and others that dig their nests in wood or plant stalks or even occupy pre-existing cavities (Michener and Szent-Ivany 1960; Krombein 1967; Bohart and Youssef 1972; Eickwort et al. 1981; Martins and Almeida 1994). The Megachilidae are also biologically interesting in the way they draw on a wide variety of material in constructing their nests, such as cut pieces of leaves and petals, chewed leaves, plant fibers, resin, clay, mud, sand, and pebbles (Stephen et al. 1969; Yanega 1994). Two other unusual features, not found in the parasitic species of this group, are the method of transporting pollen on a ventral abdominal scopa (rather than pollen-gathering hairs on the legs) and the practice of cutting pieces of leaves in constructing nests (in species of the genus *Megachile*, from which the name "leaf-cutter bees" is derived; Stephen et al. 1969; Michener 1974).

*Megachile* that nest in pre-existing cavities show differing degrees of specialization, ranging from those that nest exclusively in the empty shells of molluscs, termite nests, or deserted nests of another solitary bee species to those that use a wide variety of cavities (Michener 1953; Stephen et al. 1969; Iwata 1976; Messer 1984; Martins and Almeida 1994). The habit of using pre-existing cavities apparently has evolved, several times, from digging ancestors (Eickwort et al. 1981).

*M. assumptionis* Schrottky is at one end

of this specialization ranking, as it nests exclusively in the deserted nests of another solitary bee, in the family Apidae (=Anthophoridae), *Ptilothrix plumata* Smith. This may result either from adaptation or preadaptation and could have an influence on the ecological characteristics of the species, such as a limit to population growth (Martins and Almeida 1994).

Unfortunately, there has been a scarcity of detailed studies into the ecology and behavior of solitary bees in the Neotropics (Roubik 1989, but see Martins and Antonini 1994; Martins and Almeida 1994; Martins and Figueira 1992; Martins *et al.* 1996). In Brazil, despite the great richness of *Megachile* species (Sakagami *et al.* 1967), displaying remarkable interactions in complex and varied environments, the lack of studies has meant that knowledge of these insects is limited.

The aim of our study was to provide information on the nesting behavior and dynamics of *M. assumptionis* from the foundation of the nests to their closure, and later on, emergence of the new adults. A further objective was to compare the biology of *M. assumptionis* with that of *M. brevis*, a well-studied species in the Nearctic region (Michener 1953).

## METHODS

The work was undertaken in the Ecological Station of the Campus-Pampulha of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. This station comprises 156 ha of mixed vegetation, which is crossed by a number of trails and dirt roads, as described in Martins and Almeida (1994). Preliminary observations relating to *M. assumptionis* and its interactions with *P. plumata* were made in May 1992 but most of the present data was obtained from January 1993 to September 1994, totalling 485 hours of observation (225 and 260 hours, respectively).

The *ad libitum* and "focal individual" methods were used to study nesting behavior (Martin and Bateson 1993). A 700m trail was visited between 0900 and 1300 hours, the peak hours of bee nesting activity. From April to September visits were more frequent (at least 10 days per month). From October to March visits were more sporadic as there is usually no adult activity in this period; only routine checks were required to see whether new individuals had emerged.

We analyzed selection of nesting site, cell construction, provisioning, nest closure, mating, male patrolling, longevity and adult mobility. Captured individuals had their scutum marked with fast-drying paint. If recaptured, they were recorded, remarked if necessary, and released again.

Nesting dynamics were studied by recording every single *P. plumata* and *M. assumptionis* nest along the same trail. The nests were identified and labelled with metallic arrows (4 cm long by 5 mm wide) nailed to the ground. The arrows were either distinguished by different colours corresponding to those colours marked on their respective founding females or else marked by numbers. After the nests had been closed by the females, marked plastic cup emergence traps were nailed over the entrances to record the period of egg-adult development and emergence of brood parasites.

Twenty-three nests were excavated in 1993 and 10 in 1994 in order to study their inner structures, the material used in their construction, and the development of the immature stages. The method of determining the degrees to which water would penetrate a cell was to submerge it in water for 24 hours.

We measured height and width of six cells and tunnels and calculated average and standard deviation for all these measurements. Voucher specimens of the bee species were deposited at the Laboratório de Ecologia e Comportamento de Insetos of the Departamento de Biologia Geral, ICB-UFMG, Belo Horizonte, Minas Gerais, Brazil. Two *M. assumptionis* females were also deposited in the Snow Entomological

Museum of the University of Kansas, Lawrence, KS, USA.

## RESULTS AND DISCUSSION

*Nesting Site Selection and Cavity Occupation.*—The main factor which constrains the nesting behavior of *M. assumptionis* is the availability of *P. plumata* nests, as the former species nests exclusively in deserted nests of the latter (Martins and Almeida 1994). No females were observed either digging or nesting in any sort of potentially suitable cavities such as crevices in the soil and sand banks, termite burrows, or vacant nests of *Diadasina distincta* Holmberg (Apidae); all of these are used, for example, by *M. neoxanthoptera* Cockerell, another syntopic and cavity-generalist megachilid (Martins and Almeida 1994; Martins and Antonini 1994).

Females of *P. plumata* adopt a scattered-nesting behavior which influences the searching behavior of *M. assumptionis* females. They fly over the area and select one from a number of potentially available nests. The searching flight itself and the exact moment of selection was not observed, but the females would explore cavities and decide about its occupation by flying in a sinuous or zigzag course, close to the ground, investigating sticks and other possible nesting places, in the same way as females of *M. brevis*. The flight is continuous apart from irregular and often rather long interruptions which occur while a bee crawls into a hole (Michener 1953). The precise factors that determine whether or not *M. assumptionis* and *M. brevis* females will decide to occupy a cavity are presently unknown.

Only one kind of flight has been recognized as characteristic of *M. assumptionis* females. This flight helped to distinguish females from males (see below). It was a fast flight, about 50 cm above the ground, along the trail, without any pause for an investigation of cavities. One explanation for this flight might be that it is associated with the nest-provisioning phase.

There were two cases of reoccupation of *M. assumptionis* nests, from which adults had already emerged, apart from the occupation of deserted nests of *P. plumata*. These nests were reoccupied by other females, 2–7 days after their emergence. Nest reoccupation was not observed for *M. brevis* (Michener 1953).

The females and males have also been seen inside either deserted or active nests of *P. plumata* and even in other shallower and narrower cavities (between 1–2 cm). In these cavities, the individuals often stayed for an undefined period (from a few minutes to one hour) or even stayed overnight, with the abdomen visibly raised, close to the nest entrance. There is no evidence that either the males or the females spend the night inside their own nests, or those of conspecifics. However, *M. brevis* females spend the night in their nests and also probably hiding in curled leaves or seeking similar protection (Michener 1953). Females of *M. assumptionis* may, however, remain in the nest during strong rains. This was observed for a female that was coming back from a provisioning trip. She entered the nest tail-first and remained there with her head close to the nest entrance. When the rain had started, she exited and re-entered the nest, head first, keeping her abdomen up (the only visible part) and blocking the nest entrance. At the same time, two females of *P. plumata* were in a similar position in their own nests, next to the *M. assumptionis* nest; this behavior might be attributed to the need to protect provisions from rain water and was not observed in *M. brevis*.

*Male Patrolling Behavior.*—The males were normally seen patrolling the nesting site. They fly just above the ground, investigating a variety of cavities, such as deserted or active nests of *M. assumptionis* or *P. plumata*, nests of *D. distincta*, or any other sort of cavity. When they interrupt their flight, they may or may not stop near the cavity entrance, possibly entering as far as the level of the thorax or else com-

pletely. The time spent in a cavity varies and sometimes they are accompanied by a female who is already there, and in the morning sometimes they remain in the cavities for over an hour.

The males are able to patrol the whole of the trail extension; four individuals were located 600 m from where they had been marked. The scattered-nesting pattern influences the behavior of the males and might be one of the primary reasons for patrolling (Martins and Almeida 1994).

Males were often observed near the entrances of active nests, adopting a peculiar posture, which may be described as the "guard position". When in this posture, their wings were half-open or entirely closed. They would also perform a brief flight and then come back again soon afterwards. As this phenomenon was only observed in active nests, it can be explained by the presence of a female either provisioning or preparing the nest for provisioning.

*Mating.*—Matings were observed on the soil near the nest entrances and on flowers of *Vernonia rubriramea*. Although both sexes were promiscuous, up to 6 matings were observed for a single couple. Between one mating and the next, the male would visit flowers to drink nectar, as was seen once on a bush of *Waltheria americana* (Sterculiaceae).

The pattern of the mating process was as follows: the female remains inside the nest with the male standing in the 'guard position'. Then he enters up to the level of the thorax or half the body and probably touches the female abdomen before leaving the nest. Shortly afterwards, the female leaves too, and allows the male to mount her. He holds her body with his front legs and sometimes opens his wings before going away. Copulation lasts for about 3 seconds. Then, the female starts gathering pollen again. The male either disappears or else mates with another female in a nearby nest.

Not every male succeeds; sometimes the
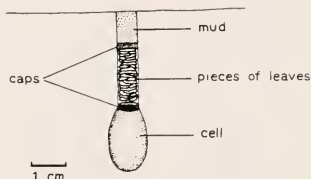


Fig. 1. Structure of a nest of *M. assumptionis*, in a deserted nest of *Ptilothrix plumata*, showing the closing "caps."

females did not allow them to approach, and even after the male had mounted, mating was not always finished because the female would fly away. When there were no females, the males would stay inside the active nests, only leaving when the resident female returned, to let them inside. Sometimes, while flying back to their nests, the females were followed by the males. On other occasions, the males would stay inside the nests, together with the females, for about one minute. There is no clear explanation for this behavior.

In *M. brevis*, males occasionally pursued the females and tried to approach them. However, not enough mating was observed during the three years of study for any definite conclusions to be drawn (Michener 1953). Apparently mating tended to occur very soon after emergence. By contrast, mating of *M. assumptionis* was observed throughout the reproductive season, with matings recorded in April (late), May (early), July (early), and August (early), and males present throughout the season.

*Cell Construction and Provisioning.*—After selecting a deserted nest, the female starts working in it, keeping the basic structure intact (Fig. 1). Cells averaged 1.55 ± 0.18 cm in height and 1.14 ± 0.06 cm in width and were linked to the outside by tunnels averaging 2.38 ± 0.55 cm in height and 0.50 ± 0.03 cm in diameter (n = 6). The female first lines the inner cell
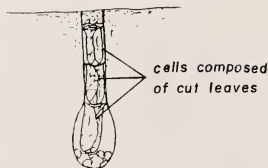
Fig. 2. Structure of the brood cells in a nest of *Megachile neoxanthoptera* in a deserted nest of *Ptilothrix plumata*.



Fig. 3. Closed nest entrance of *Megachile assumptionis*, showing the small pebbles used in the process and the intact turret.

wall, spreading a paste made of masticated leaves mixed with a presumed mandibular or salivary secretion. It is unknown whether the unusual clypeal horn of this species is used in the process. This results in a lining that eventually turns into a dry and darker thin material, hardly separable from the wall.

Due to their specialized behavior in using deserted nests of *P. plumata*, the cells of *M. assumptionis* do not follow the general pattern adopted by leaf cutter bees, as in *M. brevis* (Michener 1953), *M. neoxanthoptera* (Martins and Almeida 1994), or *M. instita* (Yanega 1994). Usually, these and other species of the same genus cut long pieces of leaves and/or petals to make brood cells in the form of an overlapped leaf structure, sometimes called a "cup", which is easily detachable (Fig. 2). These species also cut round pieces of leaves and petals to make the caps that block the nests'/cavities' entrances.

*Megachile assumptionis* does not utilize the free room available in the tunnel to construct more cells. This behavior differs from that of *M. neoxanthoptera*, which, for example, once occupied a deserted nest of *P. plumata*, with three cells placed end to end and snugly fitted (Fig. 2). In comparison, *M. brevis* may construct 1–11 cells, using all room available in the hollow (Michener 1953). After the cell has been lined, provisioning is started, the final product being a semisolid mass composed of pollen and nectar. A part of this mate-

rial comes from *Vernonia rubriramea* (Asteraceae) plants, where some females were observed gathering pollen and where bees of both sexes were seen drinking nectar. *M. brevis* uses a pollen and nectar mixture in provisioning its nests, as well (Michener 1953), as do all *Megachile* species.

When the provisioning has finished, the female lays an egg on top of the surface of the provision mass as in *M. brevis* (Michener 1953). The egg is about 5 mm long, with a similar shape but larger than that of *M. brevis*, which is 3 mm long.

Mature larvae of either species construct a cellophane-like waterproof cocoon that, in the case of *M. assumptionis*, helps preserve a favorable microhabitat during the period of immature dormancy (which is sometimes long; see below).

*Nest Closure.*—After laying the egg, the female blocks the cell entrance with a small cap, made of a mixture of chewed leaves, grains of sand and a secretion, probably glandular. Then she fills in the tunnel, just above the cell, with several layers of cut and overlapped leaves, that are pressed and compacted by the mandibles. As she cuts the leaves, the bee turns its body so that a piece is cut out with the mandibles working like scissors, in semicircular movements.

When the tunnel is filled in, the female leaves the nest, comes back with water, and then starts, close to the nest, to collect sand and/or pebbles. This material is gathered by the front legs and is then transferred to the mandibles, where it is mixed with water to produce mud. The pebbles are either obtained around the nest entrance, left over from *P. plumata* ex-
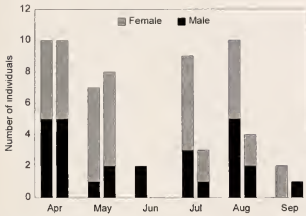
Fig. 4. Number of individuals of *Megachile assumptionis* marked in 1993 (gray bars) and 1994 (black bars).



Fig. 5. Number of nests founded by *Megachile assumptionis* in 1993 (gray bars) and 1994 (black bars).

cavation (Martins *et al.* 1996), or even taken from leaf-cutter ant colonies (*Atta* sp.). The female seems to push the mud by using her mandibles, and in this way constructs another cap, at ground level. The number of caps constructed in the nests could be 1–2. When there were 2 caps present, another layer made of cut leaves was found between them.

The process of nest closing might be interrupted by the female in order to get some nectar. This happened in the case of one female, which flew to one *V. rubriramea* close to her nest.

The last step in nest closure consists of gathering sand and/or pebbles with the mandibles and putting them together on top of the nest entrance (Fig. 3). In this process the bee avoids destroying the little turret (about 1.5 cm) constructed by the *P. plumata* female (Martins *et al.* 1996). This particular behavior of *M. assumptionis* makes clear the difference between her closed nests and those of *P. plumata*, whose females usually destroy the turret during nest closure (Martins *et al.* 1996).

*Nesting Activity, Life Span and Dormancy.*—*M. assumptionis* is a locally rare species, which makes generalizations on phenology difficult. However, observations on a total of 66 individuals in two consecutive years indicate activity from April to September (Fig. 4).

The adult population varies during the year with two peaks. The first one is in April and May and the second in July and August. During June and from September to March, the adults were hardly seen or not seen at all. For unknown reasons there was a steep fall in number between these two peaks in June in both years (Fig. 4).

During the active season, 43 and 14 nests were founded in 1993 and 1994 respectively (Fig. 5). The bees are more active from April to May and from July to August, with a sharp decrease in July and September (Martins and Almeida 1994). However, we found a smaller number of founded nests in the first portion of the second year as compared to the same time in the previous year (Fig. 4). This difference might be related to a reduced availability of nests of *P. plumata*: 404 in 1992, 275 in 1993 and 270 in 1994 (Martins *et al.* 1996). The decrease in the nesting activity might also have been due to environmental factors; drought might have made it difficult for the bees to dig their nests.

There is a time lag of 1 month between the peak of nests founded by *M. assumptionis* and *P. plumata*. This time lag in nest founding occurs because of the delay in adult emergence time resulting from *M. assumptionis* prepupal dormancy (Martins and Almeida 1994). *M. assumptionis* prepupae also become dormant throughout the rainy season, from October to January,

Table 1. Recorded emergences of *Megachile assumptionis* in 1993 and 1994.

| Egg laying date | Nest number | Emergence date | Generation | Egg laying-emergence adults interval |
|---|---|---|---|---|
| 27-04-1993 | 1 | 17-08-1993 | 2nd | 112 |
| 08-05-1993 | 2 | 23-08-1993 | 2nd | 107 |
| 09-05-1993 | 3 | 27-07-1993 | 2nd | 79 |
| 24-05-1993 | 4 | 05-08-1993 | 2nd | 73 |
| 05-07-1993 | 5 | 02-05-1993 | 1st | 302 |
| 07-07-1993 | 6 | 21-04-1993 | 1st | 289 |
| 16-08-1993 | 7 | 02-05-1993 | 1st | 260 |

Table 2. Mortality, survival and desertion of nests in *Megachile assumptionis* in 1993 and 1994 (percentage in parentheses).

| Nest status | Number of nests | |
|---|---|---|
| | 1993 | 1994 |
| Marked | 43 | 14 |
| Deserted | 1 | 2 |
| Founded | 42 (100) | 12 (100)* |
| Lost | 12 (29) | — |
| Survival | 11 (26) | 5 (50) |
| Mortality | 19 (45) | 5 (50) |

* Two nests from 1994 were left in the field.

when the first few nests are founded (Fig. 5). This dormancy can be interpreted as an adaptation or preadaptation of *M. assumptionis* which allows synchronization of the reproductive peaks between species. This synchronization is important for *M. assumptionis* reproduction because the number of available deserted nests was higher in the *P. plumata* nesting peak (Martins and Almeida 1994).

It was not possible to exactly determine the egg-adult developmental time. The reason for this is that upon reaching maturity, the larvae can halt development and stay in diapause as prepupae. However, it was possible to record the time between egg laying and the emergence of adults and make observations of the time of 7 emergences (Table 1). These intervals were either about 9 months (5–7) or 2 to 3 months (1–4).

The adult emergence pattern (n = 7) confirms that there are at least two generations per year (Table 1). The first one is represented by the progeny of the last individuals from the previous year, which remain dormant for about 9 months. Three emergences were recorded from April to May in 1994 and they correspond to nests founded in July and August in 1993. The second generation was characterized by four emergences recorded in July and August in 1993, which correspond to nests founded in April and May of the same year. Individuals of this second generation remain in dormancy for 2–3 months. On the other hand, we found one larva that had been dormant for about 7 months, in one nest founded in April 1993 that was excavated in October of the same year. This indicates a possible variability in larval developmental time, as recorded for other temperate megachilid species, called parsivoltinism by Torchio and Tependino (1982). Additionally, in species of other megachilid genera, *Prochelostoma*, *Osmia* and *Hoplitis*, a period of 2 years in dormancy has been observed (Danks 1987), indicating that *M. assumptionis* may possibly have the ability to remain in dormancy for longer than the 9 months recorded. This suggests that wide variability in emergence times recorded for other solitary bees and wasps should also be common at seasonal tropical sites (Martins *et al.* 1996; Martins unpublished data).

Survival and mortality rates were calculated from emergence and nest excavation data. Twenty-three nests were excavated in 1993 and 10 nests in 1994, with all nests containing dead individuals, mold, or lacking evidence of successful brood considered as dead and excavated nests which contained pupae or healthy larvae considered successful.

Discounting the number of lost nests, the mortality rate was 45% in 1993 and 50% in 1994 (Table 2). The causes of the high immature mortality rate are un-

known. In at least 17% of the excavations there was no sign of any cell, tunnel or immatures. Furthermore, in 1993, 12 nests were lost due to work done by a bulldozer in the study area. According to Martins *et al.* (1996), one possible reason for the loss of the contents of bee nests is ground modifications resulting from termite activity or even the intense predation by ants nesting in the vicinity.

Diptera rather than termites are more commonly known as natural enemies of solitary bees. Among them, larvae of *Anthrax* sp. (Bombyliidae) have previously been observed consuming *Megachile* larvae (Roubik 1989). Although species of *Anthrax* occurred in the nesting site of *M. assumptionis* and were recorded parasitizing *P. plumata* nests (Martins *et al.* 1996), no individuals emerged from any of the *M. assumptionis* nests. This might be partially due to parasite preference for another apid, *Diadasina distincta*, that nests in the same area and is heavily parasitized (Martins and Antonini 1994).

*Adult Longevity and Mobility.*—The recovery rate of marked bees was 45%. These figures are satisfactory when compared to those found for *M. brevis*—8% (Michener 1953). The low numbers found by this author are accounted for by the remarkable mobility of the individuals. The bees would concentrate in an attractive patch of flowers and then disperse when they ceased to bloom. The result was an apparent drop in the population size (Michener 1953). In contrast, *M. assumptionis* individuals were more sedentary, since they were locally confined to the nesting site of *P. plumata*. In 1994, for example, all recoveries occurred in the same place where the bees had been marked, indicating low mobility (Martins and Almeida 1994).

The data recorded for *M. assumptionis* show male bees may live about twice as long as females. In both years, the individuals were recovered between 2 to 48 days after being marked. In 1993, the maximum

values observed were 48 days for a male and 19 days for afemale. In 1994, the values recorded were 28 days for a male and 16 days for a female. As regards *M. brevis*, the maximum time interval between the marking and the recovery was 22 days for a male, although there is some evidence to suggest that the individuals can live for approximately one month (Michener 1953).

This also suggests that longevity in individuals of tropical solitary bee species can be longer than in temperate regions, but much more data on other species is needed to verify this possibility, as there is a lack of information (Roubik 1989).

## CONCLUSION

The behavior and nesting dynamics of *M. assumptionis* show that it is a rare species in this locality and specialized in that it uses deserted nests of *P. plumata*. Unlike most of the species in the genus whose nesting biology is known, *M. assumptionis* does not construct rows of brood cells of cut leaf pieces in natural cavities or burrows of its own making, but instead uses the pre-existing, empty cells constructed by another solitary bee, provisioning only a single cell in each nest. It may therefore experience a scarcity of suitable nesting sites and some restrictions on fecundity, and we suppose that the limiting resource in the ecology of this species is nest sites rather than pollen availability or predator/parasite pressure. In contrast, *M. brevis* is one of the commonest *Megachile* species in North America, presumably because it is so generalized in its use of nesting substrates.

## ACKNOWLEDGMENTS

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# Phylogeny of the Ammobatini and Revision of the Afrotropical Genera (Hymenoptera: Apidae: Nomadinae)

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*Abstract.*—The phylogeny of the genera of Ammobatini was studied using cladistic methods and the classification is consequently revised. The tribe forms a monophyletic group that comprises five monophyletic genera: *Pasites* Jurine, *Sphecodopsis* Bischoff, *Ammobates* Latreille, *Melanempis* Saussure and *Oreopasites* Cockerell, and one monotypic genus *Spinopasites* Warncke. They all occur in the Afrotropical Region except *Oreopasites*, and the Afrotropical species are revised. *Pasites* (*Morgania* Smith, *Omachthes* Gerstaecker and *Pasitomachthes* Bischoff, **new synonymy**) includes 17 Afrotropical species, *Sphecodopsis* (*Pseudopasites* Bischoff and *Pseudodichroa* Bischoff, **new synonymy**) 10 species, and *Ammobates* and *Melanempis* are each known from a single Afrotropical species. Ten **new species** are described (all attributed to Eardley alone): *Pasites nilssoni*, *P. paulyi*, *P. humectus*, *P. gnomus*, *P. namibiensis*, *P. somalicus*, *Sphecodopsis vespericena*, *S. longipygidium*, *S. namaquensis* and *Ammobates auster*. Thirty-four species names are **newly synonymized**: *Pasites nigerrimus* Friese and *Pasitomachthes argentatus* Baker = *Pasites barkeri* (Cockerell); *Morgania chubbi* Cockerell, *M. nigritula* Bischoff and *M. peratra* Cockerell = *Pasites friesei* Friese; *Omachthes nigripes* Friese, *Morgania fortis* Cockerell, *M. subfortis* Cockerell, *M. stordyi* Cockerell, *M. voiensis* Cockerell and *M. altior* Cockerell = *Pasites carnifex* (Gerstaecker); *M. nigrithorax* Strand = *P. dichrous* Smith; *Omachthes alboguttatus* Friese, *Morgania natalensis* Cockerell and *M. ogilviei* Cockerell = *Pasites jenseni* (Friese); *Morgania histrio transvaalensis* Bischoff, *M. alivalensis* Cockerell and *M. rufitarsis* Cockerell = *Pasites histrio* (Gerstaecker); *Morgania marshalli* Cockerell = *Pasites jonesi* (Cockerell); *Omachthes abessinicus* Friese, *Morgania fulviventris* Bischoff, *M. rhodesiana* Bischoff, *M. apicalis* Bischoff, *M. turneri* Cockerell, *M. polituta* Cockerell, *M. indecisa* Cockerell, *M. nudicauda* Cockerell, *M. bechuanica* Cockerell and *M. breviceps* Cockerell = *Pasites appletoni* (Cockerell); *Morgania rufula* Cockerell = *Sphecodopsis minutissima* (Cockerell); *Pasites pygmaeus* Friese, *Morgania leonis* Cockerell = *Sphecodopsis rufescens* Bischoff, *S. algoensis* Bischoff and *Morgania perpunctata* Cockerell = *Sphecodopsis aculeata* (Friese); *Morgania leonis* Cockerell = *Sphecodopsis semirufa* (Cockerell). Keys to the genera and Afrotropical species are provided.

The purpose of this study is to provide a comprehensive revision of the systematics of the Afrotropical Ammobatini (Apidae: Nomadinae). To attain this objective, three main aspects were investigated. The first was to establish whether the Ammobatini is a monophyletic taxon and, in so doing, establish its validity. The second was to review the generic classification of the Ammobatini and gain an understanding of the relationships among the genera. The third was to acquire a sound knowledge of the identity of the Afrotropical species and the relationships between species.

The Ammobatini are cleptoparasitic bees, also known as cuckoo-bees. They lay their eggs in the nests of pollen-collecting bees that provision each larval cell with sufficient food for the larva to develop to maturity. Like other Nomadinae, the ammobatines lay each egg in a hole in the wall of the host's larval cell. When the egg hatches the tiny mobile first-instar larva,

which has elongate sharp-pointed mandibles, kills the host larva or egg and then consumes the food provided for the host. An outstanding account of cleptoparasitism is given by Alexander (1990).

Pollinating bees are one of the most important groups of beneficial insects. It is therefore important to study the systematics and biology of their cleptoparasites because they affect the population dynamics of pollen-collecting bees. Bees of the ammobatine genus *Sphecodopsis* Bischoff, for example, are known to parasitise species of *Scrapter* Lepeletier & Serville (Rozen & Michener 1968). Both of these genera are endemic to southern Africa. *Scrapter* species pollinate indigenous plants and are potentially important in the pollination of agricultural crops. The genus is prevalent in the semi-arid regions of southern Africa where insect-pollinated indigenous plants form an important component of the ground cover and pasture.

Cleptoparasitism among bees is a derived trait and it has evolved independently several times within the bees (Alexander 1990). The features that are unique to cleptoparasitic bees, such as the loss of the scopa, are derived, although they may resemble the primitive state for the bees as a whole. Other features that separate cleptoparasitic bees from pollen-collecting bees are the thickened integument and the more robust sting (Alexander 1990). There are many other convergent traits in the cleptoparasitic bees which, as indicated by Alexander (1990), complicate attempts to trace their phylogeny.

In spite of the difficulties involved in the study of the phylogeny of cleptoparasitic bees, the Nomadinae, the largest and most diverse lineage of cleptoparasitic bees (about 1200 described species), has been well studied by Rozen (1966, 1974, 1977, 1991), Rozen et al. (1978), Roig-Alsina (1987, 1991), Alexander (1990) and Roig-Alsina & Michener (1993). Roig-Alsina (1991), Rozen (1991) and Roig-Alsina

& Michener (1993) defined the Nomadinae to include only those genera that comprise a monophyletic group, namely the Ammobatini, Ammobatoidini (including *Holcopasites* Ashmead), Biastini, Caenoprosopidini, Epeolini, Neolarrini, Townsendiellini, Hexepeolini, Nomadini and Brachynomadini. Other groups that were previously included in the Nomadinae (now Anthophorinae) are: Isepeolini, Protepeolini, Osirini (including Epeoloidini and *Parepeolus* Ducke, Roig-Alsina 1989) and *Coelioxoides*, now in the Tetrapediini (Alexander 1990, Roig-Alsina & Michener 1993).

The Nomadinae has its greatest diversity in the Nearctic and Neotropical Regions, is fairly well represented in the Afrotropical and Palaearctic Regions and is poorly known from the Oriental and Australian Regions. In the Afrotropical Region, it comprises four tribes: Nomadini, Epeolini, Ammobatoidini and Ammobatini. The Nomadini, Epeolini and Ammobatoidini are represented there only by their nominate genera. The Nomadini and the Epeolini were revised by Eardley & Schwarz (1991) and Eardley (1991), respectively. The Ammobatoidini is known from the Afrotropical Region from a single female specimen described as *Ammobatoides braunsi* Bischoff. The Ammobatini is the largest and most diverse tribe of Afrotropical nomadine bees.

The Ammobatini occur mainly in the Nearctic, Palaearctic and Afrotropical Regions. Although they have not been recorded from the Oriental Region, several Palaearctic species are known from areas that border the Oriental Region and these species possibly extend into that Region. They do not occur in the Neotropical and Australian Regions. The Nearctic (Rozen 1992) and Palaearctic (Warncke 1983) faunas have been well studied and the Afrotropical fauna is revised here.

Most of the previous work on the systematics of the Afrotropical Ammobatini consists of descriptions of new species and

distribution records. The original descriptions are generally vague, without illustrations and inadequate for the recognition of the species. Bischoff (1923) provided a comprehensive revision of the Afrotropical Ammobatini, but his work has several shortcomings (e.g., he did not study much of the type material and it has become outdated. The present study is the first treatment of these bees that has included an examination of nearly all the type material and a study of male and female terminalia.

Authorship of the new species described in this paper is attributed to CDE only.

## HISTORICAL REVIEW OF THE AMMOBATINI

The history of the classification of this group of closely related bees may be outlined as follows. An early attempt to arrange them into a system of higher classification was by Dalla Torre (1896). He placed all bees in the family Apidae and placed the genera that are currently considered to belong to the Ammobatini, namely *Ammobates* Latreille, *Pasites* Jurine and *Omachthes* Gerstaecker, together with several other genera, in the subfamily Coelioxyinae. Ashmead (1899) divided the Apidae into several families and transferred the Coelioxyinae to the family Stelidae, which included most of the parasitic bees.

Michener (1944) provided the first comprehensive study in which bees were assigned to tribes. He placed *Oreopasites* Cockerell, *Ammobates*, *Morgania* Smith, *Omachthes* and *Pasites* in the tribe Ammobatini (Apidae: Anthophorinae). Michener (1944) also suggested that *Caesarea* Friese, *Melanempis* Saussure, *Parammobatodes* Friese, *Pasitomachthes* Bischoff, *Pseudodichroa* Bischoff and *Sphecodopsis* Bischoff might belong in the Ammobatini.

Popov (1951) divided Michener's (1944) Ammobatini into two distinct tribes, the Ammobatini and the Pasitini, placed in

the subfamily Anthophorinae of the family Anthophoridae. Popov's Ammobatini contained the genera *Ammobates* (for which he described two new subgenera, *Xerammobates* Popov and *Euphileremus* Popov), *Caesarea*, *Parammobatodes* Popov and *Oreopasites*. His Pasitini consisted of *Pasites*, *Morgania*, *Omachthes*, *Pseudopasites*, *Sphecodopsis*, *Pasitomachthes* and *Pseudodichroa*. He made no mention of *Melanempis*. Sûstera (1958), in contrast, placed the Nomadini, Ammobatini and Pasitini in the Andrenidae.

Baker (1971), in his discussion on *Pasitomachthes*, supported Popov's (1951) classification. Rozen & McGinley (1974) found evidence in their study on the systematics and phylogeny of the larvae of these bees that *Oreopasites* and *Pasites* are closely related, with *Ammobates* somewhat divergent and *Sphecodopsis* farthest away.

Warncke (1983), in a revision of the Palaearctic fauna, took a completely different approach and placed almost the entire Palaearctic and Afrotropical faunas of ammobatine bees (*sensu* Michener) into the genus *Pasites*, which he subdivided into six subgenera: *Parammobatodes*, *Spinopasites* Warncke, *Micropasites* Warncke, *Euphileremus*, *Ammobates* and *Pasites*. He considered *Morgania*, *Omachthes*, *Pasitomachthes*, *Pseudopasites* and *Sphecodopsis* to be junior synonyms of *Pasites* (*sensu stricto*). Warncke (1983) did not give a detailed explanation for his actions and made no mention of *Oreopasites* and *Melanempis*, except that in changing the name *Phileremus ater* Saussure (= *Melanempis atra*) to *Pasites madagascarensis* he indicated that he considered *Melanempis* to be a synonym of *Pasites*.

Subsequent to Warncke's (1983) study, the tribal classification of the Nomadinae, based on adult morphology, was studied by Roig-Alsina (1987, 1991) and Alexander (1990), neither of whom adopted Warncke's (1983) classification. Roig-Alsina (1987), in his discussion on the phylogenetic relationship between the Caeno-

prosopidini, Biastini and Ammobatini, defined the Ammobatini in the 'sense of Michener (1944)'. Alexander (1990), in his table on the distribution and host records of the Nomadinae, stated that he did not use Warncke's (1983) classification because he had not studied the group in sufficient detail. Rozen (1992) discussed the tribal characters in detail without recognising either tribes.

Roig-Alsina (1987, 1991) and Alexander (1990) demonstrated that the Caenoprosopidini is the sister group of the Ammobatini. In the Ammobatini the sixth metasomal sternum (S6) of the female is bifurcate or secondarily simple posteriorly, and in the Caenoprosopidini this structure is bilaterally separated. The inference, by the above mentioned authors, that the bifurcate female S6 in the Ammobatini gave rise to the bilaterally separated condition in the Caenoprosopidini implies that the Caenoprosopidini is a monophyletic group. The monophyly of the Ammobatini, however, was not demonstrated by either Roig-Alsina (1987, 1991) or Alexander (1990).

In his studies on the phylogeny of the Nomadinae, Roig-Alsina (1987) demonstrated the sister taxon of the (Ammobatini + Caenoprosopidini) clade to be the Biastini. Alexander (1990), however, indicated that the Neolarrini was possibly the sister group of this clade. Subsequently Roig-Alsina (1991), using different characters, came to the same conclusion as Alexander (1990). The absence of a pygidial plate, as mentioned by Roig-Alsina (1987) is not a synapomorphy of the ((Ammobatini + Caenoprosopidini) + Biastini), as several species of *Pasites* have well developed pygidial plates. Recently, Roig-Alsina & Michener (1993) considered them to belong in the Apidae. The current familial placement of these bees, a topic that is beyond the scope of the study, has been accepted.

## MATERIALS AND METHODS

In an attempt to demonstrate the monophyly of and elucidate the generic classification of the Afrotropical Ammobatini, all the known Afrotropical species (represented by over 800 specimens) and all available extra-African representatives of the tribe (183 specimens from the Palaearctic and Nearctic Regions) were studied. All the available type material of the Afrotropical species was examined during the course of the study. The type material of eight species was not studied because it could not be obtained: *Pasitomachthes argentatus* Baker was identified from the detailed description and comparison with type material of other species; *Omachthes capensis* Friese, *Pseudodichroa fumipennis* Bischoff and *Phileremus (Melanempis) ater* Saussure were reliably identified from authoritatively determined material; *Pasites atratulus* Friese, *Omachthes gabonensis* Vachal, *Morgania rotundiceps* Bischoff and *Morgania tropica* Cockerell remain *incertae sedis*. The study of extra-African taxa was based mostly on previously determined material. Information on the labels of type specimens is recorded verbatim from the labels. For other material, the locality, date, collector and floral record are given in that sequence. The **distribution** records of material that was not studied are given under 'Other published distribution records'. **Vegetation types** are from White (1983). The **acronyms** for the museums from which material was borrowed are listed in the acknowledgements section. Where geographic coordinates are given, they are in degrees and minutes (separated by a period), not decimal degrees. Where reference is made to 'the Code', this means the International Code of Zoological Nomenclature, 3rd Edition (International Commission on Zoological Nomenclature 1985).

**Morphology.**—The terminology mainly follows that of Michener (1944). Sexual dimorphism in adult Ammobatini is slight

and, apart from *Sphecodopsis*, *Oreopasites*, *Melanempis* and *Spinopasites* in which males have eleven flagellar segments, is largely confined to the posterior region of the metasoma. A single detailed description for both sexes of each species has therefore been given, with the diagnostic sex-limited characters of each sex explicitly described. The abbreviations **T** and **S** are used for the metasomal terga and sterna, respectively (e.g. T1 and S1 refer to the first metasomal tergum and sternum, respectively). **Vestiture** generally refers to the relatively fine hairs and where setae are specifically mentioned these are thicker hairs. The sixth metasomal tergum of the female of some species has a brush posteriorly (located below the pygidial plate when this structure is present). This brush has been referred to as the **subpygidial brush** (Fig. 6); when it has thick hairs dorsally and fine vestiture ventrally it has been referred to as differentiated. In certain taxa the posteromedian region of the **fifth metasomal sternum** of the female, when viewed from behind, forms a distinct furrow. Rozen's (1968a) terminology has been used for this structure which he referred to as being 'gutter-like'. In the illustrations of the **male terminalia** the anterior end is at the bottom and the posterior end is at the top.

**Cladistics:** Adults of each included species were thoroughly examined and each character for which distinct states occurred in different species was included in the matrix. Polarization of characters was based strictly on out-group comparison and the putative sister group was taken as the out group. In the analysis attempting to demonstrate the monophyly of the Ammobatini as a whole, the sister group of the Ammobatini, the Caenoprosopidini, was included in the in group. The Neolarrini (represented by *Neolarra vigilans* (Cockerell)), which is the sister group of (Ammobatini + Caenoprosopidini) (Roig-Alsina 1991), was then taken as the out group. For one character (50) the state in

the Neolarrini was entirely different from that in the (Ammobatini + Caenoprosopidini), and the sister group of the (Neolarrini + (Ammobatini + Caenoprosopidini)), the Townsendiellini (Roig-Alsina 1991) (represented by *Townsendiella californica* Michener) was used to polarize that character (the relationships between the Ammobatini + Caenoprospidini and the Neolarrini, Townsendiellini and Ammobatoidini were questioned by Alexander (pers. comm.) following additional research, however). Where a possible evolutionary progression could be determined between different states of a character within the in group, successive derived states (0 = primitive; 1, 2 & 3 = successive derived states), with nonadditive binary coding, was used.

The different states of each character were incorporated in data matrices. A question mark (?) was used where the state in a species could not be studied, such as sex-limited characters for species in which the appropriate sex is unknown or was not available for study. In order to root the cladogram, a hypothetical ancestor with all characters coded as 0 was added. The first matrix (Table 1) gives all the relevant information on each species. In the formation of the second data matrix (Table 2) some species were grouped into species groups (reasons given below), each of which is represented by the ground plan of that group (derived as explained below). The third matrix (Table 4) includes only ground plans of the genera and was derived from the second matrix.

Cladograms were generated using Hennig86, version 1.5 (Farris 1988). The first, second and fourth cladograms (Figs. 1, 2 & 4) originate from the analysis of the information in Tables 1, 2 & 4, respectively, without using character weighting (commands m*; bb*). The third cladogram (Fig. 3) resulted from the use of successive approximations character weighting (repeated application of m*; bb*; xs w) in the analysis of the information in Table 2.

Table 1.  Data matrix of character states for species (characters and coding of states according to Appendix 2).

| Taxon | Characters | | | | | |
|---|---|---|---|---|---|---|
| Ancestor | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 00000000 |
| *Sph. capicola* | 2001111101 | 0110010001 | 0012110100 | 1000010001 | 1001001101 | 10000000 |
| *Sph. vespericena &* | | | | | | |
| *Sph. longipygidium* | 20011111?1 | 0110010001 | 0012110110 | 1000010001 | 1001001101 | 1???????? |
| *Sph. villosa* | 2001111101 | 0110010001 | 0012110100 | 100001???? | ?????????? | ?0000000 |
| *Sph. namaquensis* | 2001111171 | 0110010001 | 0012110100 | 1000010001 | 1001001101 | 1??????? |
| *Sph. minutissima* | 2001111001 | 0110010001 | 0012111100 | 1000010001 | 1001001101 | 10000000 |
| *Sph. aculeata* | 2001111101 | 0110010001 | 0012110100 | 1000010001 | 0001001101 | 10000000 |
| *Sph. semirufa* | 2001111101 | 0110010001 | 0012110100 | 1000010001 | 0001001201 | 10000010 |
| *Sph. capensis &* | | | | | | |
| *Sph. fumipennis* | 2001111?1 | 0110010001 | 0012110100 | 1000010001 | 0001002301 | 2??????? |
| *P. barkeri* | 1001100011 | 0110010101 | 0021001010 | 1010010000 | 0110010001 | 10000000 |
| *P. friesei* | 1001100011 | 0110010101 | 0021001010 | 1110110100 | 0110010001 | 10010000 |
| *P. nilssoni* | 1001100011 | 0110010101 | 0021001010 | 1?1011???? | ?????????? | ?0010000 |
| *P. paulyi* | 1001100011 | 0110010101 | 0021001000 | 1110110100 | 0210010001 | 10010000 |
| *P. braunsi* | 1001100071 | 0110010101 | 0021001010 | 1110110100 | 0210010001 | 1??????? |
| *P. humectus* | 1001100011 | 0110010101 | 0021001000 | 1110110110 | 0110010001 | 10010000 |
| *P. bicolor* | 1001100011 | 0110010101 | 0021001010 | 1010110110 | 0110010001 | 10010000 |
| *P. tegularis* | 1001100011 | 0110010101 | 0021001010 | 1010110100 | 0110010001 | 10010000 |
| *P. gnomus* | 1001100011 | 0110010001 | 0021001000 | 1110010000 | 0110010001 | 12010100 |
| *P. carnifex* | 1001100011 | 0110010101 | 0022110100 | 1110010000 | 0210010001 | 10000000 |
| *P. dichrous* | 1001100011 | 0110010101 | 0022110110 | 1110010000 | 0210010001 | 10010010 |
| *P. jenseni & P. histrio* | 0011100011 | 0110010101 | 0011001010 | 1110010000 | 0210020001 | 10000000 |
| *P. namibiensis & P. jonesi* | 0111100012 | 0110012101 | 0011001010 | 1110010000 | 0210020001 | 10000000 |
| *P. rufipes* | 2001111?1 | 0110010101 | 0022110010 | 0111001000 | 0210020001 | 1??????? |
| *P. appletoni* | 1001100011 | 0110010101 | 0021001010 | 1110010100 | 0210020001 | 10000000 |
| *P. somalicus* | 1001100071 | 0110010101 | 0021001010 | 1110010100 | 0210020001 | 1??????? |
| *P. maculatus* | 1011100011 | 0101010101 | 0021001010 | 1111010000 | 0210020001 | 10000000 |
| *Spi. spinotus* | 1001100071 | 0100010111 | 0021001000 | 1100000001 | 0001001201 | 2??????? |
| *M. atra* | 2101100112 | 1001011111 | 0022110010 | 0000001010 | 0001001301 | 10010000 |
| *O. vanduzeei* | 1001100002 | 1000011011 | 0020010000 | 1100010001 | 0001001201 | 11000000 |
| *O. linsleyi* | 1001100002 | 1000021011 | 0020010000 | 1100010001 | 0001001201 | 11000000 |
| *A. verhoeffi* | 1001100002 | 1000011111 | 0021000000 | 0010010001 | 0000101211 | 11000010 |
| *A. rostratus* | 0111100002 | 1000010111 | 0020001000 | 0110000001 | 0001101211 | 11000010 |
| *A. robustus* | 0111100002 | 1007?10111 | 0020001000 | 01??????01 | ?????????? | ???????? |
| *A. teheranicus & A. baueri* | 0111100002 | 1000010111 | 0020001000 | 0110000001 | 0001101211 | 1??????? |
| *A. hipponensis* | 0111100002 | 1000011111 | 0020001000 | 0?1000???? | ?????????? | ?1000010 |
| *A. mavromoustakisi* | 0111100002 | 1000010111 | 0020001000 | 1110000001 | 0001101211 | 10000010 |
| *A. handlirschi* | 0111100002 | 1007?11011 | 0020001000 | 111000???? | ?????????? | ?1000010 |
| *A. depressus* | 0111100?2 | 1000010111 | 0020001000 | 0100000001 | 1000101211 | 11000020 |
| *A. punctatus* | 1011100002 | 1000010111 | 0020001000 | 0110010101 | 0000101211 | 11000000 |
| *A. ancylae* | 1111100002 | 1007?10111 | 0020001000 | 1110010001 | 0000101201 | 11000020 |
| *A. solitarius* | 1011100?2 | 1000010111 | 0020001000 | 1110010001 | 0000101201 | 1??????? |
| *A. vinctus* | 1011100?2 | 1000010111 | 0020001000 | 1110010001 | 0000101211 | 11000010 |
| *A. auster, A. similis,* | | | | | | |
| *A. niveatus & A. syriacus* | 1011100002 | 1000010111 | 0020001000 | 1110010001 | 0000101201 | 11000010 |
| *A. rufiventris* | 1011100002 | 1000011111 | 0020001000 | 1110010001 | 0000101201 | 11000010 |
| *A. iranicus* | 1011100002 | 1000011111 | 0020001000 | 1110010001 | 0000101201 | 11000020 |
| *A. dubius* | 1011100002 | 1000010111 | 0020001000 | 1110010001 | 0000101201 | 11000020 |
| *A. assimilis* | 1011100002 | 1000010111 | 0020001000 | 111001???? | ?????????? | ?1000020 |
| *A. opacus* | 1011100?2 | 1007?10111 | 0020001000 | 1110010001 | 0000101201 | 1??????? |
| *A. armeniacus* | 1011100002 | 1007?10111 | 0020001000 | 1110010001 | 0000101201 | 11000020 |
| *A. sanguineus* | 1011100002 | 1000010111 | 0020001000 | 1110010001 | 0000101201 | 11000020 |
| *A. biastoides* | 0001100002 | 1000010111 | 0020001000 | 1111010001 | 0000101201 | 11000010 |

Table 1. Continued.

| Taxon | Characters |
|---|---|
| A. persicus | 1011100002 1000010111 0020001000 1010010001 0000101201 1100?010 |
| A. minutus | 1001100012 1000011111 0020001000 1110010001 0000101201 1100100? |
| A. orientanus | 1001100012 0100010001 0020001000 1110010001 0000101201 1100?0?0 |
| A. aegyptiacus | 1001100002 0100010001 0020001000 11???10001 00??????21 1??????? |
| A. muticus | 1011100002 1000010111 0022011000 1100011001 0000101101 1100001? |
| A. oraniensis | 1011100002 1000010111 0022011000 1100011001 00001012?1 2?0??0?1 |
| A. latitarsis | 1011100002 1000010111 0022011000 1100011001 0000101201 1107??7? |
| A. oxianus | 1001100006 000??10101 1020001000 1110010001 0000101201 11000?0? |
| A. lebedevi | 1001100021 1000?10111 1020001000 1110010001 0000101201 1??????? |
| C. crabronina | 2010011001 0000101110 1110001101 0010010001 1000000002 10101001 |

Character weighting was applied to give an indication of which cladogram derived without weighting might be preferred. (For the fourth analysis, using the data in Table 4, only one most parsimonious tree was obtained (Fig. 4), making successive approximations character weighting unnecessary.) Plotting of characters on the cladograms was done using Clados, version 1.2 (Nixon 1992) the accelerated transformation option, a criterion of Farris (1970) in which reversals are maximised and parallelisms minimized. On theoretical grounds this approach was preferred by Pinna (1991). Characters for which states are unknown in some taxa were 'squeezed' (Nixon 1992) to avoid the indication of apparent synapomorphies based only on sharing of missing states. Each homoplastic state was considered individually to determine whether the homoplasy could be more appropriately explained by a parallelism rather than by a reversal, but no such state was found.

During the characterization of the species and species groups only adult morphological characters were taken into account, as insufficient larval material was available. Some larvae were investigated by Eardley (1994), but no synapomorphies were found. In spite of the excellent work on ammobatine larvae by Rozen (1954, 1966), Rozen & McGinley (1974) and Rozen & Roig-Alsina (1991), Rozen & McGinley (1974) clearly stated that insuffi-

cient data were available on ammobatine larvae for a phylogenetic analysis of the tribe, and little additional information has subsequently accrued.

The reason for not including zoogeographical information is that it is not genetic but historical, and therefore should not be included in the analysis of the genealogy. It was, however, used to evaluate the results of the study.

The initial analysis (all species considered separately) resulted in over 1200 equally parsimonious cladograms, and the strict consensus tree had several polytomies, some of which contained numerous branches (Fig. 1). The polytomies made it difficult to analyze the result. The optimisation and placement of characters on consensus trees is often problematic because of the conflicts in the underlying data; the character distributions shown (in Figs. 2 & 3) should thus be treated appropriately.

A study of the species data matrix (Table 1) indicated that missing data, such as the sex-limited characters for species only known from one sex, contributed significantly to the poor resolution of the cladogram. This problem was overcome to a large extent by grouping morphologically similar species into species groups. Appendix 1 is a list of the species that were studied and their groupings. Species were generally grouped on the basis of overall similarity of the characters coded in Ap-

Table 2. Data matrix of character states for species groups (characters and coding of states according to Appendix 2).

| Taxon | Character | | | | | |
|---|---|---|---|---|---|---|
| Ancestor | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 00000000 |
| *Sph.* capicola group | 2001111101 | 0110010001 | 0012110100 | 1000010001 | 1001001101 | 10000000 |
| *Sph.* minutissima | 2001111101 | 0110010001 | 0012111100 | 1000010001 | 1001001101 | 10000000 |
| *Sph.* aculeata | 2001111101 | 0110010001 | 0012110100 | 1000010001 | 0001001101 | 10000000 |
| *Sph.* semirufa | 2001111101 | 0110010001 | 0012110100 | 1000010001 | 0001001201 | 10000010 |
| *Sph.* capensis group | 2001111171 | 0110010001 | 0012110100 | 1000010001 | 0001002301 | 2???????? |
| *P.* barkeri | 1001100011 | 0110010101 | 0021001010 | 1010010000 | 0110010001 | 10000000 |
| *P.* friesei group | 1001100011 | 0110010101 | 0021001000 | 1110110100 | 0110010001 | 10010000 |
| *P.* gnomus | 1001100011 | 0111010001 | 0021001000 | 1110010000 | 0110010001 | 12010100 |
| *P.* carnifex group | 1001100011 | 0110010101 | 0022110100 | 1110010000 | 0210010001 | 10010000 |
| *P.* jenseni group | 0011100011 | 0110010101 | 0011001010 | 1110010000 | 0210020001 | 10000000 |
| *P.* rufipes | 2001111171 | 0110010101 | 0022110010 | 0111001000 | 0210020001 | 1??????? |
| *P.* appletoni group | 1001100011 | 0110010101 | 0021001010 | 1110010100 | 0210020001 | 10000000 |
| *P.* maculatus | 1011100011 | 0110010101 | 0021001010 | 1111010000 | 0210020001 | 10000000 |
| *Spi.* spinotus | 1001100071 | 0100010111 | 0021001000 | 1100000001 | 0001001201 | 2??????? |
| *M.* atra | 2101111102 | 1001011111 | 0022110010 | 0000011010 | 0001001301 | 10010000 |
| *O.* vanduzeei group | 1001100002 | 1000011011 | 0020010000 | 1100010001 | 0001001201 | 11000000 |
| *A.* verhoeffi | 1001100002 | 1000010111 | 0021000000 | 0010010001 | 0000101211 | 11000010 |
| *A.* rostratus group | 0111100002 | 1000010111 | 0020001000 | 1110000001 | 0000101211 | 11000010 |
| *A.* punctatus group | 1011100002 | 1000010111 | 0020001000 | 1110010001 | 0000101201 | 11000010 |
| *A.* biastoides | 0001100002 | 1000010111 | 0020001000 | 1111010001 | 0000101201 | 11000010 |
| *A.* persicus | 1011100002 | 1000010111 | 0020001000 | 1010010001 | 0000101211 | 11000010 |
| *A.* minutus | 1001100012 | 1000011111 | 0020001000 | 1110010001 | 0000101211 | 11001020 |
| *A.* orientanus group | 1001100012 | 0100010001 | 0020001000 | 1110010001 | 0000101201 | 11001020 |
| *A.* muticus group | 1011100002 | 1000010111 | 0022011000 | 1100011001 | 0000101201 | 11000010 |
| *A.* oxianus group | 1001100001 | 1000?10111 | 1020001000 | 1110010001 | 0000101201 | 11000020 |
| *C.* crabronina | 2010011001 | 0000101110 | 1110001101 | 0010010001 | 1000000001 | 10101001 |

pendix 2. Where different states of a character were found in a single putative group each character was considered in the light of the degree of homoplasy found in an analysis of the entire data matrix (Table 1), and each group was delimited to ensure that only characters which are also homoplastic elsewhere are those which have different states in the group. For *Oreopasites*, whose species were not studied in detail, the two species groups represent the two subgenera (Rozen 1992). As much of the missing data was among the sex-limited characters of species of which only one sex was available, the assumption was made that species that closely resembled one another in one sex would be similar in the opposite sex. Because the grouping was done primarily to overcome the problem of missing data, it was done conservatively to minimise the

possibility of grouping species for which the states of the opposite sex were different. Known intra-group differences represent highly homoplastic states that appeared to have little significance in grouping species in this tribe.

The grouping of species required the development of a ground plan of character states for each species group. This was done by first developing a ground plan comprising the most primitive state of each character that occurs in that species group. The resultant data matrix was analyzed (command used: m*) and the tree length recorded. Then, for each character for which more than one state occurs within the species group the matrix was systematically altered, taking one character at a time, by replacing the primitive state with the derived state (for characters represented by more than two states in a

Table 3. Weight assigned to each character during analysis of data in Table 2 after successive approximations character weighting (maximum weight = 10).

| Weight | Character |
|--------|-----------|
| Weight 10: | 4, 5, 15, 16, 20, 21, 22, 30, 35, 39, 42, 43, 45, 47, 49, 50, 53, 56, 58. |
| Weight 5: | 10, 46, 48, 52, 57. |
| Weight 4: | 9, 25, 29, 44. |
| Weight 3: | 23. |
| Weight 2: | 6, 7, 8, 11, 13, 26, 28, 33, 40, 41, 54, 55, 57. |
| Weight 1: | 1, 12, 18, 19, 24, 32. |
| Weight 0: | 2, 3, 14, 17, 27, 31, 34, 36, 37, 38, 51. |

single species group, the matrix was altered in a stepwise manner from the most primitive to the most derived state). After each alteration the resultant matrix was re-analyzed and the tree length compared with that of the former analyses. The data set that gave the shortest tree was chosen. Where the different states provided cladograms of equal length, each state was studied for evidence suggesting which state was primitive for the group. In the absence of such evidence the more primitive state was chosen. This procedure was repeated for each species group.

For *Ammobates*, in the oxianus group the more derived state for characters 10, 11 & 19 gave the shortest tree (i.e., state 1). In both the rostratus and punctatus groups the more derived state for character 31 (i.e., state 1) and in the rostratus group for character 52 (i.e., state 2) gave a shorter tree and was therefore preferred. In the punctatus group character 57 is represented by three different states (i.e., states 0, 1 & 2), of which state 1 gave the shortest tree.

The same approach was adopted in the development of ground plans for the genera (Table 4), which resulted in the more derived state (i.e., state 1) being preferred for two characters in *Ammobates*. For character 1 states 0 and 1 gave trees of similar length. State 1 was preferred because it is apparently more primitive for the group, being reversed in *A. rostratus*. In *Ammobates* state 1 is more common and this state also occurs in *Spinopasites* and *Oreopasites*, whereas state 2 occurs in (*Melanempis* + *Sphecodopsis*) (Fig. 2). For character 31 the derived state (i.e., state 1) gave the shortest tree.

## PHYLOGENY OF THE AMMOBATINI

As indicated above, an analysis including all species separately was not successful because of missing data. The analysis of ground-plan adult character states (Appendix 2) of the species groups (Table 2), however, resulted in 48 most parsimonious cladograms, each with a length of 154 steps. The study of each of these 48 trees, and the strict consensus tree (Fig. 2) indicated a con-

Table 4. Data matrix of character states for genera (characters and coding of states according to Appendix 2).

| Taxon | Characters |
|-------|-----------|
| Ancestor | 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 |
| Sphecodopsis | 2001111101 0110010001 0012110100 1000010001 0001001101 1000000000 |
| Pasites | 0001100011 0100010101 0011000000 0010000000 0110001002 1000000000 |
| Spinopasites | 1061100021 0100010111 0021001000 1100000001 0001001201 1001017 |
| Melanempis | 2121111102 1001011111 0022110010 0000001010 0001001301 1001000 |
| Oreopasites | 1001100002 1000011011 0020010000 1100010001 0001001201 1100000 |
| Ammobates | 1001100002 0000010111 0020000002 1100000001 0000101201 1100000 |
| Caenoprosopis | 2010071001 0000101110 1110001101 0010010001 1000000002 1010100 |

sistent pattern of seven major clades. The basal branch consistently represented the Caenoprosopidini, which was included in an attempt to demonstrate the monophyly of the Ammobatini, while the other six major clades more or less represented the ammobatine genera as defined by Michener (1944). The consistency in the composition of these six clades led to their being considered here to constitute genera (*Pasites, Spinopasites, Oreopasites, Ammobates, Sphecodopsis* and *Melanempis*, Fig. 1). Most of the trees differed only in the relative positions of the species groups within each clade.

Analysis of the data using successive approximations character weighting resulted in 12 most parsimonious trees, each with a raw length of 156 steps. The differences in the lengths of the trees produced with and without character weighting apparently resulted from the different configurations of the species groups within each genus and not from differences in the configuration of the genera. The final weight assigned to each character in the weighted analysis is recorded in Table 3.

The only difference in the relationships between the genera in the 48 most parsimonious unweighted cladograms was the relative position of *Oreopasites*. In some of the cladograms it formed the sister group of *Ammobates*, with (*Sphecodopsis* + *Melanempis*) as the sister group of (*Ammobates* + *Oreopasites*) (Fig. 3), while in the other cladograms it formed the sister group of (*Sphecodopsis* + *Melanempis*), with *Ammobates* as the sister group of (*Oreopasites* + (*Sphecodopsis* + *Melanempis*)). This resulted in a polytomy for *Oreopasites, Ammobates* and (*Sphecodopsis* + *Melanempis*) in the consensus tree (Fig. 2). The position of *Oreopasites* in the consensus tree, produced using successive approximations character weighting (Fig. 3), was the same as that which occurred most frequently among the trees produced without character weighting and was accepted as the most probable phylogeny. Evidence supporting this choice is the reduction in the male pygidial plate (state 52.1), which associates *Ammobates* and *Oreopasites* and was given a weight of 5 in the analysis using successive approximations character weighting (Table 3). The mandibles posterolaterally directed in repose (18.0) and the undifferentiated vestiture on the ventrolateral region of the mesepisternum (27.0), which group *Oreopasites* with (*Melanempis* + *Sphecodopsis*), have weights of 1 and 0 respectively (Table 3). The grouping of *Oreopasites* with *Ammobates* can also be more easily explained when considering the biogeography of these bees, the former genus is Neotropical and the latter mainly Palaearctic, where as the other ammobatine genera are primarily Afrotropical.

The analysis of generic ground plans (Table 4), without character weighting, gave a single most parsimonious tree (Fig. 4). The configuration of the tree differs from that produced by the former analyses (Figs. 1–3) only in the placement of *Spinopasites*. The difference is significant because it makes *Oreopasites* the sister group of *Ammobates*, whereas in the analysis of species and species groups *Oreopasites, Ammobates* and (*Melanempis* + *Sphecodopsis*) (Figs. 2 & 3) are more closely related to one another than to *Spinopasites*. The reason for the change is that in the generic ground plans of *Spinopasites, Oreopasites* and *Ammobates* the hind tibia has thick setae (32.1) and the posteromedian region of the female S5 has a distinct protuberance (48.2). In *Sphecodopsis* and *Melanempis* the hind tibia has fine vestiture (32.0). *Sphecodopsis* has a small posteromedian protuberance on the female S5 (48.1) and *Melanempis* has a large, gutter-like protuberance (48.3), making the derivation of the posteromedian protuberance on the female S5 dichotomous. Because of the absence of information on the male of *Spinopasites* it is possible that discovery of the male may alter the interpretation of the relationship between *Spinopasites* and its congeners.

Discussion of the generic relationships is based mainly on the cladogram of the
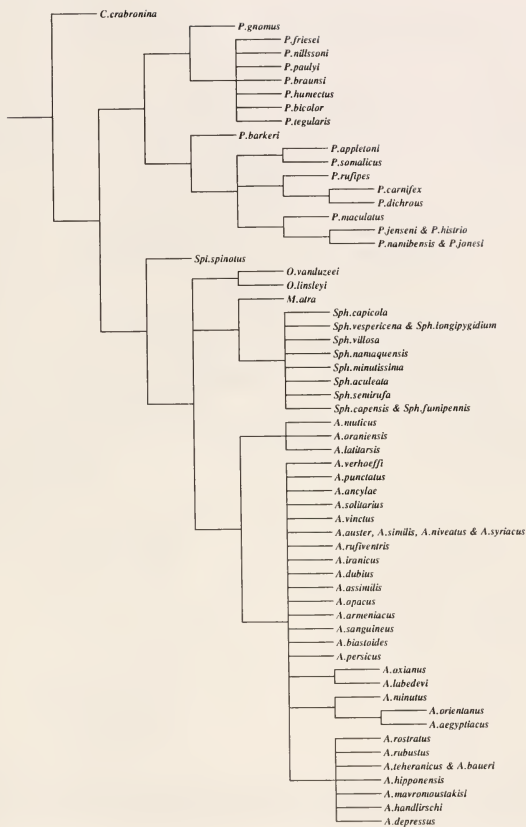
Fig. 1.  Strict consensus tree of over 1200 equally most parsimonious cladograms from analysis of data in Table 1 (species), without character weighting (length 190, consistency index (CI) 38, retention index (RI) 83).
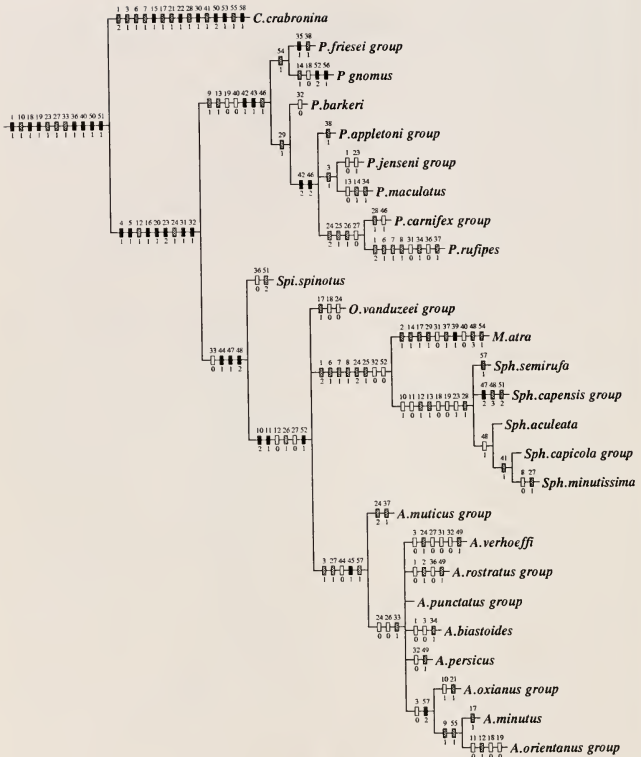
Fig. 2. Strict consensus tree of 48 equally most parsimonious cladograms from analysis of data in Table 2 (species groups), without character weighting (length 156, CI 45, RI 73). Character transformation symbolised as follows: black=unique derivation; grey=convergent derivation; open=reversal (unique or convergent).

species groups derived without weighting of characters (Fig. 2). Emphasis has not been placed on the generic analysis because the formation of generic ground plans for the more diverse genera, such as

*Ammobates*, resulted in the loss of information. The loss of information in the formation of ground plans for species groups was minimal.

The Caenoprosopidini is the sister
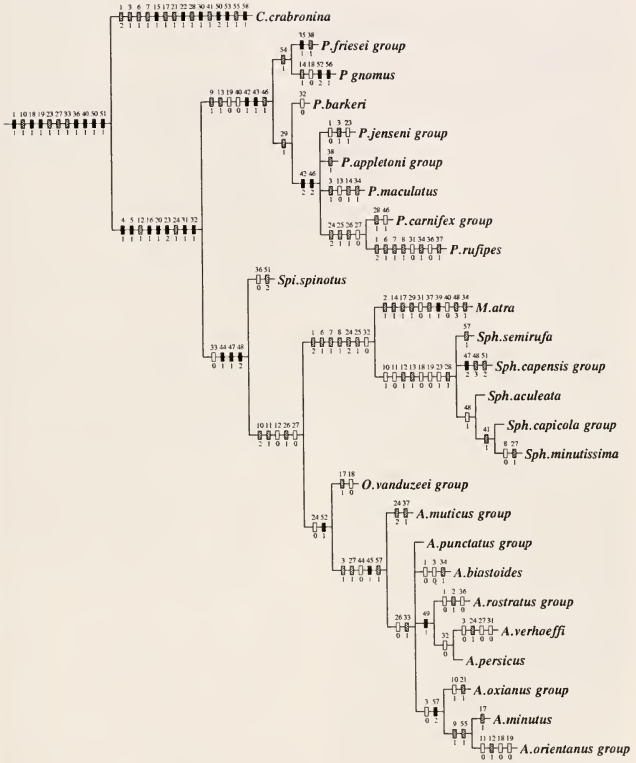
Fig. 3. Strict consensus tree of 12 equally most parsimonious cladograms from analysis of data in Table 2 (species groups), using successive approximations character weighting (raw length 158, CI 72, RI 88). For symbols see Fig. 2.

group of the Ammobatini, as was demonstrated by Roig-Alsina (1987, 1991) who adequately discussed the relationship between these two tribes. Roig-Alsina (1987, 1991) clearly demonstrated the Caenopro-

sopidini to be monophyletic by the presence of several unique synapomorphies, but was unable to demonstrate the monophyly of the Ammobatini in this way. By including *C. crabronina* in this study, to
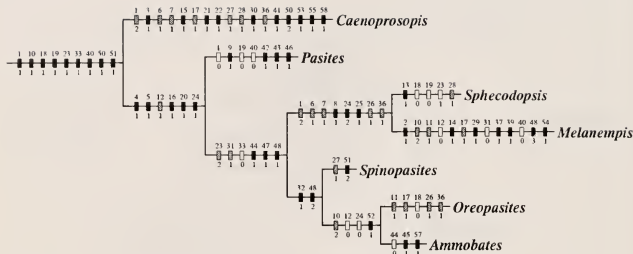
Fig. 4. Single most parsimonious cladogram from analysis of data in Table 3 (genera using adults), without character weighting (length 88, CI 69, RI 52). For symbols see Fig. 2.

represent the Caenoprosopidini, the monophyly of the Ammobatini was demonstrated by the presence of several unique, unreversed, synapomorphies. They are the position of antennal sockets in the middle of the face and the associated relatively long subantennal suture (4.1, 5.1), presence of the paraocular carina (16.1) and the declivous, gently concave, glabrous anterior surface of the pronotum (20.1). The modification of the posteromedian region of the female S5 as a whole is also unique to the Ammobatini, but it forms two separate characters within the tribe. In *Pasites* the posterior margin is clothed with fine vestiture and is not lengthened (44.1, 46.1 & 2), whereas in the other Ammobatini the posterior margin is naked and elongate (44.0, 47.1 & 2).

*Pasites* forms the first major clade of the Ammobatini (Figs. 1–4) and is monophyletic. Its monophyly is demonstrated by three unique synapomorphies, the presence of a subpygidial brush in the female (state 42.1); the fine vestiture and structure of the posteromedian region of the female S5 (43.1, 46.1). Supporting character states are: 10-segmented male antennal flagellum (9.1); spatulate labrum (13.1); position of the mandibles when in repose in both sexes (19.0) and presence of a pygidial plate in the female T6 (40.0).

The remaining ammobatine genera together form a distinct clade which is the sister group of *Pasites*. The monophyly of this clade is demonstrated by the unique structure of the female S5, which is concave posteromedially (47.1) and has a naked posteromedian protuberance (44.1 & 48.2).

*Spinopasites* is monotypic and forms the sister group of the clade ((*Sphecodopsis* + *Melanempis*) + (*Oreopasites* + *Ammobates*)) in the species-group analysis (Figs. 1–3). The distinguishing features are the gently curved propodeum (36.0) and the single posterior spine on the female S6 (51.2), neither of which is unique to this genus. In the generic analysis, *Spinopasites* forms the sister group of (*Oreopasites* + *Ammobates*), with (*Melanempis* + *Sphecodopsis*) as the sister group of (*Spinopasites* + (*Oreopasites* + *Ammobates*)) (Fig. 4). Here the apically pointed labrum (12.1), sparsely pubescent ventral region of the mesepisternum (27.1) and the single posterior spine on the female S6 (51.2) are the distinguishing characters. The reason for the different distinguishing characters in the two trees is the changes made in the development of ground plans for the genera and possible ambiguities resulting from the use of consensus trees for the species-group analyses. The discovery of the male of this ge-

nus may unambiguously demonstrate its relationship to the other genera in the tribe.

The remaining four genera form two separate clades, (*Ammobates* + *Oreopasites*) and (*Melanempis* + *Sphecodopsis*). In the accepted cladogram of the species groups, these two clades form sister groups (Fig. 3) and in the generic analysis *Spinopasites* is the sister group of (*Ammobates* + *Oreopasites*). (*Ammobates* + *Oreopasites*) forms a monophyletic group defined by the absence of the male pygidial plate (52.1), which is peculiar to these two genera, and by the strongly appressed scutal vestiture (24.0). Each of these two genera is itself apparently monophyletic. In *Ammobates* the structure of the posterior margin of the female S5 (45.1) is unique. Other states that help to define *Ammobates* are the short, unmodified, naked posterior margin of the female S5 (44.0) and the posterior region of the male S8 that is at least as wide as the anterior region (57.1). A unique synapomorphy was not found for *Oreopasites*, which is largely defined by the presence of an occipital carina (17.1), crossing of the mandibles when in repose (18.0) and undifferentiated vestiture on the lower region of the mesepisternum (27.0).

(*Melanempis* + *Sphecodopsis*) is not defined by a unique synapomorphy. The combination of character states that defines this clade is as follows: the lateral region of the vertex is flat (1.2); facial vestiture is generally simple (6.1), erect (7.1) and fairly sparse (8.1); scutal vestiture is mostly erect (24.2) and fairly sparse (25.1); vestiture on the ventrolateral region of the mesepisternum is not obviously different from that on the upper region (27.0); setation on the hind tibia is more or less uniform (32.0) and the male pygidial plate is well developed (52.0). *Melanempis* is clearly monophyletic, defined primarily by the truncate female T6 which is naked and surrounded by a small carina (39.1). Of the

other states that define this genus the most significant are the absence of a maxillary palp (14.1), presence of a mediolongitudinal carina on the dorsal surface of the female T6 (37.1) and the gutter-like structure on the posteromedian region of the female S5 (48.3). *Sphecodopsis* is defined by a combination of several states, the most important being the quadrate, apically pointed labrum (10.0, 11.0, 12.1, 13.1), mandibles which cross each other behind the labrum when in repose (18.0, 19.0), simple scutal vestiture (23.1) and the extension of the pre-epistomal groove below the scrobal groove (28.1).

The classification of Michener (1944) is compatible with the results of the current study. The only difference is that some of his genera have been synonymized. Popov's (1951) division of the current Ammobatini into two distinct tribes (Ammobatini = *Ammobates* + *Oreopasites* and Pasitini = *Pasites* + *Sphecodopsis*) is incompatible with the results of this study as *Sphecodopsis* and *Pasites* belong to separate monophyletic clades, but does associate *Ammobates* and *Oreopasites*. The inclusion of all the Ammobatini into a single genus (Warncke 1983) obscured the fact that the tribe can be divided into definite groups which facilitate the understanding and study of these bees. The differences between the genera, as delimited above, appear to be more consistent with the differences used to define genera in other groups of bees, and a subgeneric classification could even be gainfully applied to certain of the ammobatine genera, expressly *Pasites* and *Ammobates*.

Five of the ammobatine genera are confined to the Old World: *Sphecodopsis* (southern Africa; 9 species) and *Melanempis* (Madagascar, four species, R.W. Brooks pers. comm.) are Afrotropical; *Pasites* is predominantly Afrotropical (23 species) but has 1 species in the Palaearctic Region; *Spinopasites* is Palaearctic (Tunisia, 1 species), and *Ammobates* is predominantly Pa-

laearctic (Mediterranean, eastern Europe and Iran, 47 species being revised by M. Schwarz (pers. comm.)) but has 1 species in southern Africa. *Oreopasites* is the only New World genus and its 11 species occur in the southwest of the Nearctic Region (Rozen 1992).

The sister group of the Ammobatini, the Caenoprosopidini (Roig-Alsina 1987, 1991), is Neotropical and its species occur mainly in the Patagonian Subregion of South America (Roig-Alsina 1987; Kuschel 1969). This suggests that the common ancestor of the (Caenoprosopidini + Ammobatini) occurred in that part of Gondwanaland which today forms southern Africa and the southern part of South America. It also suggests that the Ammobatini evolved subsequent to the separation of South America from southern Africa, about 120 million years ago (Smith *et al.* 1981). The common ancestor of the (Caenoprosopidini + Ammobatini) must, however, have occurred before that time. Therefore, it may be assumed that the Ammobatini originated in the Old World, and most probably in the Afrotropical Region because *Pasites*, which forms the basal clade of the Ammobatini, is primarily Afrotropical (the Palaearctic *P. maculatus* Jurine is one of the most derived species in the genus). The Ammobatini are assumed to have spread from the Afrotropical into the Palaearctic Region. *Ammobates* and *Oreopasites* are evidently sister groups, and the colonization of the Nearctic probably took place from the Palaearctic Region.

Our knowledge of the paleovegetation in Africa is inadequate to facilitate a detailed hypothesis on the vegetation types that the ancestors of the extant ammobatine genera inhabited. Soon after the breakup of Gondwanaland the vegetation in Africa was vastly different from that of today (Axelrod & Raven 1978) and it consisted largely of rain forest and woodland.

Although most of the extant Ammobatini live in the semi-deserts of southern Africa and the Mediterranean Region, *Pasites* inhabits a variety of different vegetation types, and occurs in rain forest, woodland and desert. This supports the conclusion that *Pasites* is the oldest ammobatine genus and suggests that the habitation of arid areas is derived for the tribe. The occurrence of *Ammobates auster* spec. nov. in the arid areas of southern Africa suggests that *Ammobates* was previously more widely distributed in Africa.

## REVISION OF AFROTROPICAL AMMOBATINI HANDLIRSCH

The tribe Ammobatini was first proposed by Handlirsch (1925). Ammobatine bees are small to medium sized (2.3–12.5 mm long). They are mostly black to reddish with short, densely plumose, appressed vestiture and the metasoma is strongly convex dorsally. Most species of *Sphecodopsis*, however, have long, weakly plumose, semi-erect vestiture and the metasoma is flattish. The principal diagnostic features of the Ammobatini are: paraocular carina well developed on lower half of face; male with a tuft of hairs on lower lateral part of labrum, except *Melanempis*; pronotal collar carinate laterally; female T5 lacks a pseudopygidial area, S5 concave posteromedially when viewed from behind; apex of concavity of female S5 extended into a protuberance that may be gutter-like in all genera except *Pasites*; female S6 reduced and largely internal, visible externally as one or two sclerotized spines, not longitudinally separated, without coarse setae.

Many of the species are dealt with in groups (Appendix 1). The purpose of the species groups is to facilitate the description and discussion of closely related species, and should also facilitate the recognition of the species.

KEY TO THE GENERA OF AMMOBATINI
(Males and Females)

1. Distal ends of mandibles crossing diagonally in repose . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
– Distal ends of mandibles entirely overlapping in repose . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2. Labrum short (about quadrate) and pointed apicomedially, mandibles closing behind labrum (Afrotropical) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Sphecodopsis* Bischoff
– Labrum long (about 1,4× as long as wide) and truncate distally, mandibles traversing labrum so that distal end of labrum is visible posterior to closed mandibles (Nearctic) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Oreopasites* Cockerell
3. Female; metasoma with six exposed terga . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
– Male; metasoma with seven exposed terga . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
4. S5 with posteromedian region naked (often entire posterior margin naked) and with a small protuberance or a weak to well developed gutter posteromedially . . . . . . . . . . . . . . . 5
– Always with entire posterior margin of S5 clothed with fine vestiture, and devoid of any modifications as described above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Pasites* Jurine
5. S6 forming a single spine posteriorly (North Africa) . . . . . . . . . . . . . *Spinopasites* Warncke
– S6 bifurcate posteriorly . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6. T6 with posterior end naked and circumscribed by a carina (Madagascan) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Melanempis* Saussure
– T6 with posterior end setose, without a peripheral carina (southern African and Palaearctic) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ammobates* Latreille
7. Antenna 13-segmented; posterior end of T7 convex (except *Melanempis* which has 12 antennal segments and posterior end of T7 concave) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
– Antenna 12-segmented, and T7 convex posteriorly . . . . . . . . . . . . . . . . . . . . . . *Pasites* Jurine
8. T7 spatulate, devoid of a pygidial plate and concave posteriorly (Madagascan) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Melanempis* Saussure
– T7 usually with a pygidial plate, never concave posteriorly (southern African and Palaearctic) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ammobates* Latreille

## GENUS *PASITES* JURINE

*Pasites* Jurine 1807:224. Type species: *Pasites maculatus* Jurine 1807 (original designation).
*Pasites* (*Pasites*) Jurine; Warncke 1983:261–347.
*Morgania* Smith 1854:253; Cockerell 1933c:106; Warncke 1982:104–105 [synonymised]. Type species: *Pasites dichrous* Smith 1854 (monobasic).
*Morgania* (*Morgania*) Smith; Bischoff 1923:586.
*Omachthes* Gerstaecker 1869:154. Type species: *Omachthes carnifex* Gerstaecker 1869 (designated by Sandhouse 1943). Warncke 1983:291 [synonymized].
*Homachthes* Gerstaecker; Dalla Torre 1896:499 [unjustified emendation for *Omachthes*].
*Morgania* (*Omachthes*) Gerstaecker; Bischoff 1923:586.
*Omachtes* [sic.] Gerstaecker; Friese 1909:436–438 [lapsus].
*Pasitomachthes* Bischoff 1923:596; Warncke 1983:

291 [synonymised]. Type species: *Pasites nigerrimus* Friese 1922 (original designation).
*Pasitomachtes* [sic.] Bischoff; Sandhouse 1943:586 [lapsus].

The name *Pasites* is masculine according to the Code, Article 30(b), which specifies this for names with the suffix *-ites*. (Although Jurine gave no derivation for the name, it was probably derived from *pas* (Greek, all) and the suffix *-ites* (Greek, like), since he listed the ways in which the genus was similar to four other genera.) Jurine (1807) gave the specific epithet of the type species ('*maculata*') a feminine ending, however, indicating that he considered the name to be feminine. According to the Code this must be considered an error, which was apparently first corrected by Gerstaecker (1869).

Smith (1854), at the end of his original

description of *P. dichrous* (as '*dichroa*'), stated that 'It is very probable that the present species may be separated from *Pasites* by a monographer of these parasitic genera, in which case we would propose the name of *Morgania*'. According to the Code, Article 11(d)(i), this made the name *Morgania* Smith, 1854 available. Subsequently, Gerstaecker (1869) described the genus *Omachthes* for *P. carnifex*, a species that closely resembles *P. dichrous* in all respects. Thereafter the names *Pasites*, *Morgania* and *Omachthes* were commonly applied, in an inconsistent manner, to this group of bees.

Bischoff (1923) provided the first monographic study of the Afrotropical cuckoo bees, and clearly stated that *Pasites* does not occur in the Afrotropical Region. He placed the Afrotropical species that had previously been placed in *Pasites* into *Morgania* (which he divided into two subgenera, namely *Morgania sensu stricto* and *Omachthes*) except for two species that were previously assigned to *Pasites* for which he described the genus *Pasitomachthes*. The two species are *P. nigerrimus* (= *P. barkeri* (Cockerell)) and *P. bicolor* Friese. The only information that Bischoff (1923) provided on his interpretation of *Pasites*, *Morgania*, *Omachthes* and *Pasitomachthes* was in a key to the ammobatine genera. The characters referred to in the key were either poorly described, which does not allow for an accurate interpretation of his ideas, or unreliable (Cockerell 1933c). Bischoff (1923) did not state whether he had studied the type species of *Morgania* and *Omachthes*, *P. dichrous* and *O. carnifex* respectively, which are clearly more closely related to one another than to any of the other species that he placed in either *Morgania sensu stricto* or *Omachthes*. The characters that Bischoff (1923) used to identify *Pasites* are, furthermore, clearly evident in some of the Afrotropical species. It is, therefore, inexplicable as to why he stated that *Pasites* does not occur in Africa. It is also not clear why he described the genus

*Pasitomachthes* for two species that apparently conform with his interpretation of *Morgania*. The current study, during which the type species of *Pasites*, *Morgania*, *Omachthes* and *Pasitomachthes* were studied, demonstrated that these four taxa are synonymous.

*Pasites* is primarily Afrotropical. *P. maculatus* Jurine, which is Palaearctic, is the only species in the genus that does not occur in the Afrotropical Region. There are 15 subsaharan species, namely: *P. barkeri* Cockerell, *P. friesei* Cockerell, *P. paulyi* spec. nov., *P. braunsi* Bischoff, *P. humectus* spec. nov., *P. gnomus* spec. nov., *P. carnifex* (Gerstaecker), *P. dichrous* (Smith), *P. jenseni* (Friese), *P. namibiensis* spec. nov., *P. histrio* (Gerstaecker), *P. jonesi* (Cockerell), *P. rufipes* (Friese), *P. appletoni* (Cockerell) and *P. somalicus* spec. nov. Three species are endemic to Madagascar: *P. nilssoni* spec. nov., *P. tegularis* Friese and *P. bicolor*.

The species of *Pasites* are very small to large (3.9–12.5 mm long) and their colour varies from completely black to almost entirely reddish-orange. The diagnostic features of the genus are as follows: vertex, frontal view, distinctly convex (Figs. 5, 42), except that of *P. rufipes* in which vertex is flat laterally, raised between lateral ocelli (*cf.* Fig. 63); face with short brown to white or whitish vestiture, that on lower half of face densely plumose and that on upper half relatively sparse and mostly simple (Figs. 5, 42), except *P. rufipes* in which entire face is sparsely clothed with long, black, weakly plumose vestiture (*cf.* Fig. 63) and *P. maculatus* in which only area around antennal socket has plumose vestiture; antenna 12-segmented in both sexes; labrum variable in length and shape, ranging from little shorter to distinctly longer than its maximum width and from pointed apicomedially to more or less truncate distally (Fig. 14); mandibles behind labrum in repose; scutellum gently and evenly curved mediolongitudinally, gently swollen paramedially; last exposed metasomal tergum (T6 female, T7

male) either with or without pygidial plate; female S5 with strong conical (posterior apices of S5 diverging, Fig. 6) or elliptical concavity (posterior apices of S5 converging, Fig. 46), without posteromedian protuberance, border of concavity clothed with fine vestiture; female S6 bifurcate posteriorly.

The diagnostic characters of the species are diverse, ranging from their general colour, sculpture and vestiture to the structure of the maxillary palp, pygidium and S5 of the female, and the male terminalia, as described below. Males are difficult to identify, but can usually be associated with conspecific females taken from the same area, by their colour and sculpture. This, together with the fact that the males of three species are unknown, has made it difficult to produce a reliable key to the males.

The genus has been divided into eight species groups, four of which are monotypic (Appendix 1). A diagnosis of *P. maculatus* has been included in order to bring this single extra-Afrotropical species into context with the remainder of the group.

KEY TO SPECIES OF *PASITES*
(Males and Females)

1. Palaearctic; upper paraocular area distinctly swollen, resulting in it being strongly incurved above antennl sockets and dorsomedially . . . . . . . . . . . . . . . . *P. maculatus* (Jurine)
 – Afrotropical; upper paraocular area flat to slightly swollen, resulting in it being gently curved above antennal sockets and dorsomedially . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2. Occurring in subsaharan Africa . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
 – Madagascan (ater group, part) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22
3. Head, viewed perpendicular to lower region of clypeus, with upper margin of vertex between eye and lateral ocellus straight (*cf.* Fig. 63); facial vestiture weakly plumose and black; metasoma black; pygidial plate absent (male unknown) . . . . . . . . . . *P. rufipes* (Friese)
 – Vertex convex (Figs. 5, 42); facial vestiture densely plumose near antennal sockets and usually whitish, if brown or black then metasoma orange; metasoma black, reddish black or orange; female with well developed pygidial plate . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
4. Very small, 2.3–2.5 mm long; pygidial plate absent in both sexes, female with subpygidium well developed posteriorly, about half as long as its maximum width and densely clothed with fine brownish-yellow vestiture (Fig. 29); male S8 with two well developed anterior lobes (Fig. 31); gonocoxite of genitalia broadly rounded posteriorly (Fig. 32) . . .
 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. gnomus* Eardley
 – Small to large, 3.7–12.5 mm long; pygidial plate always present, but sometimes reduced; female with subpygidial brush short, distinctly less than half as long as its maximum width (Figs. 6, 15, 19, 20, 24, 28); male terminalia otherwise . . . . . . . . . . . . . . . . . . . . . . . 5
5. Metasoma orange and largely naked, with a little orange vestiture; vestiture on head and mesosoma brown to white (large, 7.0–12.5 mm long) (carnifex group) . . . . . . . . . . . . . . 6
 – Metasoma with integument usually black or blackish, sometimes reddish to orange, always with white plumose vestiture; vestiture on head and mesosoma always pallid (small to large, 3.7–8.8 mm long) (Males are difficult to identify and for some species are unknown, females are usually required for a positive identification.) . . . . . . . . . . . . . . . . . . . 7
6. First flagellomere 1.2× as long as second flagellomere; female subpygidial brush expanded dorsally (Fig. 38); male S8 parallel-sided posteriorly and weakly concave posteromedially (Fig. 39) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. dichrous* Smith
 – First flagellomere 2.5× as long as second flagellomere; female subpygidial brush not expanded dorsally (Fig. 34); male S8 tapering posteriorly and with posterior end distinctly emarginate (Fig. 36) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. carnifex* (Gerstaecker)
7. Female with posteromedian concavity on S5 conical [posterior apices diverging] (Figs. 6,

15, 19, 20, 24, 28); male integument usually completely black to blackish, legs always black; pygidial plate of male tapering posteriorly when viewed from above . . . . . . . . . . 8
– Female with posteromedian concavity on S5 elliptical [posterior apices converging] (Figs. 43, 47, 50, 51, 53, 57, 58); male integument black to orangish; pygidial plate with posterior end more or less parallel-sided in dorsal view, except for *P. appletoni* in which legs and metasoma orangish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 12
8. Female with pygidial plate well developed laterally and posteriorly (Fig. 6); vestiture on posterior margin of T2-T4 directed laterally . . . . . . . . . . . . . . . . . . . . *P. barkeri* (Cockerell)
– Female pygidial plate either well developed laterally and notched posteriorly or entire plate strongly reduced (Figs. 15, 19); vestiture on posterior margin of T2-T4 directed posteriorly (ater group, part) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
9. Female with entire pygidial plate strongly reduced laterally, only posterior margin clearly visible (Fig. 20); male S7 tapering evenly towards posterior end which is distinctly emarginate (Fig. 21) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. humectus* Eardley
– Female pygidial plate well developed laterally, notched posteriorly (Figs. 15, 19); male S7 otherwise . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10
10. Maxillary palp five-segmented . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. paulyi* Eardley
– Maxillary palp two or three-segmented . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11
11. Maxillary palp two-segmented . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. friesei* Eardley
– Maxillary palp three-segmented (male unknown) . . . . . . . . . . . . . . . . . *P. braunsi* (Bischoff)
12. Metasoma with six exposed terga and five exposed sterna, excluding highly modified S6; terminal tergum (T6) with a well developed subpygidial brush; terminal sternum (S5) strongly concave posteromedially (female) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 13
– Metasoma with seven exposed terga and six exposed sterna; terminal tergum without a subpygidial brush; terminal sternum entire (male) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18
13. Pygidial plate distinct laterally, either notched or absent posteriorly (Figs. 53, 57) (appletoni group, part) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
– Pygidial plate never notched posteriorly, sometimes reduced laterally (Figs. 43, 47, 50) (jenseni group, part) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15
14. Pygidial plate fully developed, except for a small notch posteromedially (Fig. 53) . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. appletoni* (Cockerell)
– Pygidial plate only visible laterally, without a distinct posterior margin (Fig. 57) . . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. somalicus* Eardley 16
15. Propodeum with mediolongitudinal region punctate and clothed with fine vestiture . . . 16
– Propodeum with mediolongitudinal region glabrous and naked . . . . . . . . . . . . . . . . . . . 17
16. Pygidial plate well developed both laterally and distally (Fig. 43); labrum tuberculate apicomedially . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. jenseni* (Friese)
– Pygidial plate reduced laterally so that it exists only as a distinct carina on posterior end of T6 (Fig. 50); labrum with a transverse carina apically . . . . . . . . . . . *P. jonesi* (Cockerell)
17. Labrum relatively long, 1.2–1.3× as long as its maximum width . . . *P. namibiensis* Eardley
– Labrum quadrate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. histrio* (Gerstaecker)
18. Head and mesosoma mostly black, with mandible, labrum, antenna, pronotal lobe, tegula and legs orangish, and metasoma orange; scutum fairly densely covered with small, well separated punctures; propodeum with a broad, naked, glabrous mediolongitudinal band; S8 strongly expanded laterally and weakly emarginate posteriorly (Fig. 55) (appletoni group, part) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. appletoni* (Cockerell)
– Generally with head, mesosoma and metasoma mostly black; if with orange coloration similar to that described above, then with large widely spaced scutal punctures and mediolongitudinal region of propodeum either hisute or with glabrous area greatly expanded dorsally; S8 either moderately expanded laterally and pointed posteriorly or weakly expanded laterally and truncate posteriorly (Figs. 45, 49) (jenseni group, part) . . . . . . . . . 19
19. Propodeum with mediolongitudinal region punctate and clothed with fine vestiture . . . 20
– Propodeum with mediolongitudinal region glabrous and naked . . . . . . . . . . . . . . . . . . . 21

20. Labrum tuberculate apicomedially . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. jenseni* (Friese)
– Labrum with a transverse carina apically . . . . . . . . . . . . . . . . . . . . . . . *P. jonesi* (Cockerell)
21. Labrum relatively long, 1.2–1.3× as long as its maximum width . . . *P. namibiensis* Eardley
– Labrum quadrate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. histrio* (Gerstaecker)
22. Integument of head and mesosoma mostly reddish; S7 acutely pointed posteriorly and
carinate posteroventrally (Fig. 11) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. nilssoni* Eardley
– Integument of head and mesosoma black; S7 parallel-sided posterolaterally with posterior
end emarginate (Fig. 25), without a posteroventral carina (males of the following two
species are indistinguishable) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 23
23. Female pygidial plate absent (Fig. 24) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. bicolor* Friese
– Female pygidial plate well developed laterally and notched posteriorly (Fig. 28) . . . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. tegularis* Friese

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## BARKERI SPECIES GROUP

This species group is monotypic.

### *Pasites barkeri* (Cockerell), comb. nov.
(Figs. 5–10)

*Morgania barkeri* Cockerell 1919:189–190.
*Pasites nigerrimus* Friese 1922:39; Cockerell 1932: 115 [part].
*Pasitomachthes nigerrimus* (Friese); Bischoff 1923: 596–598.
*Pasitomachthes argentatus* Baker 1971:3–8. **Syn. nov.**
*Pasites obscurus* Warncke 1983:291–292 [*nom. nov. pro Pasitomachthes nigerrimus* Bischoff *nec Pasites nigerrimus* Friese].

*Pasites nigerrimus* was described from two female specimens, one from Durban (South Africa), the other from Kigonsera (Tanzania). Both syntype have been studied and were found to belong to different species, as first pointed out by Bischoff (1923) who considered them to be generically distinct. He proposed the generic name *Pasitomachthes* for the syntype from Durban but retained the specific epithet, calling his new species *Pasitomachthes nigerrimus*. The types of *barkeri* and *Pasitomachthes nigerrimus* closely resemble one another and are clearly conspecific, which suggests that Friese (1922) was not aware that the species had been described by Cockerell (1919) (*Pasites nigerrimus* Friese is a junior synonym of *friesei*, q.v.). Baker (1971) described *argentatus* in detail, and compared it with the original description

of *Pasitomachthes nigerrimus* (he did not examine the type material of *Pasitomachthes nigerrimus*). Although the type material of *argentatus* (female holotype, in D. Baker's private collection, Oxford, England) was not available for study, comparison of the detailed original description of *argentatus* with the holotypes of *barkeri* and *Pasitomachthes nigerrimus* led to the opinion that *argentatus*, *barkeri* and *Pasitomachthes nigerrimus* are synonyms. Warncke (1983) transferred *Pasitomachthes nigerrimus* to the genus *Pasites* making it a subjective homonym of *Pasites nigerrimus* Friese, and consequently renamed *Pasitomachthes nigerrimus* as *P. obscurus*.

*Description.*—Length of head 1.6–2.0 mm; scutum 1.3–1.7 mm; fore wing 6.4–7.9 mm; body 6.3–8.8 mm. Integument black to reddish-black. Vestiture mostly white, scutal vestiture brownish-yellow; ventral surfaces of tarsi yellowish; T5 of female with yellowish tinge, distal region of S5 brownish-yellow; T6 with subpygidial brush brownish-orange. Vestiture on head mostly short, dense and plumose, vertex moderately dense and simple (Fig. 5); mesosomal vestiture dense, short and simple on scutum, moderately sparse on ventrolateral region of mesepisternum, very sparse on trochanters and femora, very dense on ventral surfaces of tarsi; T1 with anterior surface and posterolateral regions with dense plumose vestiture, vestiture on remainder of T1 sparse; T2–T4 with anterior regions sparsely, distal regions with moderately dense fringes of laterally directed vestiture; female T5, male T5–T6 with vestiture of distal fringes directed posteriorly; female T6 with subpygidial brush (Fig. 6); metasomal venter moderately sparsely to densely pubescent, with velvety vestiture surrounding distal concavity of S6. Labrum quadrate,
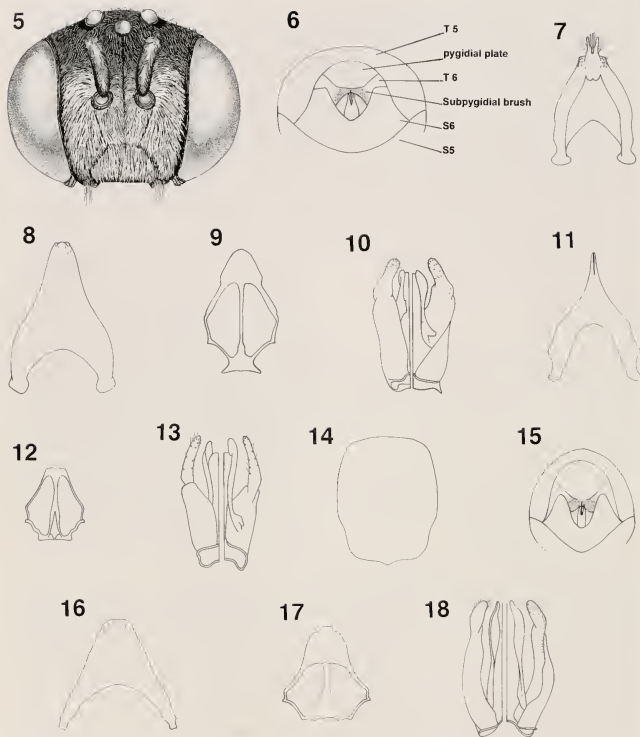
Figs. 5–18. *Pasites* spp. 5–10. *P. barkeri*. 5. Head, front view, ♀; 6. Terminalia, posterior view, ♀; 7. S6, ♀; 8. S7, ♂; 9. S8, ♂; 10. Genital capsule, left half dorsal, right half ventral, ♂ (♂ terminalia: anterior below, posterior above). 11–13. *P. nilssoni*, ♂. 11. S7; 12 S8; 13. Genital capsule. 14–18. *P. friesei*. 14. Labrum, ♀; 15. Terminalia, posterior view, ♀; 16. S7, ♂; 17. S8, ♂; 18. Genital capsule, ♂.

apex carinate with carina strongly tuberculate medially, rounded apicolaterally; maxillary palp five-segmented, about twice as long as pedicel of antenna; scutum densely punctate, punctures small and separate; scutellum strongly convex, but only slightly swollen paramedially; mesopleuron generally moderately densely punctate, punctures fairly large and separate; propodeum largely punctate, narrowly glabrous medioposteriorly; pygidial plate broad and well developed in both sexes; female with subpygidial brush short and devoid of ventral tuft (Fig. 6); female S5 with deep, conical concavity (Fig. 6), S6

narrowly bifid (Fig. 7); male S7, S8 and genital capsule as in Figs. 8–10.

*Distribution.*—Tropical and subtropical regions of Africa, mostly in forest and woodlands; known from Zaïre, Uganda, Burundi, Tanzania, Zimbabwe and east coast of South Africa.

*Discussion.*—This is the only species that is black or blackish with short simple vestiture on the scutum, laterally directed vestiture on T2-T4 and a well developed pygidial plate in the female.

It resembles certain of its congeners, the friesei species group, *P. gnomus* and the carnifex species group, in that the lateral margins of the posteromedian concavity of the female S5 diverge (Figs. 6, 15, 29, 34). The structure of the male gonocoxite (Fig. 10) resembles that of *P. paulyi* and *P. nilssoni* (Fig. 13), both of which belong to the friesei group, more closely than to any other species in the genus. In the cladistic analysis (Fig. 2) it is demonstrated as the sister species to the clade that comprises the appletoni, carnifex and jenseni groups, *P. rufipes* and *P. maculatus*.

Cockerell (1933c) recorded the host of this species as possibly being *Nomia garua* Strand (Halictidae: Nomiinae).

*Type material examined.*—*Morgania barkeri*, holotype ♀: 'Durban, Natal, 9.iii.1918, C.N. Barker; *Morgania barkeri* Ckll. Type; TYPE' (DMSA). *Pasitomachthes nigerrimus*, holotype ♀ & *Pasites nigerrimus*, paralectotype ♀: 'Durban 10.3.1, Hayar 1219 [on reverse side of label]; *Pasitomachthes nigerrimus* Bisch. Typ. ♀; War Cotype des *Omachthes nigerrimus* Fr.!, Coll. Friese; Typus; Zool Mus Berlin' (ZMHB).

*Additional material examined.*—17♀ 11♂: ZAIRE: 'SL Edourd, Bitshumbi (925m), Parc Nat. Albert', 22.iv.1936, L. Lippens (1♂ MRAC). ZIMBABWE: Victoria Falls, 20.i.1927 (1♀ 5♂ SAMC, 1♂ SANC). SOUTH AFRICA: Kosi Bay, 26.58S 32.48E, 10–11.ii.1990, C.D. Eardley (1♂ SANC); Mfongosi, iv & xii.1916 & iii.1917, W.E. Jones (9♀ SAMC, 1♀ SANC); Charters Creek, St Lucia, 28.12S 32.25E, 14–16.i.1981, R. Oberprieler (1♀ SANC); Durban, Bluff, 26.ii.1921, C.N. Barker (1♂ DMSA); Burman Bush, 8–18.iii.1963, H. Empey (2♀ 2♂ SANC); Montclair, Durban, 25.iii.1945 (1♀ DMSA, 1♀ SAMC); Port St. John, 19.iii.1969, L.C. Starke (1♀ SANC).

*Other published distribution records.*—TANZANIA: Kigonsera (Friese 1922); ZAIRE: Dilolo

& 50 km S. Bukavu (Cockerell 1932); LIBERIA: Monrovia, GHANA: Aburi, UGANDA: Kampala, TANZANIA: Uvira (Cockerell 1933c); CAMEROON & GHANA (Medler 1980); and ZIMBABWE: Bulawayo (Baker 1971).

## FRIESEI SPECIES GROUP

This species group comprises the following seven species: *P. nilssoni*, *P. friesei*, *P. paulyi*, *P. braunsi*, *P. humectus*, *P. bicolor* and *P. tegularis*. In most of these species the head and mesosoma are black and the metasoma ranges from black to reddish. In *P. nilssoni* the head, mesosoma and metasoma are reddish. The most useful diagnostic characters of the group are the conical posteromedian concavity of the female S5 in combination with the female subpygidial brush which is undifferentiated and either longer than wide or quadrate (Figs. 15, 19, 20, 24, 28). The female of *P. nilssoni* is unknown. The females are generally more distinctive and can be separated more easily than the males.

### *Pasites nilssoni* Eardley, spec. nov.
(Figs. 11–13)

This species is named for the collector, Prof. L.A. Nilsson, of Uppsala University, Sweden, who recognized it as being new.

*Description.*—Male (female unknown). Lengths: head 1.4 mm; scutum 1.1 mm; fore wing 4.8 mm; body 5.3 mm. Integument of head mostly orange with upper region of face and posterior region of gena partly black; mesosoma orange with mediolongitudinal region of scutum, anterior and ventral areas of pleuron, venter and propodeum black to orangish-black; legs more or less with ventral surface of femora, most of tibia and entire tarsi black or blackish; metasoma mostly orangish-black anteriorly, blackish-orange posteriorly. Vestiture mostly white to whitish, scutum with pale yellow tinge, ventral surfaces of tarsi pale yellow, S6 yellowish. Vestiture generally ranges from strongly to weakly plumose, fairly dense; upper region of face, vertex, most of scutum and scutellum, lower region of mesopleuron, trochanters and femora mostly with simple vestiture; propodeum with lateral surface and mediolongitudinal region of posterior surface naked; T1 mostly pubescent, distal margin naked; T2-T6 mostly with fine vestiture anteriorly and dense pubescent cross-bands posteriorly; T7 with sparse simple vestiture on pygidial plate; metasomal venter largely densely pubescent, S6 with

simple vestiture. Structure similar to *P. barkeri* except as follows: labrum without distinct carina or tubercle; maxillary palp little longer than pedicel of antenna (1.4:1); scutellum strongly convex with distinct mediolongitudinal cleft; propodeum with naked areas laterally, glabrous posteriorly; pygidial plate weakly pointed posteriorly; posterior end of S7 pointed and distinctly keeled ventrally (Fig. 11); S8 and genital capsule as in Figs. 12–13.

*Distribution.*—Morondava, forested west coast of Madagascar.

*Discussion.*—Within the group, this species can be easily recognized by the unique orangish integument of the male head and mesosoma. A more precise determination of the relationship between this and the other species in the group must await the discovery of the female.

*Type material.*—Holotype ♂: 'MADAGASCAR: OUEST: Toliary Morondava, Florêt de Kirindy, 25.xi.1989, PL. REPR. ECOL. PRO.' (NCUS).

### *Pasites friesei* Cockerell
### (Figs. 14–18)

*Pasites ater* Friese 1909b:148 [*nec Pasites ater* Spinola 1806].

*Morgania (Omachthes) ater* [sic.] (Friese); Bischoff 1923:588.

*Pasites friesei* Cockerell 1910:217. [*nom. nov. pro P. ater* Friese *nec* Spinola].

*Morgania friesei* (Cockerell); Cockerell 1933c: 109–110.

*Pasites nigerrimus* Friese 1922:39; Cockerell 1932: 115 [part]. **Syn. nov.**

*Morgania (Omachthes) nigerrimus* [sic.] (Friese); Bischoff 1923:596.

*Morgania nigerrimus* [sic.] (Friese); Cockerell 1933c:108.

*Morgania chubbi* Cockerell 1919:189–190. **Syn. nov.**

*Morgania (Omachthes) nigritula* Bischoff, 1923: 588. **Syn. nov.**

*Omachthes nigritulus* (Bischoff); Anonymous 1958:32.

*Morgania peratra* Cockerell 1933c:109–110. **Syn. nov.**

Although *P. ater* Friese is a junior objective homonym of *P. ater* Spinola (1806), the latter was synonymized with the Palaearctic species *Biastes brevicornis* (Panzer 1798) by Dalla Torre (1896). *Biastes brevicornis* is the senior synonym of *Pasites uni-*

*color* Jurine, one of the two species originally placed in *Pasites* by Jurine (1807).

The type material of *Pasites nigerrimus* has been studied and comprises two distinct species, as originally noticed by Bischoff (1923) who described the Durban syntype as *Pasitomachthes nigerrimus*. The syntype from Kigonsera is designated here as the lectotype of *Pasites nigerrimus*; it is clearly conspecific with the holotype of *P. ater*.

Cockerell (1919) described *chubbi* from a single female from Durban. He did not give a comparison between this species and any of its congeners. Bischoff (1923) separated *ater* and *nigritula* primarily on the structure of the distal fringe on the female T5, and he did not refer to *chubbi*. As *nigritula* closely resembles *chubbi*, it appears that Bischoff (1923) was not aware of Cockerell's (1919) paper. During the course of this study much material of this species, from numerous localities, was studied and the species was found to be widely distributed and the extent of the vestiture variable. The study, which included the examination of the type material, revealed that *friesei*, *chubbi* and *nigritula* are synonyms.

The male of this species was first described by Cockerell (1933c) as *M. peratra*. The association of the sexes, by the study of specimens of both sexes taken together resulted in the synonymy of *friesei* and *peratra*.

*Morgania nigritula* was described from two females, from Sunday's River and Plat River (eastern Cape, South Africa). The Sunday's River specimen is the only syntype that was traced, and it is here designated as the lectotype.

*Description.*—Length of head 1.3–2.0 mm; scutum 0.8–1.8 mm; fore wing 4.4–6.9 mm; body 4.5–7.1 mm. Integument black, except tegula, legs and metasoma sometimes reddish. Vestiture mostly white, ventral surfaces of tarsi, female T5, S5 and male T6, S6 with pale yellow tinge; female subpygidial brush brownish-orange. Head mostly densely pubescent, upper region of face and vertex with sparse vestiture (*cf.* Fig. 5); mesosoma with pronotal collar, most of

pronotal lobe, lateral regions of mesopleuron (excluding lower hypoepimeral area) and posterolateral regions of propodeum densely pubescent; remainder of mesosomal vestiture sparse; vestiture on legs dense, except trochanters and femora sparse to very sparse, ventral surfaces of tarsi very dense; T1 anterior surface and posterolateral region with dense plumose vestiture, remainder with sparse, simple vestiture; T2 and sometimes T3 posterolaterally with dense, directed, vestiture posterolaterally, anterior regions of each tergum with sparse, simple vestiture; female T3/T4-T5, male T3/T4-T6 with moderately dense distal fringes of laterally directed hairs (vestiture sparse and simple anteriorly); female T6 with sparse vestiture and with weakly developed subpygidial brush (Fig. 15); female S2-S4 with vestiture fairly sparse anteriorly, dense posteriorly, S5 with moderately dense vestiture, distal margin velutinous; male metasomal venter moderately densely pubescent. Labrum little longer than wide, weakly tuberculate apicomedially (Fig. 14); maxillary palp two-segmented, less than one-half as long as pedicel (except three-fourths as long as pedicel in one specimen); scutum 1.1× as long as narrowest width, punctures moderately large, often confluent; scutellum strongly convex but only slightly swollen paramedially; propodeum distinctly glabrous mediolongitudinally; mesopleuron mostly densely punctate, hypoepimeral and ventral regions sparsely punctate; female T6 without distinct pygidial plate, but with weak carina posterolaterally (Fig. 15), pygidial brush short, devoid of ventral tuft, shallowly concave ventrally (Fig. 15); male with well developed, broadly rounded pygidial plate; female S5 with deep conical concavity (Fig. 15), S6 narrowly bifurcate (cf. Fig. 7); male S7, S8 and genital capsule as in Figs. 16–18.

*Distribution.*—Widespread through greater part of subsaharan Africa, occurring in a variety of different biomes from semi-desert to rain forest.

*Discussion.*—*Pasites friesei* differs from the other species in the group by the two-segmented maxillary palp, female pygidial plate which is well developed laterally and notched posteriorly and subpygidial brush which is completely brownish-orange. In *P. friesei* the male S7 tapers gradually towards the gently rounded posterior end.

*Floral records.*—Asteraceae: *Ageratum* sp., *Aspilia africana* (Pers.) C.D. Adams, *Aspilia helianthoides* Benth. & Hook. f. Gsn., *Emilia coccinea* Sweet and *Mikania natalensis* DC.; Verbenaceae: *Stachytarpheta angustifolia* Vahl; Rubiaceae: *Spermacoce verticil-

lata* L.; Hypericaceae: *Harungana madagascariensis* Lam. ex Pair.

*Type material examined.*—*Pasites ater*, holotype ♀: 'Kilimandjaro; 6 Sept.; Typus; *Pasites ater* ♀ Fr. 1908 Friese det.' (NHRS). *Pasites nigerrimus*, lectotype ♀: 'D.O. Africa, Kigonsera, 1903; *Pasites nigerrimus* Fr. ♀ 1904 Friese det.; Typ.; *Pasites nigerrimus* ♂ (Fr.) Typ.; Coll. Friese; Zool. Mus. Berlin' (ZMHB). *Morgania chubbi*, holotype ♀: 'Natal, Bellair, E.C. Chubb, 13 Jan. 1919; *Morgania chubbi* Ckll. Type; TYPE' (DMSA). *Morgania nigritula*, lectotype ♀: 'Sunday's River, Dr Brauns, Cape Colony, 27.xii.1897; *O. nigritulus* Bisch. Typ. ♀.; *Omachthes nigritulus* TYPE Bischoff; *Omachthes nigritulus* ♀ Type No. 564' (TMSA). *Morgania peratra*, holotype ♂: 'NATAL, Weenen, iii.iv.1917, H.P. Thomasset; *Morgania peratra* Ckll TYPE; Pres. by Imp. Inst. Ent. B.M. 1933-582; B.M. TYPE HYM. 17B 81' (NHML).

*Additional material examined.*—53♀ 47♂:
**SENEGAL:** Ziguinchor, viii.1979, A. Pauly (1♂ PCGB). **BURKINA FASO:** Sources du Kou, 13.x.1079, A. Pauly (3♀ PCGB); River Lahissa S., 5.x.1979, A. Pauly, on *Aspilia helianthoides* (1♀ PCGB). **LIBERIA:** Bakratown, x.1926 (1♀ MCZC, 1♀ MRAC). **IVORY COAST:** Grand-Bérèby, 18.xii.1979, A. Pauly (1♂ PCGB); Tabou, 21.xii.1979, A. Pauly (1♀ PCGB). **TOGO:** Sokodé, xii.1982, A. Pauly (1♀ PCGB). **CAMEROON:** Wum, maquis d'Afrika, 6.24N 10.03E, 20.viii.1987, A. Pauly, on *Emilia coccinea* (2♀ PCGB), on *Aspilia africana* (1♀ 2♂ PCGB) on *Ageratum* sp. (1♂ PCGB); Kriegschiffsha, 15.iii.1892, Dr Brauns (1♀ TMSA). **CENTRAL AFRICAN REPUBLIC:** Kembe, 4.29N 21.53E, 13.viii.1985, Dollfuss (1♀ SCAA). **EQUATORIAL GUINEA:** Bioko, Sa. Isabel, 25.iii.1900, L. Conradt 9. (1♀ TMSA). **GABON:** Og. Lolo., Paris, 1.19S 12.30E, 29.i.1986, A. Pauly (1♀ 3♂ PCGB); Og. Lolo., Pana, 700m, 29.i.1986, A. Pauly, on *Mikania cordata* (1♂ PCGB); Og. Iv., Sassamongo, 2.v.1986, A. Pauly (2♂ PCGB, 2♂ SANC), on *Stachytarpheta angustifolia* (1♂ PCGB, 1♂ SANC); Botouala, 2.v.1986, A. Pauly, on *Stachytarpheta angustifolia* (1♂ PCGB); Cap, Santa Clara, 29.ix.1985, A. Pauly (2♀ 1♂ PCGB, 1♀ SANC); Sindara, riv. Ngounié, 29.xii.1985, A. Pauly, on *Spermacoce verticillata* (1♀ PCGB); Kango, 22.ix.1985, A. Pauly, on *Harungana madagascariensis* (1♀ PCGB); Ayem W., 25.xii.1985, A. Pauly, on *Aspilia africana* (1♂ PCGB); Forêt des Abeilles, 00.22S 11.52E, 1.ii.1986, A. Pauly, on *Harungana madagascariensis* (1♂ PCGB); W. NT., Bilé-Mêlen, 21.iii.1987, A. Pauly (1♂ PCGB). **BURUNDI:** Bururi, 900m, Nyamurembe, 7.iii.1953, P. Basilewsky (1♂ PCGB). **ZAIRE:** Tshuapa, Bokuma, i–iii.1954, R.P. Lootens, 3♀ MRAC; Equateur, Bokuma, ii & vii.1952, R.P. Lootens (1♀ 1♂ MRAC); Ubangi, Nouvelle Anvers, 9.xii.1952, P. Basilewsky (1♀ PCGB); Kivu, Uvira, 25–26.xii.1952, P. Basilewsky (1♀ 1♂ MRAC); Kivu, Mulungu, 5.iv.1937, H.J. Brédo (1♀ MRAC); Kivu, Bukavu, 26.vii.1931, J. Ogilvie (1♂ MRAC); Terr. de Kasongo,

riv. Lumami, i.1960, P.L.G. Benoit (1♂ MRAC); Ki-
sangani [= Stanleyville] 9.iv.1928, A. Collart (1♂
MRAC); Kisangani, 16.iv.1932, J. Vrydagh (2♂
MRAC); Kunzulu, ix.1917, R. Mayné (1♂ MRAC);
Boma, vii.1920, H. Schouteden (1♀ MRAC); Kisantu,
1932, R.P. Vanderyst (1♀ MRAC). KENYA: Karen,
Nairobi, 20.v.1967, C.D. Michener (1♀ SEMK).
RWANDA: Gitarama, 1850m., terr. Nyanza, i.1953, P.
Basilewsky (1♀ MRAC). ZIMBABWE: Victoria Falls,
4.i.1920 (1♀ TMSA); Bulawayo, 15.ii.1926, R.H.R. Ste-
venson (1♀ TMSA). BOTSWANA: Xugana, 19.03S
23.02E, 22–26.xi.1979, B. Lamoral (1♂ BCSA). NA-
MIBIA: 24 km S.E. Outjo, 23.ii.1977, J.G. & B.L. Rozen
(1♂ AMNH); Gobabis, 21.xii.1974, H. Empey (1♂
SANC). SOUTH AFRICA: Entabeni Forest Reserve,
33.00S 30.16E, 7–11.i.1987, C.D. Eardley (1♀ SANC);
Mogoto Nature Reserve, Zebediela, 24.15S 29.13E, 22–
25.x.1979, C.D. Eardley (1♀ SANC); Nylsvley Nature
Reserve, 24.39S 28.42E, 10–11.xii.1979, C.G. Moolman
(1♀ SANC); Lydenburg district, 1896, P.A. Krantz
(1♀ SANC); O.T.K. Reserve, near Loskop Dam,
25.27S 29.24E, 9–11.xii.1985, C.D. Eardley (1♀ 2♂
SANC); Weltevreden, 25.34S 31.10E, 24.i.1990, G.L.
Prinsloo (1♂ SANC); Mogol Nature Reserve, Ellisras
district, 23.58S 27.45E, 25–26.i.1982 & 27–29.ii.1984,
C.D. Eardley (2♀ SANC); D'Nyala Nature Reserve,
23.45S 27.49E, 8–12.xii.1989, C.D. Eardley (1♀ 1♂
SANC); Hope, near Ellisras, 17.xi.1962, H. Empey (1♂
SANC); Ben Alberts Nature Reserve, near Thabazim-
bi, 24.37S 27.23E, 24–28.xi.1980, C.D. Eardley (1♂
SANC); Schoongelegen, between Bulgeriver & Matla-
bas, 24.12S 27.45E, 14.i.1991, V.M. Uys (1♂ SANC);
Rustenburg, 6.xii.1969, L.C. Starke (1♂ SANC); Bo-
tanical Gardens, Pretoria, 25.45S 28.17E, 6.iv.1989,
C.D. Eardley (1♀ SANC); Johannesburg, i.1908, G.
Kobrow (1♂ TMSA); Strubens Valley, 31.xii.1965, H.
Empey (1♂ SANC); Potchefstroom, T. Ayrs (1♀
SAMC); Mfongosi, iii.1916, W.E. Jones (1♂ SAMC);
Umlaas Road, 19 km S.E. Pietermaritzburg, 23.i.1967,
C.D. Michener, D.J. Brothers (1♂ SEMK); Nagle Dam,
27 km E. Pietermaritzburg, 5.i.1967, C.D. Michener,
D.J. Brothers (1♀ SEMK); Weenen, iii.1924, H.P. Tho-
masset (1♂ SANC); Tongaat Beach, 10–11.iv.1971,
F.L. Farquharson (1♂ DMSA); Umgeni River, near
Table Mountain, 4.ii.1940, L. Bevis (1♂ AMGS);
Amanzimtoti, 10.iv.1952, C. Jacot-Guillarmod (2♀
AMGS); Drakensberg Botanic Gardens, near Harris-
mith, 28.17S 29.09E, 27.xii.1986, C.D. Eardley (1♂
SANC); Cookhouse, 14.i.1965, H. Empey (1♂ SANC);
Hilton, Grahamstown, 3–16.xi.1977, F.W. Gess (3♀
1♂ AMGS); Boesmans River, near Grahamstown,
iii.1954 (1♂ SANC); Hunts Drift, Fish River,
11.xii.1960, C. Jacot-Guillarmod (1♀ AMGS).

Other published distribution record.—
UGANDA: Kampala (Cockerell 1933c).

### Pasites paulyi Eardley, spec. nov.
(Fig. 19)

This species is named for the collector,
Dr A. Pauly (PCGB).

Description.—Similar to *P. friesei*. Length of
head 1.5–1.6 mm; scutum 1.1–1.3 mm; fore wing 4.5–
5.5 mm; body 5.0–6.4 mm. Integument black, except
tegula, legs and metasoma sometimes reddish. Ves-
titure mostly white, ventral surfaces of tarsi, female
T5, T6 and male T6, S6 with pale yellow tinge; female
T6 with subpygidial brush black medially, circum-
scribed by brownish-orange (Fig. 19, dense central re-
gion black, relatively sparse peripheral area brown-
ish-orange). Head mostly densely pubescent, upper
region of face and vertex with sparse vestiture (cf. Fig.
5); mesosoma with pronotal collar, most of pronotal
lobe, lateral regions of mesopleuron (excluding lower
hypoepimeral area) and posterolateral regions of pro-
podeum densely pubescent; remainder of mesosomal
vestiture sparse; vestiture on legs dense, except tro-
chanters and femora sparse to very sparse, ventral
surfaces of tarsi very dense; T1 anterior surface and
posterolateral region with dense plumose vestiture,
remainder of T1 sparse, simple vestiture; T2 and
sometimes T3 with dense, posterolaterally directed,
vestiture posterolaterally, anterior regions of each ter-
gum with sparse, simple vestiture; female T3/T4-T5,
male T3/T4-T6 with moderately dense distal fringes
of posteriorly directed hairs (vestiture sparse and
simple anteriorly); female T6 with sparse vestiture,
weakly developed subpygidial brush (Fig. 19); female
S2-S4 with vestiture fairly sparse anteriorly and
dense posteriorly, S5 with moderately dense vestitu-
re, distal margin velutinous; male metasomal venter
moderately densely pubescent. Labrum little longer
than wide, labrum with small tubercle apicomedially;
maxillary palp five-segmented, subequal in length to
pedicel; scutum consistently 1.1× as long as its nar-
rowest width, punctures moderately large, often con-
fluent; scutellum evenly convex, without pronounced
paramedian swelling; propodeum distinctly glabrous
mediolongitudinally; mesopleuron mostly densely
punctate, hypoepimeral and ventral regions sparsely
punctate; female pygidial plate with posterolateral
carina more strongly developed than in *P. friesei* (Fig.
19), subpygidial brush quadrate (Fig. 19), S5 deeply
emarginate posteromedially (Fig. 19), S6 narrowly bi-
fid; male with well developed, broadly rounded py-
gidial plate (cf. Fig. 7); male S7 and genital capsule as
in *P. barkeri* (cf. Figs. 8 & 10); male S8 similar to that
of *P. friesei*, except little more truncate distally (cf. Fig.
17).

Distribution.—Woodlands of northern
Cameroon.

Discussion.—In this species the maxil-
lary palp is five-segmented, female pygi-
dial plate notched posteriorly and subpy-
gidial brush brownish-orange with a black
centre. The male S7 has the lateral margins
gently concave and posterior end more or
less gently rounded (cf. Fig. 8).
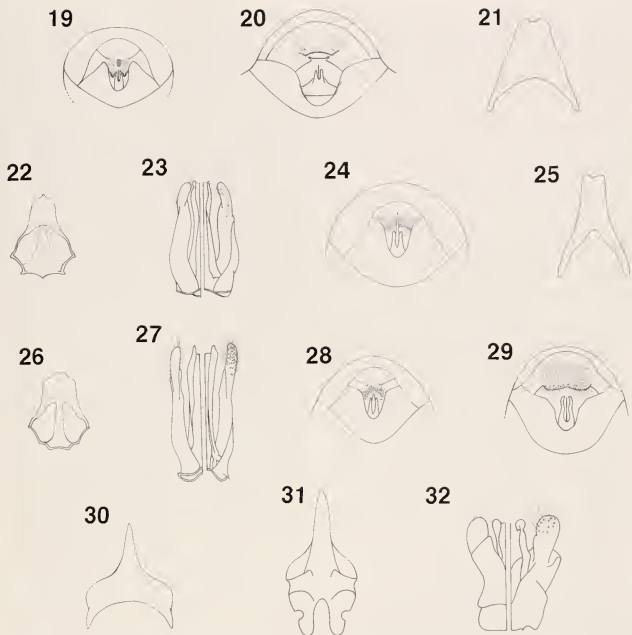
Figs. 19–32. *Pasites* spp. 19. *P. paulyi*, terminalia, posterior view, ♀; 20–23. *P. humectus*. 20. Terminalia, posterior view, ♀; 21. S7, ♂; 22. S8, ♂; 23. Genital capsule, ♂. 24–27. *P. bicolor*. 24. Terminalia, posterior view, ♀; 25. S7, ♂; 26. S8, ♂; 27. Genital capsule, ♂. 28. *P. tegularis*, terminalia, posterior view, ♀. 29–32. *P. gnomus*. 29. Terminalia, posterior view, ♀; 30. S7, ♂; 31. S8, ♂; 32. Genital capsule, ♂.

*Type material.*—Holotype ♂, paratypes 3♀: CAMEROON: Parc Nat. Waza, 11.21N 14.35E, 5.viii.1987, A. Pauly (holotype ♂ 1♀ PCGB, 1♀ SANC); Maga, 10.50N 14.59E, 3.viii.1987, A. Pauly, Fl. No. 374 (1♀ PCGB).

### *Pasites braunsi* (Bischoff), comb. nov.

*Morgania (Omachthes) braunsi* Bischoff 1923:587.
*Omachthes braunsi* (Bischoff); Anonymous 1958: 31.

*Description.*—Female (male unknown). Length of head 1.4–1.9 mm; scutum 1.2–1.6 mm; fore wing 4.7–5.8 mm; body 5.0–6.5 mm. Similar to *P. friesei* except as follows: subpygidial brush black medially, circumscribed by brownish-orange; labrum pointed, very weakly tuberculate apicomedially; maxillary palp three-segmented, subequal in length to antennal pedicel; pygidial plate with posterolateral carina more strongly developed; subpygidial brush quadrate.

*Distribution.*—Ranges from bushveld, in Zimbabwe, Namibia and parts of South Africa, to montane grassland in Lesotho.

*Discussion.*—This species closely resembles *P. paulyi* in the notched pygidial plate and black central spot in the subpygidial brush, but differs in that the maxillary palp is three-segmented.

*Type material examined.*—*Omachthes braunsi*, holotype ♀: 'Bothaville, Oranje Fr. Sta., 13.xi.1898, Dr Brauns; *Omachthes braunsi* Bisch. Typ.; Typus Bischoff; *Omachthes braunsi* Biss. Type No. 566' (TMSA).

*Additional material examined.*—31♀: ZIMBABWE: Bulawayo, 21.xii.1919 (1♀ SANC). NAMIBIA: Regenstein 32, 2217 CA, 12.xii.1973 (2♀ SMWH). 5 km S. Okahandja, 30.iii–1.iv.1979, J.G. Rozen (3♀ AMNH); 3 km S. Windhoek, 11.iii.1976, J.G. & B.L. Rozen (1♀ AMNH). LESOTHO: Mamathes, ii.1946 & i.1961, C. Jacot-Guillarmod (3♀ AMGS); Hensley's Dam Leribe, 29.ii.1948, C. Jacot-Guillarmod (1♀ AMGS). SOUTH AFRICA: Kruger National Park, Skukuza, 24.59S 31.55E, 292m, 19.i.1984, C.D. Eardley (2♀ SANC); same locality, 14–17.i.1985, G.L. Prinsloo (3♀ SANC); Bishop's Nature Reserve, Thabazimbi, 24.37S 27.32E, 24–28.xi.1980, M.W. Mansell (1♀ SANC); Johannesburg, 4.ii.1978, H.R. Hepburn (1♀ SEMC); Queenstown, 16.xii.1979, H. Empey (1♀ SANC); Whittlesea, i.1979, C.D. Eardley (1♀ SANC); Hilton, Grahamstown, 28.ii–17.iii.1978, F.W. & S.K. Gess (7♀ AMGS); Willow Glen, Grahamstown, 24.xi.1982, D.W. Gess (1♀ AMGS); Belmont Valley, Grahamstown, 24.xi.1982, F.W. & S.K. Gess, 24.xi.1982 (2♀ AMGS); Strowan, W. Grahamstown, i.1980, D.J. Brothers, P. Hulley & C. Jacot-Guillarmod (1♀ BCSA).

## Pasites humectus Eardley, spec. nov.
### (Figs. 20–23)

This species is apparently endemic to the humid regions of tropical Africa, hence the name *humectus*.

*Description.*—length of head 1.1–1.5 mm; scutum 0.8–1.2 mm; fore wing 4.0–5.6 mm; body 3.7–4.5 mm. Integument of head and mesosoma black, except labrum, mandible, antennal flagellum, tegula, pronotal lobe and legs (coxae excluded) which are mostly reddish-black; metasoma black to reddish-black. Vestiture mostly white, ventral surfaces of tarsi pale yellowish, terminal segment of metasoma brownish-orange. Head mostly moderately densely pubescent, lower half very densely pubescent (cf. Fig. 5); mesosoma with scutum and ventrolateral region of mesepisternum sparsely pubescent, remainder of mesosoma very densely pubescent; legs densely pubescent, except trochanters and femora sparsely pubescent; metasoma naked to very sparsely pubescent, except T1 with anterior (subvertical) surface mostly densely plumose, with dense posterolateral tuft; T2–T3 with broadly medially interrupted distal fring-

es; female T4–T5, male T4–T6 with well developed distal fringes; female T6 with distal end densely clothed with velutinous vestiture (Fig. 20), with weakly developed subpygidial brush (Fig. 20); male T7 largely naked; metasomal venter with sparse vestiture, except distal ends of S2–S4, in female, and S2–S5, in male, with dense distal fringes; S5 in female and S6 in male velutinous. Labrum little longer than wide (1.1:1), flattish with weakly developed tubercle apicomedially, angulate apicolaterally (cf. Fig. 14); maxillary palp two-segmented, half as long as pedicel; scutum moderately densely punctate, punctures large, sometimes convergent; scutellum gently curved with paramedian region gently swollen; propodeum with mediolongitudinal region broadly glabrous; female T6 virtually devoid of pygidial plate, but with small carina visible (Fig. 20); female S5 broadly emarginate (Fig. 20), S6 narrowly bifid posteriorly; male S7, S8 and genital capsule as in Figs. 21–23.

*Distribution.*—Wooded areas in tropical Africa, from Nigeria to Tanzania.

*Discussion.*—The pygidial plate of the female of *P. humectus* is strongly reduced, almost absent (Fig. 20). The male S7 tapers gradually towards the gently concave posterior end (Fig. 21).

*Type material.*—Holotype ♀, paratypes 17♀ 8♂: ZAIRE: Malela, 6.00S 12.40E, 8.vii.1915, Lang & Chapin (holotype ♀ AMNH); Kisangani, 25.10E 0.30N, ii & iv.1915 (1♀ 1♂ AMNH). NIGERIA: Lagos, 18.viii.1966, C.D. Michener (2♂ SEMK). CAMEROON: Bambui, near Bamenda, 1400 m, 9 & 20.vii.1966, C.D. Michener (12♀ 1♂ SEMK, 2♀ SANC); Tingoh, Menchin River, near Wum, 7100 m, 14.viii.1966, C.D. Michener (1♂ SEMK); Lolodorf, 10.viii.1920, A.I. Good (1♂ ICCM Acc 6552); same data except 6.vii.1926 (1♀ ICCM). GABON: 4.xii.1909, A.I. Good (1♂ SANC Acc 4189); same data except 23.xi.1909 (1♀ SANC). TANZANIA: Morogoro, 19.x.1956, W.E. Kerr (1♂ SEMK).

## Pasites bicolor Friese
### (Figs. 24–27)

*Pasites bicolor* Friese 1900:262.
*Pasitomachthes bicolor* (Friese); Bischoff 1923: 597–598.
*Pasites bicoloratus* Warncke 1983:291 [*nom. nov. pro P. bicolor* Friese *nec* (Lepeletier)].

Friese (1900) attributed the authorship of this species to 'de Saussure *in litt.*', but the article was clearly written by Friese, as it is in his distinct style and part of a larger paper by him. The name should therefore

be attributed to Friese, according to the Code, Article 50(a). The species was described from two females from Nossi-Bé and Antananarivo in Madagascar. Bischoff (1923) regarded the type series to contain two different species, belonging to distinct genera, and described the Antananarivo syntype as *Pasitomachthes bicolor*. Both syntypes of *Pasites bicolor* were originally deposited in the ZMHB, but the curator of that collection, Dr F. Koch, was unable to trace the syntype from Nossi-Bé. The syntype from Antananarivo is here designated as the lectotype of *Pasites bicolor*, which makes that name an objective senior synonym of *Pasitomachthes bicolor*. Should the paralectotype from Nossi-Bé be found, and prove to represent a different species, a new name may then be required for it.

Warncke (1983) renamed *P. bicolor* as *P. bicoloratus* because the name *bicolor* was preoccupied by *Ammobates bicolor* Lepeletier and he considered *Ammobates* to be a subgenus of *Pasites*. As *bicolor* Friese was rejected after 1960 and is here not considered to be congeneric with *bicolor* Lepeletier, the replacement name is invalid according to the Code, Article 59(d).

*Description.*—Length of head 1.5–1.9 mm; scutum 1.3–1.7 mm; fore wing 5.9–7.3 mm; body 5.9–7.6 mm. Integument of head, mesosoma and legs entirely black to mostly black or blackish with labrum, mandible, pronotal lobe and tegula orange to orangish, legs blackish-orange to orange; metasoma completely orange to reddish-black (latter with mottled appearance). Vestiture mostly white, anteromedian region of scutum with slight yellow tinge, ventral surfaces of tarsi pale yellow, T6 and S5 mostly pale yellowish, subpygidial brush reddish. Vestiture on lower region of face and gena plumose, upper region of face and vertex simple (*cf.* Fig. 5); mesosoma mostly pubescent, dorsum and ventral region of mesopleuron with simple to weakly plumose vestiture; vestiture on coxae plumose, remainder of legs simple; propodeum densely pubescent, except propodeal triangle which is naked; T1 with anterior surface sparse, plumose, remainder of vestiture fine and simple, except posterolateral region which ranges from naked to sparsely clothed with simple to weakly plumose vestiture (never densely plumose); distal margin of T1 naked and glabrous; T2 with sparse fine vestiture, except posterolaterally where it is dense; female T3 and male T3-T4 similar to T2, except vestiture on posteromedial

region ranges from sparse and simple to dense and plumose (where latter occurs, vestiture forms dense cross-band); female T4-T5, male T5-T6 with vestiture sparse and simple anteriorly, dense and plumose posteriorly; female T6 with sparse, erect, simple hairs, except subpygidial brush which is fairly dense (Fig. 24), male T7 sparsely pubescent; metasomal venter fairly sparsely clothed with fine, simple vestiture, except distal margin of female S5 with fine dense vestiture. Labrum quadrate, apex strongly tuberculate, rounded apicolaterally; maxillary palp three-segmented, half as long as pedicel of antenna; scutum densely punctate, punctures small, distinctly separate; tegula weakly convex, giving the impression that it is proportionately larger than in its congeners; scutellum strongly convex with deep mediolongitudinal cleft, appearing strongly swollen paramedially; propodeal triangle glabrous, weakly striated in places; mesopleuron fairly densely punctate, punctures separate; female T6 devoid of pygidial plate (Fig. 24), male pygidial plate well developed, broadly rounded distally; female subpygidial brush weakly defined (Fig. 24); female S5 distinctly concave (Fig. 24); S6 narrowly bifid (*cf.* Fig. 7); male S7, S8 and genital capsule as in Figs. 25–27.

*Distribution.*—Madagascar, forest to deforested and cultivated areas.

*Discussion.*—The females of the two Madagascan species, *P. bicolor* and *P. tegularis*, are similar, and the males are indistinguishable. The most salient diagnostic feature of the females is the complete loss of the pygidial plate in the former, as opposed to the reduced pygidial plate in the female of *P. tegularis*. Associated with the loss of the pygidial plate, the T6 is distinctly more rounded in *P. bicolor*; the remnants of the pygidial plate in *P. tegularis* form two dorsolateral carinae which give the T6 more angulate appearance. The males of *P. bicolor* and *P. tegularis* can be separated from the other species in the group by the S7 which is more or less parallel-sided posterolaterally and emarginate posteriorly (Fig. 25).

*Type material examined.*—Lectotype ♀: 'Madagasc, Annanarivo [label almost illegible] *Pasites bicolor* Sau. ♀. Madagascar; Typus; *Pasitomachthes bicolor* Bisch. Typ. ♀; Zool. Mus. Berlin' (ZMHB).

*Additional material examined.*—8♀ 4♂: **MADAGASCAR:** N.E., Fampanambo, iv.1959, J. Vadon (2♀ MRAC); Centre Province: Antananarivo, Angavokely, 17.ii.1992, 18.56S 47.45E, PL. REPR. ECOL.

PROI. (5♀ 3♂ NCUS); Centre Province, Angavokely, 17.iii.1988, L.A. Nilsson (1♀ 1♂ NCUS).

### *Pasites tegularis* Friese
### (Fig. 28)

*Pasites tegularis* Friese 1922:38–39.
*Morgania* (*Omachthes*) *tegularis* (Friese); Bischoff 1923:589.

This species is most closely related to *P. bicolor*, which Bischoff (1923) placed in *Pasitomachthes*.

*Description.*—Length of head 1.3–1.6 mm; scutum 1.0–1.4 mm; fore wing 4.2–6.1 mm; body 5.2–6.9 mm. Integument of head and mesosoma mostly black or blackish with labrum, mandible, pronotal lobe and tegula orange to orangish; legs blackish-orange to orange; metasoma completely orange to reddish-black (latter with mottled appearance). Vesiture similar to *P. bicolor* in colour except as follows: scutum mostly pale yellow, sometimes white; pygidial brush brownish; propodeum densely pubescent, except mediolongitudinal region which is naked; T1 with posterolateral region densely pubescent; female T6 with sparse, erect, simple vesiture, except with dense subpygidial brush. Structure similar to *P. bicolor* except as follows: maxillary palp three-fourths as long as pedicel of antenna; mediolongitudinal region of propodeum glabrous (dorsolateral region of propodeal triangle pubescent, glabrous area not confined to propodeal triangle mediolongitudinally), without any striations; female pygidial plate reduced to weakly developed dorsolateral carina on T6 (Fig. 28).

*Distribution.*—Madagascar, forest to deforested and cultivated.

*Discussion.*—The pygidial plate of *P. tegularis* is weakly developed laterally and absent posteriorly. It is the only known Madagascan species in which a pygidial plate occurs in the female. The male is indistinguishable from that of *P. bicolor*.

*Type material examined.*—Holotype ♀: 'Nossi-Bé, *Pasites bicolor* ♀ var.; *Pasites tegularis* ♀ Fr. 1904 Friese det.; Type; *Omachthes tegularis* (Fr.) ♂ Typ.'; Coll. Friese, Zool. Mus. Berlin' (ZMHB).

*Additional material examined.*—12♀ 7♂: MADAGASCAR: N.E., Fampanambo, J. Vadon, iv.1959 (3♀ 5♂ MRAC), vi.1960 (1♀ MRAC), xii.1962 (1♀ MRAC), 1962 (1♀ MRAC); Tamatave Province, 6 km N. Tamatave, 15.i.1985, J.W. Wenzel (2♀ SEMK); Tulear Province, 45 km S. Mahabo, 20.42S 44.38E, 24–26.xii.1986, J.W. Wenzel (1♀ SEMK); Tananarive Province, 17 km W. Ambatolampy, 19.24S 47.25E, 1650m, 30.i.1985, J.W. Wenzel (1♂ SEMK); Rogez, vii.1937, A. Seyrig (1♂ MRAC); Est. Neaux Nottes, S. St. Marie,

6.xii.1983, L.A. Nisson, L. Jonsson (1♀ NCUS); Est. Soanierana Ivongo S, 27.x.1987, L.A. Nilsson (1♀ NCUS).

## GNOMUS SPECIES GROUP

This species group is monotypic.

### *Pasites gnomus* Eardley, **spec. nov.**
### (Figs. 29–32)

The specific epithet of the name of this tiny species is New Latin and refers to its small size.

*Description.*—Length of head 0.7–0.8 mm; scutum 0.4–0.5 mm; fore wing 2.0–2.2 mm; body 2.3–2.5 mm. Integument generally black to blackish-orange, with mandible, antenna, distal ends of tibiae, tarsi, basal region of T1 and metasomal venter orange to orangish (female more extensively orange coloured than male). Vesiture mostly white; ventral surfaces of tarsi and female T6 and S5 pale yellow. Scutal vesiture largely simple; trochanters and femora sparsely pubescent; metasoma with anterior and posterolateral regions of T1 densely pubescent; T2 with broadly interrupted distal fringe, female T3-T4, male T3-T5 with continuous distal fringes; female T6 densely pubescent posteriorly (Fig. 29), with short and long vesiture (distal end of male metasoma damaged and cannot be accurately described); S1-S4 sparsely pubescent, female S5 with sparse vesiture which comprises mixture of short and long hairs. Labrum quadrate, generally flat, distinctly pointed apically; maxillary palp absent; scutum moderately densely punctate, punctures small, shallow and separate; scutellum gently and evenly convex, devoid of any exaggerated swelling paramedially; propodeum devoid of mediolongitudinal glabrous area; punctation on propodeum and mesopleuron similar to scutum; pygidial plate absent in both sexes; female T6 flattened posteromedially, this area densely clothed with short, fine vesiture, that on subpygidial area very short, subpygidial brush weakly developed (Fig. 29); female S5 conically emarginate, S6 narrowly bifid (Fig. 29); male S7-S8 acutely pointed posteriorly, S8 with two anterior lobes (Figs. 30–31); male genital capsule as in Fig. 32.

*Distribution.*—Niger, near Tahoua, which is grassland wooded with *Acacia* and deciduous shrubs.

*Discussion.*—*Pasites gnomus* is distinct from its congeners. It can be easily recognised by its small size, absence of a pygidial plate in both sexes, truncate and finely pubescent posteromedian region of the female T6, acute apices of the male S7 & S8 and two anterior lobes of the male S8

Fig. 33. *Pasites carnifex*, habitus, dorsal view (dark shading represents black integument and lightly shaded areas are orange), ♀.

(Figs. 29–31). In the cladistic analysis it is grouped with *P. friesei* by the loss of the anteromedian lobe on the male S8 (Fig. 31).

*Type material.*—Holotype ♀, paratype ♂: **NIGER:** 20km S. Tahoua, 14.45N 5.20E, 13.viii.1987, A. Pauly (PCGB).

## CARNIFEX SPECIES GROUP

Two species have been placed in the carnifex species group: *P. carnifex* and *P. dichrous*. These two species are large (7.0–12.5 mm) with the head and mesosoma black and metasoma orange. The distal fasciae of T2–T4 are sparse, with posteriorly directed vestiture. The female pygidial plate and subpygidial brush are well developed, and the S5 is conically emarginate posteromedially. Males resemble females in colour, but do not have any other obvious unique features.

### *Pasites carnifex* (Gerstaecker), **comb. nov.**
### (Figs. 33–37)

*Omachthes carnifex* Gerstaecker 1869:155.
*Omachthes nigripes* Friese 1915:276, 296, 298. **Syn. nov.**
*Morgania nigripes* (Friese); Cockerell 1919:190.
*Morgania (Omachthes) nigripes* (Friese); Bischoff 1923:591.
*Morgania fortis* Cockerell 1921:207–208. **Syn. nov.**
*Pasites magnificus* Brauns 1926:207–208.
*Morgania magnificus* [*sic.*] (Brauns); Cockerell 1933b:130 [*lapsus*].
*Morgania subfortis* Cockerell 1933c:107. **Syn. nov.**
*Morgania (Omachthes) stordyi* Cockerell 1933a: 377. **Syn. nov.**
*Morgania (Omachthes) voiensis* Cockerell 1937a: 155. **Syn. nov.**
*Morgania (Omachthes) altior* Cockerell 1937a:155. **Syn. nov.**
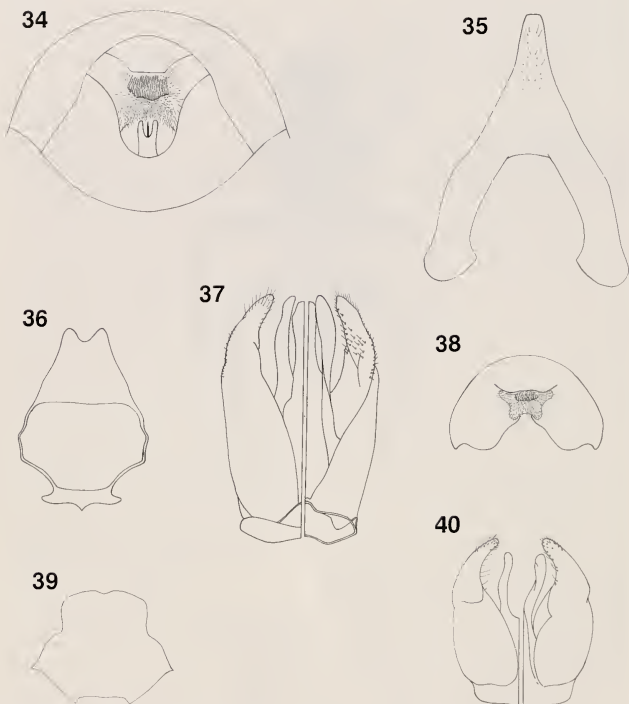
Figs. 34–40. *Pasites* spp. 34–37. *P. carnifex*. 34. Terminalia, posterior view, ♀; 35. S7, ♂; 36. S8, ♂; 37. Genital capsule, ♂. 38–40. *P. dichrous*. 38. Terminalia, posterior view, ♀; 39. S8, ♂; 40. Genital capsule, ♂.

Small differences in size, colour and wing venation of this striking species led to the description of several synonyms. *Pasites magnificus* was synonymized with *fortis* by Cockerell (1933b), and *nigripes*, *fortis*, *subfortis*, *stordyi*, *voiensis* and *altior* are here synonymized with *carnifex*. The synonymy of these six species follows the study of the type material of each species,

which was found to be within the range of variation established for this species during the study. *Omachthes nigripes* was described from a male and female from Eritrea, neither of which could be obtained for study, and a female from Usambara, Tanzania, which was studied and is here designated as the lectotype.

*Description.*—Habitus, dorsal aspect, as in Fig.

33. Length of head 2.4–2.7 mm; scutum 2.3–2.5 mm; fore wing 8.6–10.0 mm; body 11.1–12.5 mm. Colour of integument, dorsal aspect, as in Fig. 33 (darkly shaded areas illustrate black integument, light shading orange areas); head and mesosoma mostly black, distal region of mandible and sometimes antenna and labrum reddish, legs completely black to blackish proximally, orange distally; metasoma orange to reddish-orange. Vestiture on head brown to white; mesosoma mostly brownish, ventral surface of hind tarsus always orange; metasoma mostly orange, subpygidial brush mostly black, except ventral region sometimes orange or orangish. Middle and lower regions of face and gena, entire labrum densely pubescent; upper region of face and vertex with moderately dense, largely simple, vestiture; mesosoma generally densely clothed with short vestiture, peripheral fringe of pronotal lobe, coxae, tibiae and tarsi densely clothed with long plumose hairs; metasoma largely clothed with short, fine, simple vestiture; subpygidial brush well developed, not expanded dorsally, differentiated, dorsal region with thick hairs and ventral region with fine vestiture (Fig. 34); S5 velutinous. Labrum more or less quadrate, distal end generally rounded, sometimes slightly pointed picomedially; maxillary palp four-segmented, 1.4–1.7× as long as pedicel; scutum mostly very densely punctate, punctures very small and separate; scutellum weakly to moderately tuberculate paramedially; punctation on pleural and ventral regions of mesosoma and entire propodeum moderately dense to very dense; pygidial plate well developed in both sexes (female pygidial plate, as in Fig. 34); female S6 broadly bifurcate; male S7 and S8 as in Figs. 35–36; genital capsule (Fig. 37) more elongate than *P. dichrous.*

*Distribution.*—Apparently occurring throughout East and South-East Africa, and from a single locality in West Africa, mostly in forest and woodland.

*Discussion.*—In *P. carnifex* the subpygidial brush is gently concave ventrally (Fig. 34), not distinctly bilobed as in *P. dichrous* (Fig. 38). The males of these two species differ in the shape of the S8, in *P. carnifex* it tapers towards the distinctly concave posterior end, whereas in *P. dichrous* the posterior region is parallel-sided and the posterior end more or less entire (notched medially) (*cf.* Figs. 36, 39).

*Type material examined.*—*Omachthes carnifex,* holotype ♀: 'Capland, Drége S., 639; Type, *carnifex* Gerst. dichrous Klug i.l., Omachthes carnifex Gerst. 1907 Friese det.; Omachthes dichrous Spin.; Zool. Mus. Berlin' (ZMHB). *Omachthes nigripes,* lectotype ♀: 'D.O.-

Africa, Usambara, 6.1903; Omachthes nigripes ♀ Fr. 1914 Friese det., Type; Omachthes nigripes Fr. i.l. Type Bischoff ♀; Zool. Mus. Berlin' (ZMHB). *Morgania fortis,* holotype ♀: 'F.J. Kroeger, Moboki, Lydenb. Transv.; Morgania fortis Ckll. TYPE' (SAMC). *Pasites magnificus,* holotype ♀: 'Sawmills S.R., 22.3.1919. Rhodesia Museum; Pasites magnificus ♀ Type No. 571' (TMSA). *Morgania subfortis,* holotype ♀: 'Musée du Congo, Ituri: Blukwa, 3/4.xii.1928, A. Collart; Morgania subfortis Ckll. TYPE' (MRAC). *Morgania stordyi,* holotype ♂: 'Brit E. Africa, R.J. Stordy, 1912-329; Morgania stordyi Ckll. TYPE; B.M. TYPE HYM. 17B 80' (NHML). *Morgania voiensis,* holotype ♀: 'Brit E. Af., Voi., 1 800 ft. Mch. 21–23,1911, S.A. Neave, 1911-177; Morgania voiensis Ckll. TYPE; B.M. TYPE HYM. 17B 77' (NHML). *Morgania altior,* holotype ♂: 'Brit E. Afr., S.E. Slopes of Kenya, 6 000 to 7 000 ft., Mch. 3–12.1911, S.A. Neave, 1911-177; Morgania altior Ckll. TYPE; B.M. TYPE HYM. 17B 78' (NHML).

*Additional material examined.*—10♀ 2♂: **BURKINA FASO:** riv. Volta Rouge, 15 Km Kokhologo, 22.x.1979, A. Pauly (1♀ PCGB). **ZAIRE:** 'P.N.A. vers Rweru (Volc. Mikeno) 2400 m., (Bambous), 26 au 27.vii.1934, G.F. de Witte: 501' (1♀ MRAC). **ZIMBABWE:** Umtali, 26.ii.1942 (1♀ SAMC); Chimanimani, 1050 m, 25.iv.1985, J. Gusenleitner (1♀ SCAA); Sawmills, 24.ii.1925, R.H.R. Stevenson (1♀ TMSA, 1♀ SANC); Bulawayo, 16.iii.1919 (1♀ SAMC). **SOUTH AFRICA:** Uhmlali, 14.iv.1946, R.F. Smith (1♀ AMGS); Waterval Boven, 18.ii.1969, L.C. Starke (2♀ SANC); Magoebaskloof, 23.58S 30.00E, 5.ii.1986, J.S. Donaldson (1♂ SANC); Schoemanville, 26.xii.1959, H. Empey (1♂ SANC).

*Other published distribution records.*—**ERITREA** (Friese 1909b); **UGANDA:** Semliki Plain (Cockerell 1933a); **KENYA:** Laikipia Escarpment; **TANZANIA:** Sanje (Cockerell 1933c); **UGANDA:** Busongora; **MALAWI:** Mulanje & Blantyre (Cockerell 1937b).

## *Pasites dichrous* Smith
### (Figs. 37–40)

*Pasites dichroa* [sic.] Smith 1854:253 [lapsus].

*Homachthes dichrous* (Smith); Dalla Torre 1896:499.

*Morgania dichroa* (Smith); Cockerell 1904:207.

*Omachthes dichroa* [sic.] (Smith); Friese 1909a:437 [lapsus].

*Homachthes gerstaeckeri* Schulz 1906:267 [*nom. nov. pro P. dichrous* Smith *nec 'Ammobates dichrous*' Spinola, *nomen nudum*].

*Morgania gerstaeckeri* (Schulz); Cockerell 1910:217.

*Morgania (Morgania) gerstaeckeri* (Schulz); Bischoff 1923:592.

*Morgania nigrithorax* Strand 1912:310–311. **Syn. nov.**

*Morgania (Morgania) nigrithorax* Strand; Bischoff 1923:593.

When Smith (1854) described this species he suggested that it was probably generically distinct, and recommended the generic name *Morgania* for the taxon. Spinola (1843) mentioned the existence of a specimen in '*Mus, Berol*' (= ZMHB) that had been labelled *Ammobates dichrous*. According to the Code, Article 12(a), this name has no standing in zoological nomenclature, however, because the species was not described. Schulz (1906) established that Spinola's (1843) '*Ammobates dichrous*' and Smith's (1854) *Pasites dichrous* were congeneric, but not synonymous. He disregarded the fact that '*Ammobates dichrous*' had never been described and unjustifiably renamed Smith's (1854) species, which he considered to be a junior homonym, as *gerstaeckeri*.

Strand (1912), in the original description of *M. nigrithorax*, indicated that the type series comprised three females. In reality the type series consists of two females and a male (Bischoff 1923), of which one female and the male were studied. The female that was studied is here designated as the lectotype.

*Description.*—Length of head 1.8–2.0 mm; scutum 1.5–1.6 mm; fore wing 7.1–8.0 mm; body 7.0–8.6 mm. Similar to *P. carnifex* except as follows: legs with femora, tibiae and tarsi orange; vesture on head and mesosoma mostly white, scutum yellowish-brown; subpygidial brush of female mostly brownish-orange, black dorsomedially, well developed, differentiated, expanded dorsally, bilobed ventrally (Fig. 38); flagellar segment I around 0.34× as long as scape, 1.2× as long as flagellar segments II; labrum distinctly pointed apicomedially; maxillary palp 1.0–1.2× as long as pedicel; scutum moderately densely punctate, with small, well separated punctures; scutellum strongly tuberculate paramedially; punctation of area above scrobal sulcus moderately dense; female S6 narrowly bifid posteriorly; male S8 and genital capsule as in Figs. 39–40 (male S7 missing from specimen studied).

*Distribution.*—Central Zaire, Equatorial Guinea and northern Angola, dominant vegetation evergreen forest.

*Discussion.*—The female of *P. dichrous* can be separated from *P. carnifex* by the dorsal expansion and two ventral lobes of the subpygidial brush (Fig. 38). For the posterior region of the male S8 is parallel sided and the posterior end gently curved with a median notch (Fig. 39).

*Type material examined.*—*Pasites dichrous*, holotype ♂: 'dichroa Type SM.; *Morgania dichroa* TYPE Smith; B.M. TYPE HYM. 17B 79' (NHML). *Morgania nigrithorax*, lectotype ♀: 'Sp. Guinea, Uelleburg, 6–8.1908, G. Tessmann S.G.; *Morgania nigrithorax* Strand det. ♀ m.; Type; Zool. Mus. Berlin' (ZMHB); paralectotype ♂: 'Span. Guinea, Uelleburg, G. Tessmann S.G.; *Morgania nigrithorax* Strand det. ♀ m.; Type; *Morgania nigrithorax* Strd. ♂ Bischoff, Lectotype' (ZMHB).

*Additional material examined.*—2♀: ZAIRE: Kisangani (= Stanleyville), 0.30N 25.10E, 13.iv.1915, Lang & Chapin (1♀ AMNH). ANGOLA: Dundo (Distr. Lunda), ii–iv.1958 (1♀ BLCU).

*Other published distribution records.*—ZAIRE: Kasai, Dungu & Lac Kivu (Cockerell 1933c).

## JENSENI SPECIES GROUP

This species group comprises four species, *P. jenseni*, *P. namibiensis*, *P. histrio* and *P. jonesi*. These four species all have the head, mesosoma and legs mostly black; the metasoma ranges from black to orange. The vestiture on the lower half of the face is pallid, densely plumose and appressed. The most useful diagnostic features of the females of the group are the elliptical posteromedian concavity on S5, in combination with the pygidial plate, which is at least visible posteriorly (posterior margin entire), and the differentiated subpygidial brush. Males can only be identified as belonging to the group by their association with females.

### *Pasites jenseni* (Friese), **comb. nov.**
(Figs. 41–46)

*Omachthes graenicheri* var. *jenseni* Friese 1915: 298.

*Morgania graenicheri jenseni* (Friese); Cockerell 1919:190.

*Morgania (Omachthes) jenseni* (Friese); Bischoff 1923:587.

*Epeolus jenseni* (Friese); Friese 1941:101.

Fig. 41. *Pasites jenseni*, habitus, lateral view (integument black and vestiture largely white), ♀.

*Omachthes jenseni* Friese; Anonymous 1958:32.

*Omachthes (Ammobates) graenicheri* Brauns; Friese 1915:298, *nomen nudum*.

*Morgania graenicheri* (Brauns); Cockerell 1919: 190.

*Morgania graenicheri* Bischoff 1923:587–588. **Syn. nov.**

*Omachthes graenicheri* Brauns; Friese 1922:38.

*Pasites graenicheri* (Brauns); Anonymous 1958: 31.

*Omachthes alboguttatus* Friese 1922:38. **Syn. nov.**

*Morgania (Omachthes) alboguttatus* [*sic.*] (Friese); Bischoff 1923:588 [*lapsus*].

*Morgania alboguttata* (Friese); Cockerell 1933b: 130.

*Morgania natalensis* Cockerell 1933b:129–130. **Syn. nov.**

*Morgania (Omachthes) ogilviei* Cockerell 1935: 560–561. **Syn. nov.**

Friese (1915) described *jenseni* as a 'variety' of *graenicheri*, which he attributed to Brauns *in. litt.* But neither Brauns nor anybody else had described *graenicheri* at that time, so *jenseni* is the oldest available name for this species, according to the Code, Articles 12 & 23. Bischoff (1923) provided a brief description of *graenicheri* in a key and also attributed it to Brauns 'i.l.', the name was thus made available from that date.

Intraspecific variation in the colour, vestiture and punctation of the species led Friese (1922) and Cockerell (1933b, 1935) to describe three morphological variants as distinct species. Following the study of both the type and other material, *alboguttata*, *natalensis* and *ogilviei* were found to fall within the range of variation of *jenseni* and are here synonymized with it.

*Description.*—Habitus, lateral aspect, as in Fig. 41. Length of head 2.1–3.0 mm; scutum 1.8–2.7 mm; fore wing 7.3–9.8 mm; body 7.8–12.5 mm. Integument, including tegula, mostly black, reddish-black in places. Vestiture white, except mandible, ventral surfaces of tarsi and distal region of S5 pale yellow, subpygidial brush completely black to mostly black with lateral and ventral regions orangish. Middle and lower regions of face, labrum and gena very densely pubescent, upper region of face and vertex moderately densely clothed with simple vestiture (Fig. 42); me-

sosomal dorsum with moderately dense to sparse, simple vestiture, except pronotal collar very densely pubescent and posterolateral regions of scutum with plumose vestiture; periphery of pronotal lobe, subvertical (posterior) region of scutellum, metanotum and propodeum (including mediolongitudinal region) densely clothed with short to long vestiture; legs generally with coxae, most of tibiae and entire tarsi densely pubescent, remainder of legs with long, simple, sparse vestiture or naked; dorsal surface of tibiae also with reddish scales; metasoma generally with anterior and anterolateral regions of T1 moderately densely pubescent, posterolateral regions very densely pubescent; T2-T3 in females, T2-T4 in males with lateral regions of distal margins densely pubescent (T4 in female and T5 in male with distal fringe narrowly interrupted medially or continuous); female T5 and male T6 with densely pubescent distal fringe; females with subpygidial brush well developed, 1.1× as long as its maximum width, differentiated, mostly thick black hairs; metasomal venter sparsely to densely clothed with simple, white vestiture, posterolateral regions of S3-S4 sometimes plumose, distal region of S5 velutinous. Labrum quadrate and flattish, pointed and distinctly tuberculate mediodistally; maxillary palp five-segmented, generally 2–3× as long as antennal pedicel; scutum moderately densely punctate with large, deep punctures that occasionally merge; scutellum with weakly developed paramedian tubercle; pygidial plate well developed in both sexes; terminal tergum truncate in female (Fig. 43), broad and rounded posteriorly in male; female S5 with elliptical concavity (Fig 43); male S7, S8 and genital capsule as in Figs. 44–46.

*Distribution.*—South Africa, Lesotho and central region of northern Namibia. Vegetation ranges from bushveld to montane grassland.

*Discussion.*—In this species the labrum is quadrate, propodeum completely clothed with fine vestiture and female pygidial plate fully developed.

*Type material examined.*—*Omachthes jenseni*, holotype ♀: 'Transvaal, Zeerust, 1897, Jensen; Omachthes graenicheri v jenseni ♀ Fr. 1914 Friese det.; type; O. jenseni Fr. ♀; Coll. Friese; Zool. Mus. Berlin' (ZMHB). *Omachthes alboguttatus*, holotype ♂: '[locality label illegible]; Omachthes alboguttatus ♂ Fr. 1914 Friese det.; type; Coll. Friese; Zool. Mus. Berlin' (ZMHB). *Morgania natalensis*, holotype ♂: 'Natal: National Park, 3–15.iii.1932, A. Mackie, T.D.A. Cockerell Exp. to Africa 1931; Pres. by Imp. Inst. Ent. B.M. 1932-291; Morgania natalensis Ckll TYPE; B.M. TYPE HYM. 17B 98' (NHML). *Morgania ogilviei*, holotype ♂: 'AFRICA: Belmont, J. Ogilviei, 23.ii.1934, B.M. 1934-157; Morgania ogilviei TYPE; B.M. TYPE HYM. 17B 91' (NHML).

*Additional material examined.*—18♀ 7♂: **NAMIBIA:** Okozongominja, 2017CA, 6.iii.1979, V.B. Whitehead (1♂ SAMC). **LESOTHO:** Mamathes, February–March in 1949–1954, C. Jacot-Guillarmod (3♀ 2♂ AMGS); Bokong Post Office, 26.xii.1946, C. Jacot-Guillarmod (1♀ AMGS). **SOUTH AFRICA:** Kruger National Park, Letaba, 2331 DC, 16.xii.1965, A.L. & H. Braack (1♀ SKNP); Woodbush Village, xii.1918, C.J. Swierstra (1♀ TMSA); Wolkberg, 21 km S.W. Tzaneen, 11.iii.1976, R.H. Watmough (1♀ SANC); Johannesburg, iv.1906, G. Kobrow (1♀ ZMHB ['type' of *graenicheri*], 4♀ 1♂ TMSA, 1♀ SANC); Delarey [= Delareyville], 15.i.1917, H. Brauns (1♀ TMSA); Cathedral Peak Hotel, 45 km S. Winterton, 1450 m, 16.ii.1967, C.D. Michener (2♀ SEMK); Modderfontein, 18.iv.1920, H. Brauns (1♀ TMSA); Murraysburg district, iii.1931 (1♀ SAMC, 1♂ SANC); Richmond district, iii.1931 (1♀ SAMC); Stellenbosch, 5.iv.1927, F. Beyers (1♂ SANC).

*Other published distribution records.*—**SOUTH AFRICA:** George (Bischoff 1923); **KENYA:** Morijo (Friese 1941).

*Pasites namibiensis* Eardley, **spec. nov.**
(Figs. 47–49)

This new species is known to occur only in Namibia, and it takes its name from that country.

*Description.*—Similar to *P. jenseni* (habitus, lateral aspect, *cf.* Fig. 41). Length of head 2.2–2.8 mm; scutum 1.8–2.6 mm; fore wing 7.5–8.9 mm; body 8.0–12.0 mm. Integument mostly black, orange maculation limited to ventral region of clypeus, labrum, basal region of antenna, and middle and hind femora; metasomal venter usually orange or orangish. Vestiture white, except mandible, ventral surfaces of tarsi and distal region of S5 pale yellow, subpygidial brush completely black to mostly black with lateral and ventral regions orangish. Middle and lower regions of face, labrum and gena very densely pubescent, upper region of face and vertex moderately densely clothed with simple vestiture (*cf.* Fig. 42); mesosomal dorsum with sparse, simple vestiture, except pronotal collar very densely pubescent and posterolateral regions of scutum with plumose vestiture; periphery of pronotal lobe, subvertical (posterior) region of scutellum and metanotum densely clothed with short to long vestiture; mediolongitudinal region of propodeum naked; legs generally with coxae, most of tibiae and entire tarsi densely pubescent, remainder of legs with long, simple, sparse vestiture or naked; dorsal surface of tibiae also with reddish scales; metasoma generally with anterior and anterolateral regions of T1 moderately densely pubescent, posterolateral regions very densely pubescent; T2-T3 in females, T2-T4 in males with lateral regions of distal margins densely pubescent (T4 in female and T5 in male with
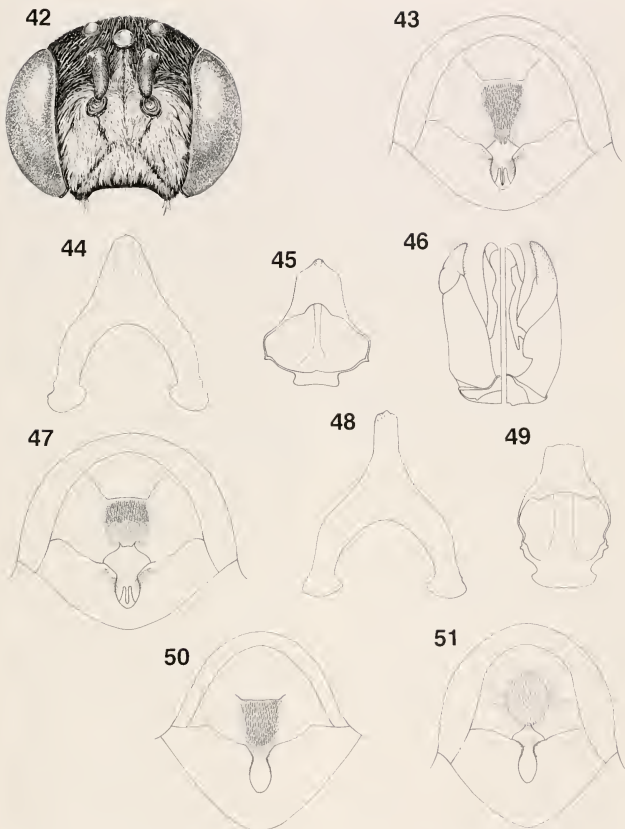
Figs. 42–51. *Pasites* spp. 42–46. *P. jenseni*. 42. Head, front view, ♀; 43. Terminalia, posterior view, ♀; 44. S7, ♂; 45. S8, ♂; 46. Genital capsule, ♂. 47–49. *P. namibiensis*. 47. Terminalia, posterior view, ♀; 48. S7, ♂; 49. S8, ♂. 50. *P. jonesi*, terminalia, posterior view, ♀. 51. *P. rufipes*, terminalia, posterior view, ♀.

distal fringe narrowly interrupted medially or continuous); female T5, male T6 with densely pubescent distal fringe; females with subpygidial brush well developed, quadrate, differentiated, mostly with thick black hairs; metasomal venter sparsely to densely clothed with simple, white vestiture, posterolateral regions of S3-S4 sometimes plumose, distal region of S5 velutinous. Labrum 1.2–1.3× as long as wide, flattish, rounded distally and weakly tuberculate; maxillary palp five-segmented, generally 2–3× as long as antennal pedicel; scutum sparsely punctate, glabrous between punctures; scutellum with weakly developed paramedian tubercle; propodeum glabrous mediolongitudinally, this region distinctly wider above than below; pygidial plate well developed in both sexes; terminal tergum truncate in female, upper half of subpygidial brush with thick black hairs and lower half with fine vestiture (Fig. 47); female S5 with elliptical concavity (Fig 47); male S7 and S8 as in Figs. 48–49, genital capsule resembles *P. jenseni* (*cf.* Fig. 46).

*Distribution.*—Arid bushveld in Namibia.

*Discussion.*—*Pasites namibiensis* has the labrum a little longer than its maximum width, posterior region of propodeum glabrous and impunctate and pygidial plate fully developed.

*Type material.*—Holotype ♀, paratypes 2♂: NAMIBIA: Spitzkoppe, 8.vii.1976, R.H. Watmough (holotype ♀ SANC); Kaoko Otavi, iii.1926 (1♂ SAMC, 1♂ SANC).

## *Pasites histrio* (Gerstaecker), comb. nov.

*Omachthes histrio* Gerstaecker 1869:155.
*Morgania histrio* (Gerstaecker); Cockerell 1904: 208.
*Morgania (Omachthes) histrio* (Gerstaecker); Bischoff 1923:589.
*Morgania (Omachthes) histrio transvaalensis* Bischoff 1923:587–589; Rozen 1969:104–106, 1974:6–16. Syn. nov.
*Morgania transvaalensis* Bischoff; Cockerell 1933c:109.
*Omachthes histrio transvaalensis* (Bischoff); Anonymous 1958:33.
*Morgania (Morgania) alivalensis* Cockerell 1933a: 380. Syn. nov.
*Morgania (Morgania) rufitarsis* Cockerell 1937a: 155–157. Syn. nov.

Bischoff (1923) described *transvaalensis* from a female and two male specimens. The female and one male are from Delareyville, in the North-West Province, and

the other male is from Willowmore, in the Eastern Cape Province, both in South Africa. A male from Willowmore was the only specimen examined that could positively be identified as constituting part of the type series and is here designated as the lectotype. *Morgania rufitarsis* was described from two males and a female, all of which were taken at Swellendam (Western Cape Province, South Africa). Only one male syntype was available for study and this specimen is here designated as the lectotype. The type specimens of *histrio*, *alivalensis*, *transvaalensis* and *rufitarsis* are almost indistinguishable and clearly conspecific.

*Description.*—Similar to *P. jenseni* except as follows: integument generally with antenna, mandible, labrum, tegula and legs reddish, metasoma reddish to orange anteriorly and black posteriorly; mesosomal dorsum sparsely pubescent, propodeum with mediolongitudinal region naked and glabrous; T3 sometimes with continuous distal cross-band; labrum quadrate, rounded distally with laterally compressed, subapical tubercle; maxillary palp five-segmented, 2.5–3.3× as long as pedicel; scutum usually very sparsely punctate with large, deep, separate punctures, glabrous between punctures.

*Distribution.*—Known from a few localities in Namibia, the North-West Province and Gauteng in South Africa (all woodland and bushland) and numerous localities in the Eastern and Western Cape Provinces of South Africa (fynbos).

*Discussion.*—In *P. histrio* the labrum is quadrate, mediolongitudinal region of the propodeum smooth and shiny, and pygidial plate well developed. The host of *P. histrio* is *Tetraloniella minuta* (Friese) (Apidae: Apinae) (Rozen 1969).

*Type material examined.*—*Morgania histrio*, holotype ♀: `Capland, Krebs S.; histrio Gerst*. caffer N. ant; Type; Omachthes histrio 1907 Friese det.; Zool. Mus. Berlin' (ZMHB). *Morgania histrio transvaalensis*, lectotype ♂: `Capland, Willowmore, 18.2.1904, Dr. Brauns; O. histrio transvaalensis Bisch. Typ.; Typus; Bischoff ♂; Omachthes histrio transvaalensis Bischoff HOLOTYPE No: 1190' (TMSA). *Morgania alivalensis*, holotype ♀: `Aliwal North, Cape Province, Dec. 1922, S. Africa, R.E. Turner; Brit. Mus., 1923-45; Morgania alivalensis Ckll. TYPE; B.M. TYPE HYM 17B 93' (NHML). *Morgania rufitarsis*, lectotype ♂:

`Cape Province, Swellendam 17-xii.31–18.i.32, S. Africa, R.E. Turner; Brit. Mus., 1932-56; Morgania rufitarsis Ckll. TYPE; B.M. TYPE HYM. 17B 89′ (NHML).

*Additional material examined.*—22♀ 10♂: **NAMIBIA:** Kaoko Otavi, iii.1926 (1♀ SANC); Gobabis, 21.xii.1974, H. Empey (1♀ 1♂ SANC). **SOUTH AFRICA:** Delarey [= Delareyville], 15.i.1917, H. Brauns (1♀ SANC); Roodeplaat, 20–25.ii.1916, Dr Breyer (1♂ TMSA); Resolution, Albany district, 23.iii.1928, A. Walton (2♂ TMSA); Strowan, Grahamstown, xi–xii.1966, C. Jacot-Guillarmod (3♀ 3♂ AMGS); Grahamstown, 7.xii.1966, C.D. Michener (2♀ AMNH); W. Grahamstown, 27.xi.1966, J.G. Rozen, D.J. Brothers (7♀ 2♂ AMNH); Grahamstown, 6–7.xii.1966, C.D. Michener (7♀ 1♂ SEMK).

*Other published distribution record.*—**SOUTH AFRICA:** near Ceres (Cockerell 1933c).

### *Pasites jonesi* (Cockerell), comb. nov.
(Fig. 50)

*Morgania jonesi* Cockerell 1921:207.
*Morgania (Morgania) marshalli* Cockerell 1937a: 157. **Syn. nov.**

As in several other cases in the genus, unreliable characters such as metasomal vestiture were used to separate species (Cockerell 1921, 1937a). The differences between the types of *jonesi* and *marshalli* are slight and clearly fall within the range of variation for this species; *marshalli* has therefore been synonymized with *jonesi*.

*Description.*—Similar to *P. jenseni* except as follows: certain specimens (from Karoo and Namaqualand, Western Cape Province) with metasoma mostly to completely orange; scutum very sparsely to moderately densely punctate; pygidial brush ranges from mostly black to mostly orange; labrum round distally with subapical carina; pygidial plate reduced to carina near top of pygidial brush (Fig. 50), subpygidial brush as in Fig. 50.

*Distribution.*—South Africa, Namibia, Zimbabwe and Kenya. Habitats range from savanna to desert.

*Discussion.*—In *P. jonesi* the labrum is quadrate, mediolongitudinal region of the propodeum punctate and clothed with fine vestiture and pygidial plate reduced laterally, so that only the posterior end is visible.

*Type material examined.*—*Morgania jonesi*, holotype ♀: 'Mfongosi, Zululand, W.E. Edwards, 1914; Morgania jonesi Ckll. TYPE' (SAMC). *Morgania marshalli*, holotype ♀: 'Mazoe, Mashonal'd, Dec. 05,

G.A.K. Marshall, 1908-212; Morgania marshalli Ckll. TYPE; B.M. TYPE HYM. 17B 90′ (NHML).

*Additional material examined.*—7♀ 1♂: **KENYA:** Karen, Nairobi, 3 & 20.v.1967, C.D. Michener (2♀ SEMK). **NAMIBIA:** 40 km N. Omaruru, 19.ii.1977, J.G. & B.L. Rozen (1♀ AMNH). **SOUTH AFRICA:** Kruger National Park, Shipandani Picket, 2331CB, A., L. & H. Braack (2♀ SANC); Dikbome, Koup, Laingsburg div., iv–v.1950, H. Zinn (2♀ SAMC); Vogelfontein, P. Albert div., iii–iv.1929, A.J. Hesse (1♂ SAMC).

*Other published distribution record.*—KENYA: Masai Reserve (Cockerell 1933c).

### RUFIPES SPECIES GROUP

This species group is monotypic.

### *Pasites rufipes* (Friese), comb. nov.
(Fig. 51)

*Omachthes rufipes* Friese 1915:298.
*Morgania rufipes* (Friese); Cockerell 1919:190.
*Morgania (Omachthes) rufipes* (Friese); Bischoff 1923:591–592.
*Pasites capensis* Warncke 1983:292 [*nom. nov. pro P. rufipes* (Friese) *nec* (Saunders)].

Warncke (1983) renamed *rufipes* Friese as *capensis* because the name *rufipes* was preoccupied by *Ammobates rufipes* Saunders, also placed in *Pasites* by Warncke. Since we consider *Pasites* and *Ammobates* to be distinct, this replacement name is invalid according to the Code, Article 59(d).

*Description.*—Female (male unknown). Length of head 2.6 mm; scutum 2.1 mm; fore wing damaged; body 10.2 mm. Integument mostly black, scape, mandible, tegula, legs and distal end of metasoma reddish. Vestiture mostly black, mediolongitudinal region of scutellum and metanotum partly white, subpygidial brush orange. Vestiture on head and mesosoma mostly moderately sparse, long and simple (similar to that which occurs on certain species of *Sphecodopsis*, Figs. 62–63); propodeum, including mediolongitudinal region, largely plumose; metasomal vestiture sparse and simple (*cf.* Fig. 62), except subpygidial brush dense (Fig. 51); S6 pallid, velutinous distally. Vertex flattish laterally, strongly raised between lateral ocelli (*cf.* Fig. 63); labrum about 1.3× as long as wide, flattish and gently rounded distally; maxillary palp five-segmented, 4.1× as long as pedicel; scutum quadrate, fairly densely punctate, punctures large, often confluent; scutellum weakly tuberculate paramedially; punctation on mesopleuron similar to scutum; pygidial plate absent (Fig. 51); S5 with

well developed, elliptical, concavity posteromedially
(Fig. 51); S6 widely bifurcate.

*Distribution.*—Known from two widely
separated localities in South Africa, name-
ly Zeerust (woodland) in the North-West
Province, and Bowesdorp, near Kamiesk-
roon (shrubland) in Namaqualand. Both
these localities are fairly arid, but Zeerust
has summer rainfall and Namaqualand
has a Mediterranean climate.

*Discussion.*—*Pasites rufipes* can be easily
recognized by the long, black, erect, weak-
ly plumose vestiture on the head and me-
sosoma in combination with the vertex
which is more or less flat laterally (*cf.* Fig.
63), absence of a pygidial plate and ellip-
tical concavity on the posteromedian re-
gion of the female S5 (Fig. 51). The struc-
ture of the vertex and vestiture on the
head and mesosoma of *P. rufipes* resem-
bles that of certain species of *Sphecodopsis*,
but the elliptical concavity of the female
S5 concurs with that of *Pasites*, and the
structure of the pygidium is unique. The
male of *P. rufipes* is unknown.

*Type material examined.*—*Omachthes rufipes*,
holotype ♀: 'Transvaal, Zeerust, 1897, Jensen;
Omachthes rufipes ♀ Fr. 1914 Friese det.; Type; Mor-
gania rufipes Fr. i.l.Bisch. Type ♀; Zool. Mus. Berlin'
(ZMHB).

*Additional material examined.*—1♀: SOUTH
AFRICA: Bowesdorp, ix.1941 (1♀ SAMC).

## APPLETONI SPECIES GROUP

*Pasites appletoni* and *P. somalicus* com-
prises this species group. The head and
mesosoma of these two species are black,
as in most of their congeners, but the legs
and metasoma are usually orange. The fe-
male S5 is elliptically concave posterome-
dially and the pygidial plate is either
notched or absent posteriorly. The most
conspicuous salient feature of the male of
*P. appletoni* is the simple, erect, yellowish
vestiture on the scutum in combination
with the legs that are usually orange. The
male of *P. somalicus* is unknown.

In the scutal vestiture and colour of the
integument, especially the orangish legs,
these two species resemble the Palaearctic

species *P. maculatus* in which the pygidial
plate is absent in the female and reduced
in the male.

### *Pasites appletoni* (Cockerell), **comb. nov.**
(Figs. 52–56)

*Morgania appletoni* Cockerell 1910:216–217.
*Omachthes abessinicus* Friese 1915:297–298. **Syn.
    nov.**
*Morgania abessinica* (Friese); Cockerell 1919:190.
*Morgania (Omachthes) abessinicus* [sic.] (Friese);
    Bischoff 1923:589–590 [*lapsus*].
*Morgania (Omachthes) fulviventris* Bischoff 1923:
    590. **Syn. nov.**
*Morgania fulviventris* Bischoff; Cockerell 1937a:
    154.
*Omachthes fulviventris* (Bischoff); Anonymous
    1958:31.
*Morgania (Omachthes) rhodesianus* [sic.] Bischoff
    1923:590 [*lapsus*]. **Syn. nov.**
*Omachthes rhodesianus* (Bischoff); Anonymous
    1958:33.
*Morgania (Omachthes) apicalis* Bischoff 1923:591.
    **Syn. nov.**
*Morgania apicalis* Bischoff; Cockerell 1933a:379.
*Omachthes apicalis* (Bischoff); Anonymous 1958:
    30.
*Morgania (Omachthes) turneri* Cockerell 1933a:
    378–379. **Syn. nov.**
*Morgania (Pseudopasites) politula* Cockerell
    1933a:382, 384 [incorrectly given masculine
    gender on p. 382]. **Syn. nov.**
*Morgania (Omachthes) indecisa* Cockerell 1936:31.
    **Syn. nov.**
*Morgania (Omachthes) nudicauda* Cockerell
    1937a:153. **Syn. nov.**
*Morgania (Omachthes) bechuanica* Cockerell
    1937a:153–154. **Syn. nov.**
*Morgania (Omachthes) breviceps* Cockerell 1937a:
    154. **Syn. nov.**

This species is widely distributed in
subsaharan Africa. Throughout its range it
varies greatly in size and moderately in
colour. The density of the vestiture varies
gradually and cannot be used to separate
species. However, specimens from the Ka-
roo and Namaqualand tend to have less
pilosity, especially on the metasoma, than
material from localities to the north of this
region. The large amount of variation that
is displayed, together with the species'

Fig. 52. *Pasites appletoni*, habitus, dorsal view (dark shading represents black or blackish integument and lightly shaded areas are orange), ♀.

wide distribution, has led to the description of a large number of synonyms. This was revealed through study of all the relevant type material.

*Description.*—Habitus, dorsal aspect, as in Fig. 52. Length of head 1.0–1.7 mm; scutum 0.8–1.3 mm; fore wing 3.3–5.8 mm; body 3.9–7.2 mm. Colour of integument of head mostly black, ventral margin of clypeus sometimes orange, antenna often partly to mostly orange or orangish, labrum and mandible usually mostly orangish (distal end of mandible blackish, labrum often with mediobasal, lateral and mediodistal regions black); mesosoma ranges from almost completely black to completely orange, most commonly with scutum, scutellum, propodeum and upper region of mesopleuron black or reddish-black, lower region of mesopleuron and mesosomal venter orange; pronotal lobe usually partly orange; tegula translucent orange; legs mostly orange, coxae sometimes black or blackish, femora, tibiae and tarsi occasionally black; metasoma generally reddish to orange, sometimes with blackish tinge and/or black distally. Vestiture on head white, except mandible white to yellowish; mesosoma mostly white, scutum yellowish except lateral region which is white, dorsal surface of scutellum concolorous with scutum; legs largely white, ventral surfaces of tarsi yellowish, outer surfaces of tibiae with few reddish scales; metasomal vestiture mostly white, subpygidial brush usually black medially, circumscribed with orange; metasomal venter orange to white vestiture, except female S5 with orange fringe surrounding posteromedian concavity. Vestiture on head usually mostly moderately dense and plumose, that on upper region of face and vertex sparse and simple, occasionally lower region partly clothed with simple hairs; mandible with few simple hairs; pronotal collar and lobe densely pubescent; scutum with short, simple moderately dense, vestiture, except lateral region which is densely pubescent; scutellum with dorsum largely similar to scutum, posterior (subvertical) surface plumose; propodeum naked mediolongitudinally; legs with femora largely naked; metasoma with T1 naked to sparsely pubescent anteriorly (subvertical surface), with dense posterolateral spots; female T2–T5, males T2–T6 with sparse to dense pubescence on posterior margins which may be interrupted medially; female T6 with well developed, subpygidial brush; differentiation of subpygidial brush unique in that thick hairs occur in centre and fine vestiture around edge (Fig. 53); male T7 sparsely clothed with pale vestiture;

**53**     **54**     **55**

**56**     **57**
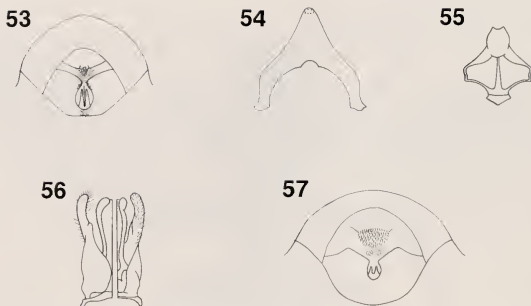


Figs. 53–57. *Pasites* spp. 53–56. *P. appletoni*. 53. Terminalia, posterior view, ♀; 54. S7, ♂; 55. S8, ♂; 56. Genital capsule, ♂. 57. *P. somalicus*, terminalia, posterior view, ♀.

metasomal venter with sparse to dense vestiture, except female S5 with fringe of short, simple hairs surrounding posteromedian concavity. Labrum about quadrate, flattish with apex pointed and weakly tuberculate; maxillary palp four-segmented, 1.5–2.2× as long as antennal pedicel; scutum fairly densely covered with small well separated punctures; scutellum gently and evenly convex to unevenly convex with paramedian regions weakly swollen; propodeum with broad glabrous area mediolongitudinally; mesopleuron mostly densely punctate, ventrolateral and ventral regions sparsely punctate; pygidial plate well developed, broadly rounded in both sexes, female with distinct notch mediodistally (Fig. 53); female S5 with elliptical concavity (Fig. 53); male S7, S8 and genital capsule as in Figs. 54–56.

*Distribution.*—Niger and Cameroon, in the north-west, Somalia, in the north-east, and from much of southern Africa. Habitat ranges from rain forest to desert.

*Discussion.*—*Pasites appletoni* can be identified by the female terminalia. The pygidial plate is notched posteromedially, the subpygidial brush is mostly orangish with a black centre and S5 with an elliptically concave posteromedially (Fig. 53). The male can be identified by the shape of the S7 and S8 (Figs. 54–55), and in orange coloured specimens, by the colour of the legs and metasoma.

*Floral records.*—Pedaliaceae: *Sesamum*

sp.; undetermined species of Boraginaceae.

*Type material examined.*—*Morgania appletoni*, holotype ♀: ʻBohotle, Somaliland, 1903, Verty. Major A.F. Appleton, 1907–89; Morgania appletoni Ckll. TYPE; B.M. TYPE HYM. 17B 84.ʼ (NHML). *Omachthes abessinicus*, holotype ♀: ʻNO.-Afrika, Eritrea, 08; Omachthes abessinicus Fr. ♀ 1914 Friese det.; Type; Zool. Mus. Berlinʼ (ZMHB). *Morgania fulviventris*, holotype ♂: ʻCapland, Willowmore, 1.12.1904, Dr Brauns; Omachthes fulviventris Bisch. ♂ Typ.; Omachthes fulviventris Biss. ♂ Type No. 569ʼ (TMSA). *Morgania rhodesiana*, holotype ♂: ʻBulawayo, S. Rhodesia, 14.12.1919, Rhodesia Museum; Omachthes rhodesianus Bisch. ♂ Typ.; Omachthes rhodesianus Biss. ♂ Type No. 572ʼ (TMSA). *Morgania apicalis*, holotype ♂: ʻCapland, Willowmore, März 10 1919, Dr Brauns; Omachthes apicalis Bisch. Typ.; Omachthes apicalis Biss. ♂ Type No. 568ʼ (TMSA). *Morgania turneri*, holotype ♀: ʻS.W.Africa, R.E. Turner, Brit. Mus., 1928-61; Okahandja, 1–12.i.1928; Morgania turneri Ckll. TYPE; B.M. TYPE HYM. 17B 83ʼ (NHML). *Morgania politula*, holotype ♂: ʻCape Province, Little Karoo, 38 m. E. of Ceres, 17–25.xi.1924, S.Africa, R.E. Turner, Brit. Mus. 1924-518; Morgania politula Ckll. TYPE; B.M. TYPE HYM. 17B 97ʼ (NHML). *Morgania indecisa*, holotype ♀: ʻS.W.Africa, Cape of Good Hope, Nelspoort, 5.xii.1933, J. Ogilvie, T.D.A. Cockerell, Exp. to Africa 1931, Pres. by Imp. Inst. Ent. B.M. 1932-291; Morgania indecisa Ckll. TYPE; B.M. TYPE HYM. 17B 92ʼ (NHML). *Morgania nudicauda*, holotype ♀: ʻAFRICA, Belmont, J. Ogilvie, 23.ii.1934, B.M. 1934-157; Morgania nudicauda; B.M. TYPE HYM. 17B

88' (NHML). *Morgania bechuanica*, holotype ♀: 'AF-RICA, Palapye, 5.iii.1934, J. Ogilvie, B.M. 1934-172; Morgania bechuanica Ckll. TYPE; B.M. TYPE HYM. 17B 86' (NHML). *Morgania breviceps*, holotype ♀: 'AF-RICA, Upington, J. Ogilvie, 21.ii.1934, B.M. 1934-157; Morgania breviceps Ckll. TYPE; B.M. TYPE HYM. 17B 87' (NHML).

*Additional material examined.*—210♀ 55♂: **NIGER:** 20 km S. Tahoua, 14.45N 05.20E, 13.viii.1987, A. Pauly, on Boraginaceae (1♀ 1♂ PCGB); Tsernaoua, 13.53N 05.20E, 13.viii.1987, A. Pauly, On *Sesamum* sp. (1♂ PCGB). **CAMEROON:** Bambui, near Bamenda, 1400 m, 5.viii.1966, C.D. Michener (1♀ SEMK). **BOTSWANA:** Serowe, 17.x.1923, R. Stevenson (1♀ TMSA); Serowe, iii.1986 (3♀ SANC); Palapye, 18.x.1923, R. Stevenson (1♀ SANC); V.-L. Kal. Exp. Kuke Pan, 21–30.iii.1930 (1♀ TMSA). **ZIMBABWE:** Sawmills, 28.xii.1919 (2♀ TMSA); Hillside, 17.ii.1923 (1♂ NHML); Sanyati Valley, ix–x.1925, R. Stevenson (1♀ TMSA); Bulawayo, December–March, various collectors (9♀ 7♂ TMSA); Bulawayo, 23.xi.1924 (2♀ SEMK). **SOUTH AFRICA:** Kruger National Park, Pafuri, 22.26S 31.12E, 264m, 20–24.i.1985, G.L. Prinsloo (53♀ 8♂ SANC); 40 km N. Louis Trichardt, 24.iii.1967, C.D. Michener (2♀ SEMK); Happy Rest Nature Reserve, 22.59S 29.46E, 10.iii.1990, C.D. Eardley (2♀ 2♂ SANC); D'Nyala Nature Reserve, Ellisras district, 23.45S 27.49E, 19.xii.1987, M.W. Mansell, G.L. Prinsloo, C.D. Eardley (3♀ SANC); Mogol Nature Reserve, Ellisras district, 23.58S 27.45E, 27–29.ii.1984, C.D. Eardley (1♀ 1♂ SANC); Ben Alberts Nature Reserve, Thabazimbi, 24.37S 27.23E, 24–28.xi.1980, M.W. Mansell, C.D. Eardley (2♀ SANC); Ellisras, 7.x.1961, 3.i.1971 & 19.ii.1972, H. Empey (1♀ 1♂ SANC); Soutpan, Pretoria district, 25.24S 28.06E, 29.i.1987, C.D. Eardley (1♀ SANC); Scottburgh, 14.ii.1926, R.H.R. Stevenson (1♀ SANC); Olifantshoek, 24.iii.1990, W. Pulawski (1♀ 2♂ CASC); Carlisle Bridge, 14.i.1965, H. Empey (1♀ SANC); Graaff-Reinet, 3.i.1978, H. Empey (1♂ SANC); Willowmore, i-ii.1911 & ii.1912, H. Brauns (1♀ 1♂ TMSA, 1♀ 2♂ SANC). **NAMIBIA:** Rundu, 10.iii.1990, W. Pulawski (1♀ CASC); Otavi, iii.1926 (1♀ SAMC); Namakunde, ii.1922 (1♀ SAMC); 61 km W. Omaruru, 22.iii.1979, J.G. Rozen (2♀ AMNH); 11–46 km W. Usakos, 14.iii.1979, J.G. & B.L. Rozen (8♀ AMNH); 17–19 km E. Usakos, 18.iii.1976, J.G. & B.L. Rozen (2♀ AMNH); 50km S.W. Usakos, 21.iii.1990, W. Pulawski (1♀ CASC); 11 km N. Karibib, 27.ii.1990, W. Pulawski (1♀ CASC); 62 km E. Karibib, 20.ii.1990, W. Pulawski (2♀ CASC); 43 km E. Karibib, 20.ii.1990, W. Pulawski (1♀ CASC); Otjituo, i.1920, W. Tucker (1♀ SAMC); 70 km N. Okahandja, 16.iii.1990, W. Pulawski (2♀ CASC); 5 km S. Okahandja, 13–17.iii.1979, J.G. & B.L. Rozen (6♀ AMNH); 5 km S. Okahandja, 30.iii.–1.iv.1979, J.G. Rozen (53♀ AMNH); 27 km S. Okahandja, 18.iii.1990, W. Pulawski (3♀ CASC); 3 km N.E.

Kalkfeld, 2.ii.1990, W. Pulawski (2♀ CASC); 15 km N. Kalkrand, 13.ii.1990, W. Pulawski (2♀ 1♂ CSAC); 23 km N. Rehoboth, 15.iii.1990, W. Pulawski (1♀ 1♂ CSAC); 24 km S. Kamanjab, 5.iii.1990, W. Pulawski (1♂ CSAC); 20km N.E. Otjiwarongo, 13.iii.1990, W. Pulawski (3♀ 2♂ CSAC); 40 km W. Witvlei, 16.ii.1990, W. Pulawski (4♀ 1♂ CSAC); 8 km W. Windhoek Airport, 11.iii.1979, J.G. & B.L. Rozen (1♂ AMNH); 36 km E. Windhoek, 16.ii.1990, W.J. Pulawski (1♀ CSAC); 20–22 km E.S.E. Seeis, 13–29.iii.1976, J.G. & B.L. Rozen (16♀ 12♂ AMNH); 9–36 km E.S.E. Seeis 16.ii.1977, J.G. & B.L. Rozen (5♀ AMNH).

*Other published distribution records.*—**ZIMBABWE:** Lonely Mine (Cockerell 1933a); **SUDAN:** Cash Delta (Cockerell 1933c).

*Pasites somalicus* Eardley, spec. nov.
(Fig. 57)

This new species is known from a single female from Somalia, and it is named for that country.

*Description.*—Similar to *P. appletoni* (cf. Fig. 52). Female (male unknown). Length of head 1.9 mm; scutum 1.7 mm; fore wing 6.5 mm; body 9.4 mm. Colour of integument of head mostly black, antenna partly orangish, labrum orange and mandible orange, except distal end which is blackish; mesosoma black; legs orange, except middle and hind coxae which are black; metasoma orange. Vestiture on head white, except mandible white to yellowish; mesosoma mostly white, scutum yellowish except lateral region which is white, dorsal surface of scutellum concolorous with scutum; legs largely white, ventral surfaces of tarsi yellowish, outer surfaces of tibiae with few reddish scales; metasomal vestiture mostly white, subpygidial brush white dorsally, orange ventrally (Fig. 57); metasomal venter with orange to white vestiture, except S5 with an orange fringe surrounding posteromedian concavity. Vestiture on head dense and plumose, that on upper region of face and vertex sparse and simple; mandible with few simple hairs; pronotal collar and lobe densely pubescent; scutum with short, simple moderately dense, vestiture, except lateral region which is densely pubescent; scutellum with dorsum largely similar to scutum, posterior (subvertical) surface plumose; propodeum naked mediolongitudinally; legs with femora largely naked; metasoma with T1 naked to sparsely pubescent anteriorly (subvertical surface), with dense posterolateral spots; T2 with dense white pubescence posterolaterally; female T3-T5 with dense white subapical fringes; T6 with well developed subpygidial brush, which has thick hairs above and fine vestiture below (Fig. 57); metasomal venter with sparse to dense vestiture, except S5 with fringe of short, simple hairs surrounding pos-
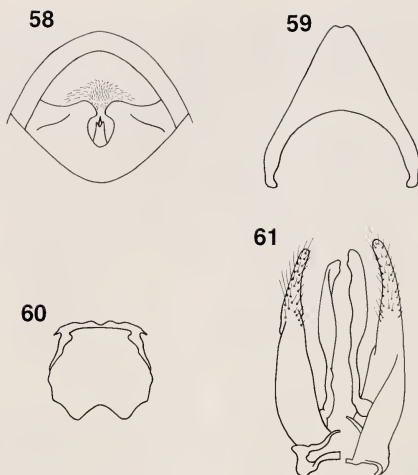
Figs. 58–61. *Pasites maculatus*. 58. Terminalia, posterior view, ♀; 59. S7, ♂; 60. S8, ♂; 61. Genital capsule, ♂.

teromedian concavity. Labrum about quadrate, flattish with apex pointed and weakly tuberculate; maxillary palp four-segmented, subequal in length to antennal pedicel; scutum fairly densely covered with small well separated punctures; scutellum with paramedian region distinctly swollen; propodeum narrowly naked mediolongitudinally; mesopleuron mostly densely punctate, ventrolateral regions sparsely punctate; pygidial plate only visible posterolaterally (Fig. 57); S5 with elliptical concavity (Fig. 57).

*Distribution.*—Somalia, *Acacia-Commiphora* woodland.

*Discussion.*—*Pasites somalicus* closely resembles *P. appletoni*. They can be separated by the structure of the female pygidium. In *P. somalicus* the pygidial plate is visible as two lateral carinae only and the subpygidial brush is black dorsally and orangish ventrally.

*Type material.*—Holotype ♀: SOMALIA: locality illegible, 25.11.53, Desert Locust Survey (AMGS).

## MACULATUS SPECIES GROUP

This species group is monotypic.

### *Pasites maculatus* (Jurine)
### (Figs. 58–61)

*Pasites maculata* Jurine 1807: 224.

*Diagnosis.*—Length of head 1.7–2.3 mm; scutum 1.2–1.5 mm; forewing 4.8–5.8 mm; body 5.8–7.3 mm. Colour of integument of head ranges from mostly black, ventral margin of clypeus, labrum and mandible orange, to completely orange; mesosoma ranges from almost completely black, except pronotal lobe and tegula orange, to completely orange, except mediolongitudinal region of propodeum black; legs mostly orange, coxae, trochanters and proximal region of femora sometimes black; metasoma generally reddish to orange, sometimes with blackish tinge and/or black distally. Vestiture mostly white to whitish, ventral surfaces of tarsi yellowish, outer surfaces of tibiae with few reddish scales, subpygidial brush of female mostly infuscated, black dorsomedially, metasomal partly orange. Vestiture on head mostly

sparse and simple, moderately dense and plumose around antennal socket; pronotal collar densely pubescent; scutum and scutellum mostly with short, simple, sparse vestiture; propodeum naked mediolongitudinally; femora with sparse vestiture; T1 with sparse vestiture; T2 with sparse to dense vestiture; female T3–T5, male T3–T6 with bands of dense pubescence on posterior region which are interrupted medially and mediolaterally; female T6 with well developed, subpygidial brush (Fig. 58); male T7 largely naked; metasomal venter with sparse vestiture, except female S5 with fringe of short, simple hairs surrounding posteromedian concavity. Labrum 1.3× as long as its maximum width, flattish with apex pointed; without maxillary palp; scutum fairly densely covered with large well separated punctures; scutellum unevenly convex with paramedian regions distinctly swollen; propodeum with mediolongitudinal area broad and glabrous; mesopleuron mostly densely punctate, ventrolateral and ventral regions sparsely punctate; pygidial plate absent in female (Fig. 58), reduced in male; female S5 with elliptical concavity (Fig. 58); male S7, S8 and genital capsule as in Figs. 59–61.

*Distribution.*—North-west Africa and Spain to Japan (Rozen 1986).

*Discussion.*—The synonymy of this species is given by Warncke (1983) and aspects of the biology are discussed by Rozen (1986) where he shows that *P. maculatus* parasitizes *Pseudapis* (Halictidae: Nomiinae).

Although *P. maculatus* resembles the appletoni species group in colour, it is most closely related to the *jenseni* species group. The female can be identified by the absence of the pygidial plate and the subpygidial brush which is mostly black and dorsoventrally differentiated (Fig. 58). In the male the elongate labrum, reduced pygidial plate and quadrate S8 (Fig. 60), in combination, are diagnostic.

*Material examined.*—4♀ 4♂: **SPAIN:** Sierra Nevada (1300 m), 18–24.vii.1980, K.M. Guichard (1♀ NHML). **SOUTH TUNISIA:** Mareth, 30.vii.1978, K.M. Guichard, G.R. & A.C. Else (1♀ NHML). **GREECE:** Rhodes Ixia, 15–29.viii.1984, M.C. Day (1♂ NHML). **ISRAEL:** Lubban (500 m), 20.v.1975, K.M. Guichard (1♂ NHML). **CYPRUS:** Akrotiri, 16.vii.1944, G.A. Mavromoustakis (1♂ NHML); Limassol, 12.vi.1929, G.A. Mavromoustakis (1♀ NHML). **AUSTRIA:** N.E. Marchfeld, Oberweiden, (Sandberge), 21.vii.1952, F. Koller (1♀ 1♂ SCAA).

## SPECIES OF UNCERTAIN IDENTITY

The following four species, *Pasites atratulus* Friese, *Omachthes gabonensis* Vachal, *Morgania rotundiceps* Bischoff and *Morgania tropica* Cockerell, could not be identified from the literature alone and the type material could not be located. Although *Omachthes* and *Morgania* have been synonymized with *Pasites*, it could not be established whether the last three species really belong in *Pasites*.

### *Pasites atratulus* Friese

*Pasites atratulus* Friese 1922:36 (syntypes 3♂).
*Morgania (Omachthes) atratulus* [sic.] (Friese); Bischoff 1923:588 [lapsus].
*Morgania atratulus* [sic.] (Friese); Medler 1980: 483.

The type material of this species comprised three males. One was placed in the ZMHB and two in the Zoologische Institut und Zoologische Museum, Universität von Hamburg, Hamburg, Germany. The first-mentioned type is not in the ZMHB, and the other two were destroyed during World War II.

### *Omachthes gabonensis* Vachal

*Omachthes gabonensis* Vachal 1903:382–383 (holotype ♀).
*Morgania gabonensis* (Vachal); Cockerell 1919: 190.
*Morgania (Omachthes) gabonensis* (Vachal); Bischoff 1923:587–588.
*Omachthes gabonensis* (Vachal); Medler 1980:483.

The holotype of this species was apparently originally deposited in Vachal's collection, now housed in the MNHN. However, it could neither be found here nor in any of the other major European museums.

### *Morgania rotundiceps* Bischoff

*Morgania (Omachthes) rotundiceps* Bischoff 1923: 588 (syntypes 2♂).

The species was described from two males, both of which were taken in Tanzania. Although Bischoff said he deposit-

Fig. 62. *Sphecodopsis capicola*, habitus, dorsal view (dark shading represents black or blackish integument and lightly shaded areas are reddish), ♀.

ed the type material in the ZMHB, it could not be found there.

### Morgania tropica Cockerell

*Morgania tropica* Cockerell 1933c:106–107 (holotype ♀, MRAC).

The type material of this species is housed in the MRAC. The material was on loan during the course of this study and the museum was unable to retrieve it.

### GENUS *SPHECODOPSIS* BISCHOFF

*Sphecodopsis* Bischoff 1923:593. Type species: *Omachthes capicola* Strand 1911 (original designation).

*Sphecodopsis* (*Sphecodopsis*) Bischoff 1923:593.

*Sphecodopsis* (*Pseudopasites*) Bischoff 1923:593. Type species: *Pasites pygmaeaus* Friese 1922 (subsequent designation, Sandhouse 1943). **Syn. nov.**

*Pseudodichroa* Bischoff 1923:586, 595; Rozen 1968a:1–10. Type species: *Omachthes capensis* Friese (subsequent designation, Sandhouse 1943). **Syn. nov.**

The following ten species comprise the genus *Sphecodopsis*: *S. capicola* (Strand), *S. vespericena* spec. nov., *S. villosa* Friese, *S. longipygidium* spec. nov., *S. namaquensis* spec. nov., *S. minutissima* (Cockerell), *S. aculeata* (Friese), *S. semirufa* (Cockerell), *S. capensis* (Friese) and *S. fumipennis* (Bischoff). Of these, *S. vespericena, S. longipygidium, S. namaquensis, S. capensis* and *S. fumipennis* are only known from female specimens, and *S. villosa* is only known from the male. The diagnostic characters of many of the species are sex-limited, and in the absence of suitable material of these species it is impossible to associate the sexes. This led to the unassociated and undescribed males of two species, of which material was available, being omitted from the study. As the males of most of the described species are unknown or cannot be identified, a key for the identification of the males has not been provided. The male terminalia have the most reliable diagnostic features of this sex and have

been illustrated for the species of which males are known. These illustrations, in combination with the descriptions, should enable the recognition of those males.

The genus is endemic to southern Africa. Five species (*S. vespericena*, *S. longipygidium*, *S. namaquensis*, *S. capensis* and *S. fumipennis*) are known only from Namaqualand and the south-western region of the Western Cape, an additional three species (*S. capicola*, *S. aculeata* and *S. semirufa*) occur in Namaqualand and the Karoo. The distribution of one of these, namely *S. aculeata*, extends eastward to Grahamstown. The other two species (*S. villosa* and *S. minutissima*) apparently occur throughout the greater part of southern Africa.

Bischoff (1923) divided *Sphecodopsis* into two subgenera. The nominotypical subgenus comprised *S. capicola* and *S. villosa*, while the subgenus *Pseudopasites* comprised *S. minutissima* and *S. aculeata*. *Sphecodopsis capensis* and *S. fumipennis* were placed in the genus *Pseudodichroa* by Bischoff (1923). Cockerell (1919 & 1933c) consistently placed the species here recognised as belonging to *Sphecodopsis* in the genus *Morgania*, and (Cockerell 1933a) considered *Sphecodopsis* and *Pseudopasites* to be subgenera of *Morgania*. In the cladistic analysis of these species, *Pasites* (= *Morgania*) and *Sphecodopsis* form distinct clades and are here considered to be distinct genera. The analysis did not reveal any characteristics that supported the subdivision of *Sphecodopsis* into subgenera, nor the placement of *S. capensis* and *S. fumipennis* in a separate genus. The only features that separate *Pseudodichroa* from *Sphecodopsis* sensu stricto are its gutter-like female S5 and the S6 which forms a single posterior spine (in the latter the female S5 has a small protuberance (Figs. 65, 80, 82, 93) and a posteriorly bifid S6 (Fig. 66)). Material of males that apparently belong to either *S. capensis* or *S. fumipennis* was studied and found to be virtually indistinguishable from *Sphecodopsis*. The two subgenera and *Pseudodichroa* have therefore been synonymized.

*Sphecodopsis* species are smallish (4.0–9.0 mm long), wasp-like bees in which the head and mesosoma are black, the metasoma is generally reddish and/or orangish anteriorly, black posteriorly; occasionally the entire metasoma is black. The genus is characterized as follows: vertex, frontal view, flat laterally, area between lateral ocelli distinctly raised (Fig. 63); antenna 12-segmented in female, 13-segmented in male; labrum more or less quadrate, pointed and weakly tuberculate apicomedially; mandibles behind labrum in repose; facial vestiture generally black (Fig. 63), white in *S. aculeata* and *S. minutissima*, long and weakly pubescence, except in *S. minutissima* which has short, dense facial pubescence; scutellum gently and evenly curved; last exposed metasomal tergum (T6 female, T7 male) without pygidial plate, but with dorsum broad and with dorsolateral region strongly incurved posteriorly, especially in male where dorsum resembles a pygidial plate; female S5 either shallowly or strongly concave distally, when viewed from behind, with weakly to strongly developed protuberance posteromedially, when viewed from below (Figs. 65, 78, 80, 82, 93); female S6 with distal end either simple or bifid posteriorly (Figs. 66, 79, 81, 83, 94).

In the discussion that follows some of the species have been placed in two species groups, on the basis of their morphology, while three species have been regarded as comprising three monotypic groups. These species groups are not clearly defined units suitable for description as distinct taxa. They have been used simply to facilitate discussion on the similarities between species. The capicola group comprises *S. capicola*, *S. vespericena*, *S. villosa*, *S. longipygidium* and *S. namaquensis*. The capensis group comprises *S. capensis* and *S. fumipennis*. The three species that have not been grouped are *S. minutissima*, *S. aculeata* and *S. semirufa*.

KEY TO SPECIES OF *SPHECODOPSIS*
(Females)

1. Metasoma with S6 simple posteriorly (capensis group) ............................ 2
– S6 bifid posteriorly ............................................................. 3
2. Posterior margin of first submarginal cell in fore wing distinctly longer than in second submarginal cell; posterior margin of S5 with area clothed with pallid vestiture distinctly pointed anteromedially (illustrated in Rozen, 1968a) ............ *S. fumipennis* (Bischoff)
– Posterior margin of first and second submarginal cell in fore wing subequal in length; posterior margin of S5 with area clothed with pallid vestiture rounded anteromedially (illustrated in Rozen, 1968a) ..................................... *S. capensis* (Friese)
3. Side of T5 notched (Fig. 75) (capicola group, part) .............. *S. longipygidium* Eardley
– Side of T5 gently curved (Fig. 64) ............................................. 4
4. Facial vestiture white ......................................................... 5
– Facial vestiture completely to mostly black ...................................... 6
5. Vestiture on lower region of face plumose, virtually obscuring facial integument; upper region of face with integument clearly visible through short, simple vestiture; T5 with well developed distal fringe medially; T6 with lateral region of distal fringe long, hairs curved outwards ......................................................... *S. minutissima* (Cockerell)
– Integument of entire face visible as a result of all facial vestiture being weakly plumose; T5-T6 devoid of clearly discernable distal fringes ..................... *S. aculeata* (Friese)
6. Median region of T5 with a well developed distal fringe of straight, posteriorly projecting setae (capicola group, part) ............................................. 7
– T5 either naked and impunctate posteriorly or with a sparse subapical fringe .......... 8
7. Distal fringe on T5 black to brownish; legs largely orange ........ *S. vespericena* Eardley
– Distal fringe on T5 white; legs black to blackish ................... *S. capicola* (Strand)
8. T5 naked and impunctate posteriorly; vestiture on anterior region long and black ......
..................................................................... *S. semirufa* (Cockerell)
– T5 densely punctate posteriorly and completely clothed with short white vestiture (capicola group, part) ..................................................... *S. namaquensis* Eardley

## CAPICOLA SPECIES GROUP

This species group is made up of the following five species: *S. capicola*, *S. vespericena*, *S. villosa*, *S. longipygidium* and *S. namaquensis*. The vestiture on the head and mesosoma is black, and consists mostly of fairly long, weakly plumose hairs, and the female T5 has a distinct apical or subapical fringe.

### *Sphecodopsis capicola* (Strand)
(Figs. 63–71)

*Omachthes capicola* Strand 1911:224–225.
*Morgania capicola* (Strand); Cockerell 1919:190, 1933c:109.
*Sphecodopsis* (*Sphecodopsis*) *capicola* (Strand); Bischoff 1923:593–595.

*Description.*—Habitus, dorsal aspect, as in Fig.

62. Length of head 1.4–2.0 mm; scutum 1.0–1.7 mm; fore wing 4.3–7.0 mm; body 4.8–7.7 mm. Integument of head black, except distal end of mandible orange; mesosoma black, except tegula, pronotal lobe, most of femora, tibiae and tarsi usually orangish; metasoma mostly orange, distal segments black. Vestiture on head black; mesosoma black, except short pubescence (described below) on scutum, scutellum and surrounding pronotal lobe white; legs generally white, femora black, dorsal surfaces of tibiae and basitarsi with black setae intermixed with white vestiture, ventral surfaces of tarsi blackish-orange; metasomal vestiture pallid in areas where integument is orange, black in regions where integument is black, except posterior region of female T5 with white vestiture (median region with well developed white distal fringe), T6 black to brownish-orange, S5 with brownish-orange tinge, especially posterolaterally; male T6 white distally, T7 completely white. Face densely clothed with long, weakly plumose vestiture (Fig. 63), lower region of gena with short and long pubescence intermixed; mesosoma with mixture of long, weakly plumose vestiture and short pubescence; legs, except

femora, generally clothed with very short, simple to weakly plumose, vestiture, femoral vestiture sparse, long and simple to weakly plumose, dorsal surfaces of tibiae and basitarsi with black setae intermixed with vestiture; metasomal vestiture very short and simple, except median region of T5 with well developed white distal fringe. Scutum with fine, dense punctation; propodeum largely punctate, propodeal triangle finely sculptured; female T5 straight posteriorly, except for weakly developed notch posteromedially (Fig. 64), pygidium short and devoid of subpygidial brush; male T7 rounded posteriorly, strongly incurved ventrolaterally (Fig. 67); female S5 broadly protuberant posteromedially, with small prominence on each side of protuberance (Fig. 65); female S6 weakly bifurcate posteriorly (Fig. 66); male S7, S8 and genital capsule as in Figs. 68–71.

*Distribution.*—Karoo and Namaqualand, in the Western and Eastern Cape Provinces.

*Discussion.*—The female of this species can be identified by the black to blackish legs in combination with the posterior fringe of white setae on T5. The male can be identified by the gonocoxite of the genitalia being truncate posteriorly (Figs. 70–71). Its closest relative is *S. vespericena*, to which it is remarkably similar. In these two species the posteromedian protuberance of the female S5 is broad with very small posterolateral prominences (Fig. 65).

*Floral Record.*—Rosaceae.—*Grielum humifusum* Thunb.

*Type material examined.*—Holotype ♂: 'Capland berg, 1774, Morgania capicola ♂ Strand det.; Type; Zool. Mus. Berlin' (ZMHB).

*Additional material examined.*—22♀ 2♂: **SOUTH AFRICA:** Willowmore, 15.viii.1920, Dr Brauns (1♀ TMSA); Ceres district, 15–30.x.1934, M. Versfeld (1♀ SAMC); 8 km W. Graafwater, 3218BA, 27.ix.1978, V.B. Whitehead (3♀ TMSA, 1♀ SANC); 20 km N. Clanwilliam, 9.ix.1982, V.B. Whitehead, on *Grielum humifusum* (1♀ SANC); Sandberg Station, 32.18BC, 11.viii.1988, V.B. Whitehead (1♀ SAMC); Biedouw Valley, Clanwilliam district, 32.08S 19.14E, 5–7.ix.1987, C.D. Eardley (1♀ 1♂ SANC); 20 km N. Klawer, 9.ix.1983, V.B. Whitehead (2♀ SAMC); 5 km S. Niewoudville, 3119AC, 2.viii.1988, 25.viii.1988, V.B. Whitehead (4♀ SAMC, 1♀ SANC); Vanrhynsdorp, 12.viii.1927, Dr. Brauns (1♀ TMSA, 1♀ 1♂ SANC); Hester Malan Nature Reserve, Springbok, 17.ix.1983, V.B. Whitehead (1♀ SAMC); Springbok, 7.ix.1966, C.D. Michener (3♀ SEMK).

*Sphecodopsis vespericena* Eardley, **spec. nov.**

The species was only known from four specimens before Drs F.W. & S.K. Gess (AMGS) discovered that the bees visit flowers in the late afternoon (after 16:00 hours). At that time they were collected in abundance. Their habit of feeding late in the day led to the derivation of the name *vespericena* from the Latin words *vesper* (evening) and *cena* (dinner).

A large series of specimens of *S. vespericena* was collected together with several specimens of *Scrapter bicolor* Lepeletier & Serville (Colletidae: Colletinae), whose host plants and foraging time were similar to those of *S. vespericena*. Parasitised nests of this species of *Scrapter* have not been found and it was not possible to ascertain through other means whether it is the host of *S. vespericena*.

*Description.*—Similar to *S. capicola* (*cf.* Fig. 62). Female (male unknown). Length of head 1.9–2.2 mm; scutum 1.6–1.8 mm; fore wing 6.4–7.4 mm; body 7.3–9.0 mm. Integument of head black, except distal end of mandible orange; mesosoma black, except tegula, pronotal lobe, most of femora, tibiae and tarsi usually orangish; metasoma mostly orange, distal segments black. Vestiture on head black, except lower region of gena with a little short white pubescence intermixed with long black vestiture; mesosoma black, except short pubescence (described below) on scutum and scutellum white, and on pleural area, venter and propodeum white to pale grey; legs generally white, femora black, dorsal surfaces of tibiae and basitarsi with black setae intermixed with white vestiture, ventral surfaces of tarsi blackish-orange; metasomal vestiture pallid in areas where integument is orange, black in regions where integument is black, except posterior region of T5-T6 black to brownish-orange (T5 with well developed blackish distal fringe medially). Face densely clothed with long, weakly plumose vestiture (Fig. 63), lower region of gena with short and long pubescence intermixed; mesosoma with mixture of long, weakly plumose vestiture and short pubescence; legs, except femora, generally clothed with very short, simple to weakly plumose, vestiture; femoral vestiture sparse, long, simple to weakly plumose; dorsal surfaces of tibiae and basitarsi with black setae intermixed with vestiture, metasomal vestiture very short, simple, except median region of T5 with well developed black distal fringe. Scutum with fine, dense punctation; propodeum largely punctate, propodeal triangle finely sculptured; T5 straight posteriorly, except for weakly
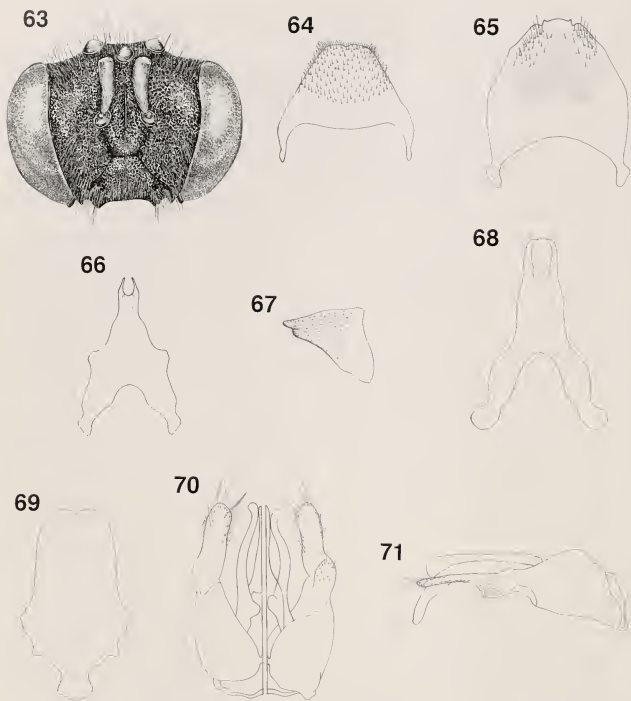
Figs. 63–71. *Sphecodopsis capicola*. 63. Head, front view, ♀; 64. T5, dorsal view, ♀; 65. S5, ventral view, ♀; 66. S6, ventral view, ♀; 67. T7, lateral view, ♂; 68. S7, ♂; 69. S8, ♂; 70. Genital capsule, dorsal left & ventral right, ♂. 71. Genital capsule, lateral view, ♂.

developed notch posteromedially (*cf.* Fig. 64), pygidium short, devoid of subpygidial brush; S5 broadly protuberant posteromedially, with small prominence on each side of protuberance (*cf.* Fig. 65); S6 widely bifurcate posteriorly (*cf.* Fig. 66).

*Distribution.*—Southern region of Namaqualand.

*Discussion.*—In *S. vespericena* the legs are largely orange and the distal fringe of the female T5 is black to brownish. Otherwise this species is remarkably similar to *S. capicola*.

*Floral records.*—Rosaceae: *Grielum humifusum*; Asteraceae: *Senecio* probably *arenarius* Thunb. and *Helichrysum* sp.; Mesembryanthemaceae: *Herrea* sp.; Scrophulariaceae: *Hemimeris montana* L.f.
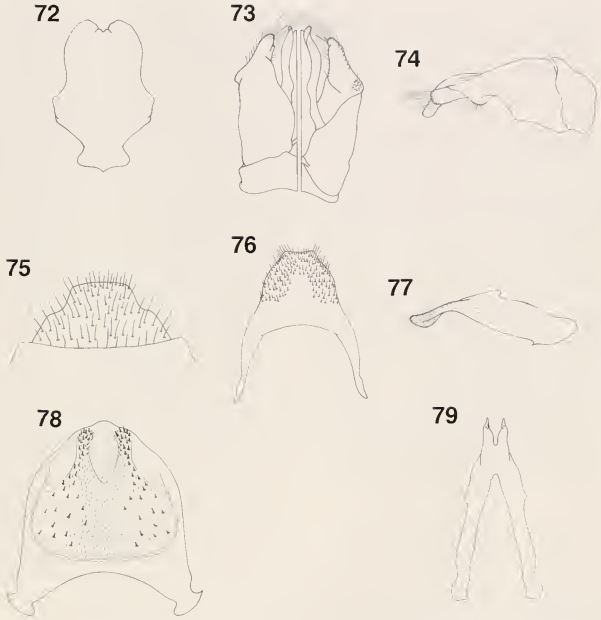
Figs. 72–79. *Sphecodopsis* spp. 72–74. *S. villosa*, ♂. 72. S8; 73. Genital capsule, dorsal left & ventral right. 74. Genital capsule, lateral view. 75–79. *S. longipygidium*, ♀. 75. T5, dorsal view; 76. T6, dorsal view; 77. T6, lateral view; 78. S5, ventral view; 79. S6, ventral view.

*Type material.*—Holotype ♀, paratypes 67♀: **SOUTH AFRICA:** 11 km W. Clanwilliam, 32.10S 18.47E, 1.x.1990, C. Eardley (holotype ♀ 24♀ SANC, 2♀ MRAC, 3♀ AMNH, 2♀ NHML, 2♀ TMSA, 2♀ SAMC, 3♀ SEMK, 2♀ MNHN, 2♀ DMSA, 2♀ ZMHB, 3♀ SCAA, 2♀ CASC); same locality, 2–8.x.1990, F. W. & S.K. Gess, on *Grielum humifusum* (1♀), *Senecio* prob. *arenarius* (1♀), *Herrea* sp. (5♀), *Helichrysum* sp. (1♀) (14♀ AMGS); Holfontein, 20 km S. Clanwilliam, 24.viii.1983, V.B. Whitehead, on *Hemimeris racemosa* (1♀ SAMC); Ramskop Camp, Clanwilliam, 3218BB, 30.viii.1984, V.B. Whitehead, M. Macpherson (1♀ SAMC); Saldanha Bay, ix.1960 (1♀

SAMC); Malmesbury Road, 20.x.1923, W.C. Eales (1♀ SAMC).

## *Sphecodopsis villosa* (Friese)
### (Figs. 72–74)

*Pasites villosus* Friese 1909a:438–439.
*Omachthes villosus* (Friese); Friese 1915:297.
*Morgania villosa* (Friese); Cockerell 1919:190.
*Sphecodopsis* (*Sphecodopsis*) *villosa* (Friese); Bischoff 1923:593–594.

*Description.*—Male (female unknown). Similar to

*S. capicola* except as follows: head and mesosoma more densely punctate (punctation difficult to quantify; refer Bischoff 1923); distal region of metasoma with area in which integument is black, clothed with black vestiture; S8 and genital capsule as in Figs. 72–74.

*Distribution.*—Namaqualand and Zeerust.

*Discussion.*—The similarity between this species and the male of *S. capicola* suggests that they are closely related. These two species can be separated only by the structure of the male terminalia. The most distinctive difference is in the shape of the posterior end of the gonocoxite, which is truncate in *S. capicola* (Figs. 70–71) and somewhat pointed in *S. villosa*. As the males of *Sphecodopsis* have not been included in the key to species, these males should be identified by the comparison of the male S8 and genitalia with the illustrations given in Figs. 72–74.

*Type material examined.*—Holotype ♂: ´Transvaal, Zeerust, 1897, Jensen; Pasites villosus Fr. ♂ 1908 Friese det.; Omachthes villosus Fr. ♂ 1914 Friese det.; Type; Zool. Mus. Berlin´ (ZMHB).

*Additional material examined.*—1♂: SOUTH AFRICA: Vanrhynsdorp, 12.viii.1927, H. Brauns (1♂ SANC).

## *Sphecodopsis longipygidium* Eardley, spec. nov.
### (Figs. 75–79)

This new species is known from a single female specimen in which the pygidial region of S5 is elongate. It is from this unique feature that the name *longipygidium* was derived.

*Description.*—Female (male unknown). Similar to *S. capicola* (cf. Fig. 62). Length of head 2.3 mm; scutum 1.8 mm (fore wing damaged in holotype); body 8.1 mm. Integument of head black, except distal end of mandible orange; mesosoma black, except tegula, pronotal lobe, most of femora, tibiae and tarsi usually orangish; metasoma mostly orange, distal segments black. Vestiture on head black; mesosoma black with short white pubescence apparently confined to scutum (scutal pubescence damaged in holotype); legs generally white, femora black, dorsal surfaces of tibiae and basitarsi with black setae intermixed with white vestiture, ventral surfaces of tarsi blackish-orange; metasomal vestiture pallid in areas where integument is orange, black in regions where integument is blackish, posterior region of T5 with

well developed, black distal fringe medially, T6 black to brownish-orange, S5 with brownish-orange tinge, especially posterolaterally. Face densely clothed with long, weakly plumose vestiture (cf. Fig. 63), lower region of gena with short and long pubescence intermixed; mesosoma with mixture of long, weakly plumose vestiture and short pubescence; legs, except femora, generally clothed with very short, simple to weakly plumose, vestiture; femoral vestiture sparse, long and simple to weakly plumose, dorsal surfaces of tibiae and basitarsi with black setae intermixed with vestiture; metasomal vestiture very short and simple, except median region of T5 with well developed black distal fringe. Scutum with fine, dense punctation; propodeum largely punctate, propodeal triangle finely sculptured; posteromedian region of T5 elongate, i.e., fringed area (Fig. 75); pygidium of T6 much more strongly elongate posteriorly than in *S. capicola* (Figs. 76–77); S5 without apicolateral prominence (Fig. 78); S6 with relatively short disc, elongate anterolaterally (Fig. 79).

*Distribution.*—Namaqualand.

*Discussion.*—The principal diagnostic feature of *S. longipygidium* is the elongation of the terminal segments of the female metasoma (Figs. 75–77). The T5 has a distal fringe that is similar to that of *S. capicola* and *S. vespericena*, which suggests that they are closely related. The structure of the apex of S5 is unlike that of *S. capicola* and *S. vespericena*, in that it does not have apicolateral prominences, and resembles that of *S. minutissima* (Fig. 82).

*Type material.*—Holotype ♀: SOUTH AFRICA: ´Namaqualand, Knersvlakte, Niewerust [= Nuwerus], ix.1941´ (SAMC).

## *Sphecodopsis namaquensis* Eardley, spec. nov.
### (Figs. 80–81)

This new species takes its name from the region it inhabits, Namaqualand.

*Description.*—Female (male unknown). Length of head 1.5–1.7 mm; scutum 1.3–1.5 mm; fore wing 5.1–5.5 mm; body 5.6–7.9 mm. Similar to *S. capicola* except as follows: pronotal lobe black; femora largely black, distal ends orangish; posterior margin of T2 slightly blackish, that of T3 black; mesopleuron with little or no white pubescence; metasomal vestiture mostly white, few black hairs occur on proximal regions of T3–T5, on S2–S5 and on pygidium; distal fringe on T5 subapical, weakly developed; S5 narrow posteriorly, with well developed apicolateral prominence (Fig. 80); S6 with disc long and slender, very narrowly bifid posteriorly (Fig. 81).

*Distribution.*—Namaqualand.

*Discussion.*—This species is distinct from the other species in this group in that it does not have a distinct distal fringe on T5. It resembles the other species in the posterolateral prominences on S5. The most important diagnostic features are the white vestiture on the female S5 and the slender, narrowly bifid female S6 (Fig. 81).

*Type material.*—Holotype ♀, paratypes 2♀: SOUTH AFRICA: Biedouw Valley, Clanwilliam district, 32.08S 19.14E, 5–7.ix.1987, C.D. Eardley (holotype ♀ SANC); Kleinberg, near Langebaanweg, 3218CC, 26.ix.1978, V.B. Whitehead (2♀ SAMC).

## MINUTISSIMA SPECIES GROUP

This species group is monotypic.

### *Sphecodopsis minutissima* (Cockerell), comb. nov.
### (Figs. 82–87)

*Morgania (Omachthes) minutissima* Cockerell 1933a:379.

*Morgania (Pseudopasites) rufula* Cockerell 1933a: 382–383. Syn. nov.

The type specimens of *minutissima* and *rufula* are remarkably similar and clearly conspecific. It is, therefore, unclear why Cockerell (1933a) described them as distinct species in different subgenera in the same article without even comparing them with one another.

The description that follows is incomplete because the metasoma is missing, except the terminal terga, sterna and genitalia, in the only known male specimen.

*Description.*—Length of head 1.1–1.3 mm; scutum 0.9–1.1 mm; fore wing 3.2–4.3 mm; body 4.6–5.8 mm. Integument of head and mesosoma black to reddish-black, antenna, mandible, pronotal lobe, tegula, most of femora, tibiae and tarsi orangish; labrum orange to black; metasoma orange. Vestiture white, except ventral surfaces of tibiae and tarsi pale orangish, female T6 and S5 pale orangish, fringe on distal end of pygidium blackish. Lower region of face and gena very densely pubescent; upper region of face and gena, and vertex sparsely pubescent, vestiture short and simple; mesosomal vestiture sparse, except pronotal collar, anterior region of scutum, lateral regions of scutellum and metanotum, posterolateral region of propodeum and most of dorsal region of mesopleuron densely pubescent; legs generally with vestiture on coxae, tibiae and tarsi dense, trochanters and femora sparse; female with vestiture on T1-T3 sparse (T2-T3 with little white pubescence posterolaterally), T4 sparse with weakly developed distal fringe, T5 sparse with distal fringe well developed medially, T6 generally sparsely pubescent (distal fringe short, sometimes blackish medially). Structurally similar to *S. capicola* except as follows: lateral region of vertex sloping upwards towards raised lateral ocelli, giving vertex convex appearance; propodeum broadly glabrous mediolongitudinally; female S5 resembles that of *S. longipygidium* in that it does not have an apicolateral protuberance (Fig. 82); female S6 very narrowly bifid, disc fairly wide, keeled mediolongitudinally (Fig. 83); male S7, S8 and genital capsule as in Figs. 84–87.

*Distribution.*—Widely separated localities in Zimbabwe and South Africa. Biotypes range from woodland to semi-desert, with either summer or winter rainfall.

*Discussion.*—This species can be easily identified by the gently convex vertex and white, appressed, pubescence on the head and mesosoma. These features are unique to this species, being more similar to *Pasites*, which makes it difficult to determine its closest relative. The female S5 resembles *S. longipygidium* in that it does not have posterolateral prominences (*cf.* Figs. 78, 82).

*Type material examined.*—*Morgania minutissima*, holotype ♀: `Aliwal North, Cape Province, 450ft., 1–13.i.1923, S. Africa, R.E. Turner, Brit. Mus., 1923-70; Morgania minutissima Ckll TYPE; B.M. TYPE HYM. 17B 72' (NHML). *Morgania rufula*, holotype ♀: `Cape Province, Little Karoo, 38 km E. of Ceres, 17–25.xi.1924, S. Africa, R.E. Turner, Brit. Mus., 1924-518; Morgania rufula Ckll TYPE; B.M. TYPE HYM. 17B 96' (NHML).

*Additional material examined.*—4♀ 1♂: ZIMBABWE: Victoria Falls, 3.i.1920 (1♀ SAMC). SOUTH AFRICA: Farm Arkoep, 6 km N. Kamieskroon, 30.19S 17.56E, 1–2.x.1990, C. Eardley (1♀ SANC); Clanwilliam Dam, 32.11S 18.53E, 3–7.x.1988, F.W. & S.K. Gess (1♀ AMGS); Vanrhynsdorp, 20.x.1968, J.G. Rozen, E. Martinez (1♀ 1♂ AMNH).
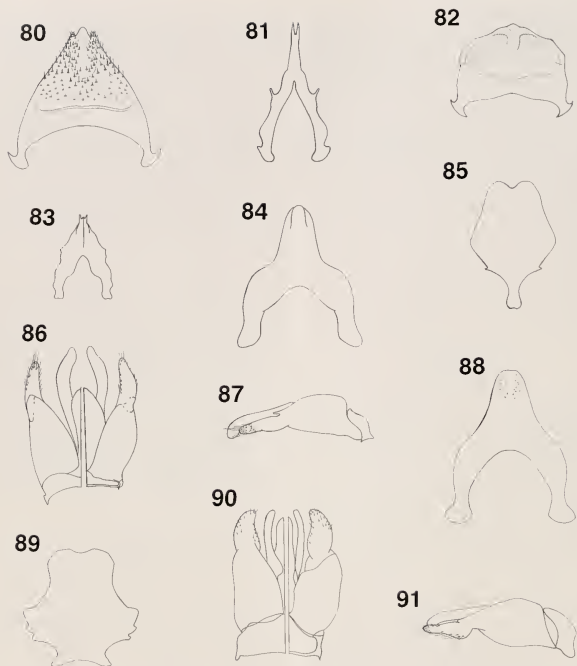
## ACULEATA SPECIES GROUP

This species group is monotypic.

### *Sphecodopsis aculeata* (Friese)
### (Figs. 88–91)

*Pasites aculeatus* Friese 1922:37.

*Sphecodopsis (Pseudopasites) aculeata* (Friese); Bischoff 1923:595.

Figs. 80–91.  *Sphecodopsis* spp. 80–81. *S. namaquensis*, ♀. 80. S5, ventral view; 81. S6, ventral view. 82–87. *S. minutissima*. 82. S5, ventral view, ♀; 83. S6, ventral view, ♀; 84. S7, ♂; 85. S8, ♂; 86. Genital capsule, dorsal left & ventral right, ♂. 87. Genital capsule, lateral view, ♂. 88–91. *S. aculeata*, ♂. 88. S7; 89. S8; 90. Genital capsule, dorsal left & ventral right. 91. Genital capsule, lateral view.

*Morgania aculeata* (Friese); Cockerell 1933a:383.
*Pasites pygmaeus* Friese 1922:37. **Syn. nov.**
*Sphecodopsis* (*Pseudopasites*) *pygmaeus* [sic.] (Friese); Bischoff 1923:595 [*lapsus*].
*Morgania pygmaea* (Friese); Cockerell 1933a:384.
*Sphecodopsis* (*Pseudopasites*) *rufescens* Bischoff 1923:593–594. **Syn. nov.**
*Sphecodopsis* (*Pseudopasites*) *algoensis* Bischoff 1923:595. **Syn. nov.**

*Morgania algoensis* (Bischoff); Cockerell 1933a: 384.
*Pseudopasites algoensis* (Bischoff); Anonymous 1958:30.
*Morgania* (*Pseudopasites*) *perpunctata* Cockerell 1933a:382–384 [specific epithet erroneously recorded as masculine on p. 382]. **Syn. nov.**

Bischoff (1923) and Cockerell (1933a)

recognized five distinct species for what is here considered to be a single taxon, mainly based on differences in the colour of the vestiture and the metasoma. An exception is the female paralectotype of *algoensis* (which could not be found) that Bischoff (1923) separated from *aculeata*, *pygmaea* and *rufescens* by its relatively long vestiture on the upper region of the head and scutum. (Confirmation as to whether that specimen was correctly described awaits its discovery.) A comparative study of the colour differences that Bischoff (1923) and Cockerell (1933a) used to separate species indicated that these differences could not be used to define distinct species.

*Morgania pygmaea* and *M. algoensis* were each described from a pair of specimens of opposite sexes. The type series of *pygmaea* was collected in Cape Town and that of *algoensis* at Algoa Bay. In each case the female could not be located. The male syntypes are therefore designated as the lectotypes of these two species.

*Description.*—Length of head 1.2–1.5 mm; scutum 0.9–1.2 mm; fore wing 4.0–5.0 mm; body 4.4–6.3 mm. Integument of head and mesosoma black to blackish, except distal end of mandible orange; posterolateral region of tegula translucent; metasoma completely black to orange anteriorly, black posteriorly. Pubescence white, except ventral surfaces of tarsi pale white. Head and mesosoma generally moderately densely pubescent, except femora sparsely pubescent; tibiae and tarsi densely pubescent; metasoma with sparse vestiture, except pygidium in which it is dense. Structurally similar to *S. capicola* except as follows: scutum moderately densely punctate, punctures large, mostly separate; propodeal triangle weakly sculptured to glabrous; female S5 similar to that of *S. namaquensis*, except without black setation (*cf.* Fig. 80); S6 narrowly bifid (*cf.* Fig. 81); male S7, S8 and genital capsule as in Figs. 88–91.

*Distribution.*—Southern region of South Africa. Vegetation types fynbos and karoo.

*Discussion.*—*Sphecodopsis aculeata* closely resembles other species in the capicola species group. This species can be recognized by the pallid, simple vestiture on the head and mesosoma, absence of distal fringe on the female T5 and expansion of

the anterior lobe of the male S8 (Fig. 89). The pallid, simple vestiture and the structure of the male S8 are unique, within the genus, to this species. The absence of a distal fringe on the female T5 suggests an affinity with both *S. namaquensis* and *S. semirufa*. The structure of the female S5 and S6 of *S. aculeata*, however, resembles that of *S. namaquensis*.

*Type material examined.*—*Pasites aculeatus*, holotype ♀: 'Cape Town, L.C. Peringuey, 1911; Pasites aculeatus Fr. ♀ 1904 Friese det.; Type, Pseudopasites; Zool. Mus. Berlin' (ZMHB). *Pasites pygmaeus*, lectotype ♂: 'Capland; Pasites pygmaeus Fr. ♂ 1904 Friese det.; Coll Friese, Pseudopasites, Type; Zool. Mus. Berlin' (ZMHB). *Pseudopasites rufescens* holotype ♀: 'T. us Afr. Pseudopasites rufescens, Type; Zool. Mus. Berlin' (ZMHB). *Sphecodopsis algoensis*, lectotype ♂: 'Algoa bay, Capland, Dr Brauns, 20.8.96; Pseudopasites algoensis Bisch. ♂ Typ.; Pseudopasites algoensis Type ♂ Bischoff; Pseudopasites algoensis Biss. ♂ Type No. 567' (TMSA). *Morgania perpunctata*, holotype ♂: 'Rapenburg, Cape Flats, 1–14.x.1920, S. Africa, R.E. Turner, 1920-424; Morgania perpunctata, B.M. TYPE HYM. 17B 95' (NHML).

*Additional material examined.*—26♀ 21♂: SOUTH AFRICA: 19 km N.W. Grahamstown, 16.xi.1970, H.V. Daly (1♀ SEMK); Grahamstown, Hilton, 12.x.1977 & 26.ix.1983, F.W. & S.K. Gess (3♀ AMGS); same locality, 9.x.1972, 29.ix.1977 & 12.x.1977, F.W. Gess (4♀ AMGS); Boknes, 33.43S 26.35E, 5.iv.1984, S.K. Gess (1♀ AMGS); Willowmore, 11.x.1904, H. Brauns (1♀ TMSA); Cango River, Oudtshoorn district, x.1937 (1♀ SAMC); Seven Weeks Poort, Ladismith district, 10.ix.1948, C.J. Jacot-Guillarmod (2♀ AMGS); Pearly Beach, Bredasdorp, ix.1959 (1♀ SAMC); Cape Town, vii & ix.1913 & 1915 (1♀ 1♂ SAMC, 2♂ SANC); Hout Bay, 15.ix.1966, C.D. Michener (3♀ 1♂ SEMK); Kommetjie, 15–25.x.1972, J.G. Rozen, R. McGinley, C.Thompson (2♀ AMNH); Kommetjie, 15.ix.1966, C.D. & B.J. Michener (4♀ SEMK); Stellenbosch, 1919, Lightfoot (1♀ AMNH); Pakhuis Pass, ix.1961 (1♂ SANC); Kamieskroonberg, near Kamieskroon, 30.32S 18.08E, 3.x.1990, C.D. Eardley (1♀ 1♂ SANC).
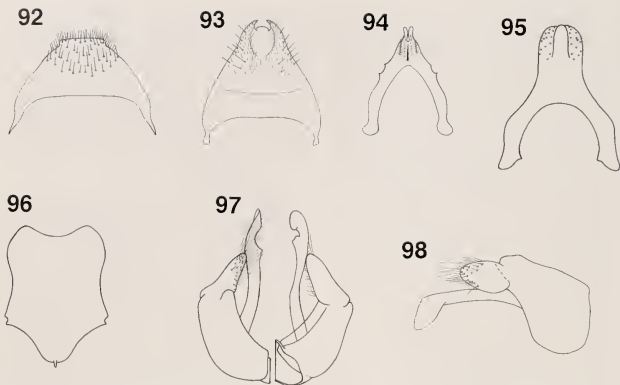
## SEMIRUFA SPECIES GROUP

This species group is monotypic.

### *Sphecodopsis semirufa* (Cockerell), **comb. nov.**
(Figs. 92–98)

*Morgania semirufa* Cockerell 1933a:380–381.
*Morgania* (*Sphecodopsis*) *leonis* Cockerell 1933a: 382, 384. **Syn. nov.**

Figs. 92–98.   *Sphecodopsis semirufa.* 92. T6, dorsal view, ♀; 93. S5, ventral view, ♀; 94. S6, ventral view, ♀; 95. S7, ♂; 96. S8, ♂; 97. Genital capsule, dorsal left & ventral right, ♂. 98. Genital capsule, lateral view, ♂.

The type specimens of *leonis* are considerably smaller than those of *semirufa*, otherwise they are almost indistinguishable.

*Description.*—Length of head 1.1–1.7 mm; scutum 0.8–1.3 mm; fore wing 3.6–5.8 mm; body 3.9–6.1 mm. Integument of head and mesosoma mostly black, distal half of mandible, antenna and pronotal lobe sometimes orange to reddish-black; tegula always orange; legs black to reddish-black, often with femur orangish; metasoma orange anteriorly, black posteriorly. Vesiture on head black; mesosoma with short, white and long, black vestiture intermixed; vestiture on coxae and trochanters largely white, femora generally black (posterodistal region of hind femur white), tibiae and tarsi pallid with few black setae on dorsal surfaces (those on middle and hind legs thick and spinose); female metasoma generally with vestiture on orange areas short and pallid, black regions long and black, except T6 and S5 mostly with mixture of black and white vestiture, posterior region pale brownish; male metasomal vestiture mostly black. Vestiture on head long and moderately dense, hairs simple to weakly plumose; mesosoma with short white pubescence intermixed with long, black, weakly plumose hairs; femora generally sparsely pubescent, dense posterodistally on hind femur; black setae on dorsal surfaces of middle and hind tibiae and tarsi thick and spinose; female metasoma generally with vestiture on areas in which integument is orange short, on areas with integument black long; metaso-

ma of male with vestiture mostly long. Scutum fairly sparsely punctate, punctures small, shallow and mostly separate; propodeal triangle glabrous, mediolongitudinal region below triangle punctate; female T6 as in Fig. 92, S5 with posteromedian protuberance small, posterolateral prominence large and incurved, forming a distinct concavity posteromedially (Fig. 93); female S6 very narrowly bifid, mediolongitudinally carinate on ventral surface (Fig. 94); male S7, S8 and genital capsule as in Figs. 95–98, genitalia with gonocoxite shorter than penis valve.

*Distribution.*—Southern and western regions of South Africa. Vegetation types fynbos and karoo.

*Discussion.*—*Sphecodopsis semirufa* can be easily identified by the sparsely pubescent, glabrous face; posteromedian concavity and enlarged apicolateral prominences of the female S5 (Fig. 93), absence of a distinct anterior lobe on the male S8 (Fig. 96) and bowed gonocoxite of the male genitalia (Fig. 97). These features are all unique within the genus. The mosaic of characters that occur in *S. semirufa* makes it difficult to determine its closest relative.

*Type material examined.*—*Morgania semirufa,*

holotype ♀: 'Worcester, Cape Province, Sept. 1928, S. Africa, R.E. Turner, Brit. Mus. 1928-457; Morgania semirufa Ckll TYPE; B.M. TYPE HYM. 17B 94' (NHML). *Morgania leonis*, holotype ♂: 'S. Africa, R.E. Turner, 1920-342, Lion's Head, Cape Town, Aug. 1920; Morgania leonis Ckll., TYPE; B.M. TYPE HYM. 17B 85' (NHML).

*Additional material examined.*—7♀: SOUTH AFRICA: Grahamstown, Hilton, 12.iv.1968, C. Jacot-Guillarmod (1♀ AMGS); Willowmore, 19.v.1903 & 5.ix.1903, H. Brauns (1♀ TMSA, 1♀ SANC); Lammerskraal, Prince Albert District, ix.1947 (1♀ SAMC, 1♀ SANC); Kamieskroon, ix.1930 (1♀ SAMC); Lambert's Bay, 32.04S 18.20E, 4.x.1974, R.H. Watmough (1♀ SANC).

### CAPENSIS SPECIES GROUP

This species group comprises *S. capensis* and *S. fumipennis*. These two species are unique in the structure of the female terminalia. The posteromedian region of S5 is gutter-like and the posterior end of S6 forms a single spine.

### *Sphecodopsis capensis* (Friese), comb. nov.

*Omachthes capensis* Friese 1915:296–297 (holotype ♀, ZMHB).
*Morgania capensis* (Friese); Cockerell 1919:190.
*Pseudodichroa capensis* (Friese); Bischoff 1923:595–596; Rozen 1968a:1–9, 1968b:3–13.

The holotype of this species was not examined during the course of the study because material that was reliably identified by Dr J.G. Rozen (AMNH), who examined the holotype (Rozen 1968a), was studied together with Rozen's (1968) outstanding redescription.

The host of this species is *Scrapter longula* (Friese) (Colletidae: Colletinae) (Rozen 1968b).

*Material examined.*—26♀: SOUTH AFRICA: Rapenburg, 1–14.x.1920, R.E. Turner (4♀ SAMC); Kommetjie, 29.x.–9.xi.1966, C.D. Michener & J.G. Rozen (7♀ AMNH); Kommetjie, 14.x.1972, J.G. Rozen, R. McGinley & C. Thompson (10♀ AMNH); 25 km E. Velddrif, 23.x.1972, J.G. Rozen, R. McGinley & C. Thompson (5♀ AMNH).

### *Sphecodopsis fumipennis* (Bischoff), comb. nov.

*Pseudodichroa fumipennis* Bischoff 1923:596; Rozen 1968a:1–9, 1968b:3–13, 1974:6–8 (syntypes 2♀, ZMHB).

Bischoff (1923) described this species from two female specimens, one from Cape Town, and the other with `Java' on the label. Bischoff (1923) regarded the accuracy of the locality label of the second specimen as questionable, and Rozen (1968a), who examined the specimen (the Cape Town syntype has been lost), shared Bischoff's (1923) sentiments. During the course of the current study, material of this species which was identified by Dr J.G. Rozen was studied and compared with his (Rozen 1968a) excellent redescription. This species is endemic to southwestern region of South Africa. It was adequately dealt with by Rozen (1968a) and requires no further comment.

The host of *S. fumipennis* is *Scrapter crassula* Cockerell (Colletidae, Colletinae) (Rozen 1968b).

*Material examined.*—10♀: SOUTH AFRICA: Kommetjie, 29.x–9.xi.1966, C.D. Michener & J.G. Rozen (4♀ AMNH); Kommetjie, 14.x.1972, J.G. Rozen, R. McGinley & C. Thompson (2♀ AMNH); Between Nieuwoudtville & top Vanrhyns Pass 29–30.ix.1990, F.W. & S.K. Gess (3♀ AMGS); Nieuwoudtville flower reserve, 31.19 AC, V.B. Whitehead & M. Macpherson, 28.viii.1984 (1♀ SAMC.)

### SPECIES OF UNCERTAIN IDENTITY

### *Sphecodopsis argyrura* (Cockerell), comb. nov.

*Morgania argyrura* Cockerell 1933c:108–109 (holotype ♀, NHML).

All that remains of the holotype is the thorax and part of the legs, which allow only for it to be recognised as belonging to *Sphecodopsis*. Cockerell (1933c) described it in the genus *Morgania*, but mentioned that it belonged to 'the genus or subgenus *Sphecodopsis*'.

### GENUS *AMMOBATES* LATREILLE

*Ammobates* Latreille 1809:169. Type species *Ammobates rufiventris* Latreille 1809 (subsequent designation by Latreille 1810:439, Sandhouse 1943).
*Phileremus* Latreille 1809:169. Type species *Epeolus punctatus* Fabricius 1804 (subsequent des-

Fig. 99.  *Ammobates auster*, habitus, dorsal view (dark shading represents black or blackish integument and lightly shaded areas are reddish), ♀.

ignation by Latreille 1810:439, Sandhouse 1943).

Ammobatoides Schenck 1869:349, not Radoszkowski 1868. Type species *Ammobates bicolor* Lepeletier 1825 (= *Epeolus punctatus* Fabricius) (monobasic, Sandhouse 1943).

Ammobates (Caesarea) Friese 1911d:142. Type species *Ammobates depressa* Friese 1911 (subsequent designation by Sandhouse 1943, Brooks pers. comm. 1997).

A single species of *Ammobates*, namely *A. auster* spec. nov., was recently discovered in southern Africa. *Ammobates* is otherwise known from the Palaearctic Region (Popov 1951), where it is particularly diverse in the Mediterranean basin. Because only one species is known from the Afrotropical Region the subgeneric classification is beyond the scope of this articel. As *A. auster* is known only from five specimens, it is difficult to speculate on the distribution of *Ammobates* in the Afrotropical Region. However, several other genera of bees, including *Meliturgula* Friese and *Mel-*

*itturga* Latreille (both Andrenidae) and *Ochreriades* (Megachilidae), occur in southern Africa and the Eremic Region and not in the intermediate area. It is, therefore, possible that *Ammobates* does not occur in the area between southern Africa and the Mediterranean Basin.

*Ammobates auster* is a medium sized (7.3–9.0 mm long) bee. The head and mesosoma are mostly black and the metasoma is at least partly orangish (posterior region sometimes black). The generic diagnostic features are: vertex, in front view, gently convex; antenna 12-segmented in female, 13-segmented in male; labrum distinctly longer than its maximum width, truncate distally; mandibles lie over labrum, their apices overlap in repose; facial vestiture white and mostly sparse, dense pubescence occurs in vicinity of antennal sockets, and appressed; scutellum essentially gently and evenly curved; female T6 without pygidial plate, male T7 with pygidial plate; female with pygidial region
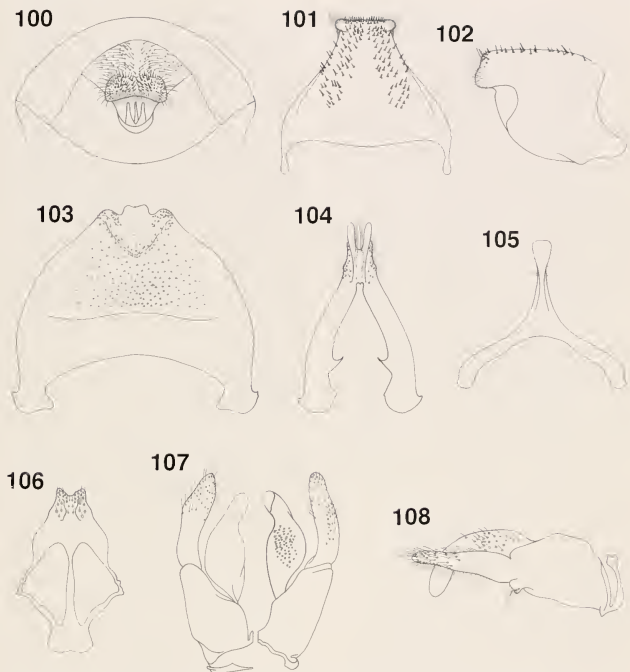
Figs. 100–108. *Ammobates auster.* 100. Terminalia, posterior view, ♀; 101. T6, dorsal view, ♀; 102. T6, lateral view, ♀; 103. S5, ventral view, ♀; 104. S6, ventral view, ♀; 105. S7, ♂; 106. S8, ♂; 107. Genital capsule, dorsal left & ventral right, ♂; 108. Genital capsule, lateral view, ♂.

densely setose (Figs. 101–102); female S5 shallowly concave posteriorly, with fairly well developed gutter posteromedially (Figs. 100, 103); female S6 bifid posteriorly (Fig. 104).

#### *Ammobates auster* Eardley, **spec. nov.**
(Figs. 100–108)

This new species takes its name from the Latin word *auster*, which means south.

It is the only species of the genus known from the southern hemisphere.

*Description.*—Habitus, dorsal aspect, as in Fig. 99. Length of head 2.0–2.7 mm; scutum 1.5–2.2 mm; fore wing 6.1–8.6 mm; body 7.3–9.0 mm. Integument of head and mesosoma mostly black, appendages generally reddish to orange; metasoma either mostly reddish to orange or orangish anteriorly, black posteriorly. Vestiture generally white, posterior surface of hind tibia and ventral surfaces of all basitarsi with dense yellow to orange setation; female T6 orangish,

female pygidium with blackish tinge; female S5 with orangish velutinous vestiture subapically, male S6 pale yellowish. Vestiture generally sparse, often dense and pubescence around antennal sockets, on lateral region of pronotal collar, edge of pronotal lobe, anterior margin of scutum, posterior region of scutellum, entire metanotum, anterodorsal region of mesepisternum, adjacent to epimeral suture, entire area above scrobal sulcus, dorsolateral region of propodeum, posterior regions of middle and hind tibiae and on posterolateral regions of female T1-T5 and male T1-T6; posterior surface of hind tibia and ventral surfaces of all basitarsi with dense setation; pygidial area with coarse, dense setation. Labrum about 1.6× as long as its maximum width, strongly incurved laterally, truncate distally; maxillary palp two-segmented, subequal in length to antennal pedicel; scutum fairly sparsely punctate, glabrous between punctures; scutellum generally gently curved, slightly concave medioposteriorly; virtually entire posterior surface of propodeum naked and glabrous; female T6 truncate posteriorly, expanded posterolaterally (Figs. 100-102); male T7 with well developed, broadly rounded, posteriorly concave, pygidial plate; female S5 with well developed gutter posteromedially (Figs. 100, 103), S6 forked posteriorly (Fig. 104); male S7, S8 and genital capsule as in Figs. 105-108.

*Distribution.*—Southern Namibia (desert), Western Cape Province (karoo) and Eastern Cape Province (fynbos).

*Discussion.*—*Ammobates auster*, for the purpose of the cladistic analysis, was grouped with *A. punctatus*. In spite of the geographical separation of *A. auster* from the rest of the punctatus group, it is remarkably similar to the other species in the group. The most important diagnostic feature of the group is the structure of the female pygidium, and within the group the female of *A. auster* can be identified by the shape of this structure. The pygidium of *A. auster* is truncate and expanded laterally (Figs. 100-102). The male can be identified by the structure of the S8 which narrows posteriorly (Fig. 106).

*Type material.*—Holotype ♀, paratypes 3♀ 1♂: **NAMIBIA:** 40 km S. Kolmanskop, 23.x.1974, R.H. Watmough (holotype ♀ SANC). **SOUTH AFRICA:** Strowan, 27.xi.1968, F.W. Gess (2♀ AMGS); 29 km E. Touwsrivier towards Hondewater, xii.1962 (1♀ SAMC); 77 km E. Barrydale, 13.xi.1966, C.D. Michener (1♂ SEMK).

## GENUS *MELANEMPIS* SAUSSURE

*Phileremus* (*Melanempis*) Saussure 1891:84. Type species *Phileremus* (*Melanempis*) *ater* Saussure 1891 (monobasic) (Sandhouse 1943).
*Melanempis* Saussure; Michener 1944:276.

*Melanempis* is endemic to Madagascar. The name, which means black spot, is feminine. The genus is known from one described species, which is the largest known ammobatine bee. It is currently being revised by R.W. Brooks and A. Pauly, who have material of three additional species (Brooks, pers. comm.). Consequently, the genus is only briefly dealt with here. During the course of this study only the type species was available for examination.

*Melanempis atra* is a large bee (11.2-15.8 mm long). The head, mesosoma and metasoma are blackish-brown in colour. The genus is characterized as follows: vertex, frontal view, weakly and unevenly convex; antenna 12-segmented in both sexes; labrum 1.4× as long as its maximum width and truncate distally; mandibles lie over labrum and their apices overlap in repose; vestiture mostly brownish-orange and sparse, fairly dense on lower region of face and distal end of metasoma; scutellum gently and evenly curved mediolongitudinally, and distinctly tuberculate paramedially; hind wing without jugal lobe; last exposed metasomal tergum (T6 female, T7 male) devoid of pygidial plate; female T6 distinctly truncate, pygidial region naked and circumscribed by small carina; male T7 abruptly curved under laterally and posterolaterally, forming pseudopygidial plate; female S5 with well developed gutter posteromedially; female S6 bifid posteriorly.

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## APPENDIX 1

Species studied and their groupings. Following each species name are: genera to which species were assigned before this study, for genera synonymized here; number of specimens studied; whether the holotype or lectotype was studied, indicated by a 'T'; and general distribution. The zoogeographic region in which each species occurs is indicated as follows: P = Palaearctic, A = Afrotropical, Na = Nearctic, Nt = Neotropical.

*Pasites*

barkeri group

   *P. barkeri* (Cockerell) [19♀ 11♂; T; A: tropical & subtropical Africa]

ater group

   *P. friesei* Cockerell [57♀ 49♂; T; A: widespread in Africa]

   *P. nilssoni* spec. nov. [1♂; T; A: Madagascar]

   *P. paulyi* spec. nov. [3♀ 1♂; T; A: Cameroon]

   *P. braunsi* (Bischoff) [32♀; A: Southern Africa]

   *P. humectus* spec. nov. [18♀ 8♂; T; A: equatorial Africa]

*P. bicolor* Friese [*Pasitomachthes*; 9♀ 4♂; T; A: Madagascar]

*P. tegularis* Friese [13♀ 7♂; T; A: Madagascar]

gnomus group

*P. gnomus* spec. nov. [1♀ 1♂; T; A: Niger]

carnifex group

*P. carnifex* (Gerstaecker) [15♀ 5♂; T; A: East & southern Africa]

*P. dichrous* Smith [4♀ 2♂; T; A: equatorial West Africa]

jenseni group

*P. jenseni* (Friese) [19♀ 10♂; T; A: southern Africa]

*P. namibiensis* spec. nov. [1♀ 2♂; T; A: southern Africa]

*P. histrio* (Gerstaecker) [24♀ 12♂; T; A: southern Africa]

*P. jonesi* (Cockerell) [9♀ 1♂; T; A: East & southern Africa]

rufipes group

*P. rufipes* (Friese) [2♀; T; A: southern Africa]

appletoni group

*P. appletoni* (Cockerell) [217♀ 59♂; T; A: widespread in Africa]

*P. somalicus* spec. nov. [1♀; T; A: Somalia]

maculatus group

*P. maculatus* Jurine [5♀ 4♂; P: Morocco to Japan]

*Sphecodopsis*

capicola group

*S. capicola* (Strand) [22♀ 3♂; T; A: southern Africa]

*S. vespericena* spec. nov. [68♀; T; A: southern Africa]

*S. villosa* (Friese) [2♂; T; A: southern Africa]

*S. longipygidium* spec. nov. [1♀; T; A: southern Africa]

*S. namaquensis* spec. nov. [3♀; T; A: southern Africa]

minutissima group

*S. minutissima* (Cockerell) [6♀ 1♂; T; A: southern Africa]

aculeata group

*S. aculeata* (Friese) [28♀ 24♂; T; A: southern Africa]

semirufa group

*S. semirufa* (Cockerell) [8♀ 1♂; T; A: southern Africa]

capensis group

*S. capensis* (Friese) [*Pseudodichroa*; 29♀; A: southern Africa]

*S. fumipennis* (Bischoff) [*Pseudodichroa*; 11♀; A: southern Africa]

*Melanempis*

*M. atra* (Saussure) [2♀ 1♂; A: Madagascar]

*Spinopasites*

*S. spinotus* (Warncke) [1♀; P: Tunisia]

*Ammobates*

orientanus group

*A. orientanus* (Warncke) [1♀ 1♂; P: Mediterranean]

*A. aegyptiacus* (Warncke) [1♂; P: Mediterranean]

minutus group

*A. minutus* (Mocsary) [4♀ 5♂; P: East Europe]

muticus group

*A. muticus* Spinola [45♀ 28♂; P: North Africa]

*A. oraniensis* (Lepeletier) [5♀ 6♂; P: South-east Europe]

*A. latitarsis* Friese [2♀ 2♂; P: East Mediterranean]

biastoides group

*A. biastoides* Friese [2♀ 1♂; P: Mediterranean]

unctatus group

*A. punctatus* (Fabricius) [5♀ 4♂; P: Mediterranean]

*A. ancylae* (Warncke) [1♀ 1♂; P: Mediterranean]

*A. solitarius* Nurse [1♀ 1♂; P: Pakistan]

*A. vinctus* Gerstaecker [6♀ 6♂; P: Mediterranean]

*A. auster* spec. nov. [4♀ 1♂; A: southern Africa]

*A. similis* Mocsary [1♀ 1♂; P: Mediterranean]

*A. rufiventris* Latreille [3♀ 2♂; P: Algeria]

*A. iranicus* (Warncke) [1♀ 1♂; P: Iran to Turkey]

*A. dubius* Benoist [1♀ 1♂; P: Egypt & Sudan]

*A. niveatus* (Spinola) [1♀ 2♂; P: Mediterranean]

*A. assimilis* (Warncke) [1♂; P: Tunisia]

*A. syriacus* Friese [1♀; P: Mediterranean]

*A. opacus* Popov [1♀; P: Bulgaria]

*A. armeniacus* Morawitz [1♀ 1♂; P: Turkey]

*A. sanguineus* Friese [1♀ 1♂; P: Turkey & Greece]

rostratus group

*A. rostratus* Friese [3♀ 3♂; P: Mediterranean]

*A. robustus* Friese [1♀ 1♂; P: Turkey]

*A. teheranicus* Mavromoustakis [1♂; P: Iran]

*A. hipponensis* Pérez [2♂; P: Algeria]

*A. baueri* (Warncke) [1♀; P: Mediterranean]

*A. mavromoustakisi* Popov [2♀ 2♂; P: Mediterranean]

*A. handlirschi* Friese [1♂; P: Algeria]

*A. depressus* Friese [1♀; P: Turkey]

verhoeffi group

*A. verhoeffi* Mavromoustakis [1♀ 1♂; P: North Africa]

persicus group

*A. persicus* Mavromoustakis [1♀ 1♂; P: Iran]

oxianus group

*A. oxianus* Popov [1♀ 1♂; P; Turkey]

*A. lebedevi* Popov [1♀; P; Turkey]

*Oreopasites*

vanduzeei group

*O. vanduzeei* Cockerell [1♀ 1♂; Na: western U.S.A.]

*O. linsleyi* Rozen [1♀ 1♂; Na: western U.S.A.]

*Caenoprosopis*

*C. crabronina* Holmberg [1♀ 1♂; Nt: Argentina, Paraguay & south-eastern Brazil]

## APPENDIX 2

Adult morphological characters used in the cladistic analysis and their states. The states assigned to taxa are recorded in Tables 1, 2, & 4. Characters are treated as additive. Polarity was determined with reference to Neolarrini as the out group, except for character 50.

1. Vertex contour, when viewed perpendicular to lower region of inner eye margins: strongly convex laterally, lateral ocelli distinctly below vertex (Fig. 42) (0); gently convex, lateral ocellus slightly protuberant above vertex or a little below vertex (Fig. 5) (1); straight, lateral ocellus mostly protuberant above lateral region of vertex (Fig. 63) (2).

2. Vertex length: relatively short, less than twice diameter of lateral ocellus (0); elongate, at least twice as long as diameter of lateral ocellus (1).

3. Vertex profile: curved gently downwards to occiput (0); extending more or less straight behind lateral ocellus, curved abruptly downwards posteriorly (1).

4. Position of antennal socket: on lower half of face, much closer to ventral edge of clypeus than to lateral ocellus (0); near middle of face, usually closer to lateral ocellus than to ventral edge of clypeus (Fig. 5) (1).

5. Length of subantennal suture: much shorter than clypeus (0); subequal in length to clypeus (Fig. 5) (1).

6. Facial vestiture, hair structure: densely plumose, at least in area surrounding antennal sockets (0); simple to weakly plumose (1).

7. Facial vestiture, hair posture: appressed (0); erect (1).

8. Facial vestiture, hair density: dense, at least on lower region of face (Fig. 5) (0); sparse over entire face (Fig. 63) (1).

9. Segmentation of male antennal flagellum: 11-segmented (0); 10-segmented (1).

10. Length of labrum: distinctly shorter than its maximum width (0); quadrate (1); clearly longer than wide, about 1,2–1,9 times as long as its basal width (2).

11. Shape of labrum, apical truncation: apex gently rounded (or pointed) (0); truncate, distal end straight to weakly concave medially (1).

12. Shape of labrum, apex pointed: apex gently rounded (or truncate) (0); pointed apicomedially (1).

13. Shape of apex of labrum: unmodified (0); spatulate (1).

14. Maxillary palp: present (0); absent (1). The number of segments in the maxillary palp is highly variable in several species groups, and sometimes within a single species. However, what appeared to be of significance is that some species have lost the maxillary palp.

15. Length of segments of labial palp: segment 2 about twice as long as segment 3 (0); segment 2 at least four times as long as segment 3 (1).

16. Paraocular carina: absent (0); present (1).

17. Occipital carina: absent (0); present and short (1); long, extending down posterior edge of gena (2).

18. Angle of mandibles, in repose: directed posterolaterally so that they clearly cross one another, and their apices do not overlap (illustrated by Rozen 1968a) (0); directed mesad so that their distal ends overlap in repose (1).

19. Position of mandibles, when in repose, in relation to labrum: mandibles close behind labrum (0); close over or in front of distal edge of labrum (1).

20. Pronotum: curved distinctly upwards posteromedially, but not declivous (0); declivous with vertical surface usually gently concave and glabrous (1).

21. Lateral region of pronotal collar: rounded (0); carinate (1).

22. Lateral edge of axilla: curved gently downward to wing base (0); carinate (1).

23. Scutal vestiture, hair structure: densely plumose (0); with weakly plumose and densely plumose vestiture intermixed (1); simple (2).

24. Scutal vestiture, hair posture: strongly appressed (0); weakly appressed (1); mostly erect (2).

25. Scutal vestiture, hair density: dense (0); sparse (1).

26. Mesepisternal vestiture, hair structure: densely plumose (0); mostly weakly plumose (1)

27. Ventrolateral region of mesepisternum: vestiture similar to remainder of sclerite (0); sparsely pubescent to naked, in strong contrast to densely pubescent upper region of mesepisternum (1).

28. Pre-episternal groove: extending from near wing base to scrobal groove (0); extending below scrobal groove (1).

29. Mediolongitudinal region of scutellum: unmodified or weakly raised (0); strongly swollen (1).

30. Dorsolateral edge of scutellum: rounded (0); carinate (1).

31. Shape of median region of metanotum: swollen or tuberculate (0); flat (1).

32. Setae on hind tibia of female: all setae fine, not thickened and spine-like (0); fine setae mixed with greatly thickened, spine-like, setae (1).

33. Anterior region of S1: flat to gently curved (0); strongly swollen (1).

34. Posterior region of S1: more or less in same plane as S2 (0); strongly declivous (1).

35. Mediolongitudinal region of S1: gently rounded (0); carinate anteriorly (1).

36. Mediolongitudinal region of propodeum: gently and evenly curved (0); declivous (1).

37. Dorsal surface of female T6: flat to gently convex (0); carinate mediolongitudinally (1).

38. Posterior end of female pygidial plate: fully de-

veloped (Fig. 6) or absent **(0)**; reduced, including posteromedian notch **(1)**.

39. Female T6 truncate, following loss of pygidial plate: Pygidial plate present, fully developed or reduced (or absent with distal end of T6 spatulate) **(0)**; absent, posterior end of T6 truncate and setose **(1)**; absent, posterior end of T6 truncate and naked, circumscribed by a small carina **(2)**.

40. Female T6 spatulate, following loss of pygidial plate: pygidial plate present, either fully developed or reduced (or absent with distal end of T6 truncate) **(0)**; pygidial plate absent, posterior end of T6 spatulate **(1)**.

41. Posterior fringe on female T6: absent **(0)**; present **(1)**.

42. Female subpygidial brush: absent **(0)**; present, but not differentiated (Fig. 6) **(1)**; well developed and differentiated dorsoventrally (Figs. 34, 38, 43, 47, 50, 51, 53, 57) **(2)**.

43. Posterior margin of female S5: posteromedian region naked **(0)**; clothed with fine vestiture **(1)**.

44. Posteromedian elongation of naked posterior margin of female S5: naked posterior margin short and of uniform length (or elongate and more or less of uniform length throughout its width) **(0)**; elongate posteromedially only, due to the apparent recession of the vestiture, more or less pointed anteromedially **(1)**.

45. Posterior elongation of naked posterior margin of female S5: naked posterior margin short and of uniform length (or elongate posteromedially) **(0)**; naked posterior margin widely elongate due to an apparent elongation of naked posterior margin, of uniform length **(1)**.

46. Posteromedian concavity of female S5 in species in which the posterior margin is clothed with fine vestiture, when viewed from behind: broadly and moderately concave (or variable with posterior margin naked) **(0)**; with a well developed, conical concavity (Figs. 6, 15, 19, 20, 28, 29, 34) **(1)**; concavity well developed and elliptical (Figs. 43, 47, 50, 51, 53, 57) **(2)** (see character 47).

47. Posteromedian concavity of female S5 in species in which the posterior margin is naked, when viewed from behind: broadly and moderately concave (or strongly concave with posterior margin clothed with fine vestiture) **(0)**; with a well

developed, conical concavity **(1)**; concavity well developed and more or less elliptical **(2)**. The structure of the posterior margin of the female S5 differs between those bees in which this structure is naked and those in which it is clothed with fine vestiture. Apparently the posteromedian concavity evolved independently in these two groups of bees in response to similar requirements associated with the laying of the eggs in the cell wall of the host's nest.

48. Posteromedian protuberance of female S5: posterior edge entire or concave and without a posteromedian protuberance (Figs. 65, 78, 82) **(1)**; with a very small posteromedian protuberance distinct (Fig. 80) **(2)**; protuberance gutter-like (illustrated by Rozen 1968a) **(3)**.

49. Carina on female S5: absent **(0)**; present **(1)**.

50. Structure of female S6: external **(0)**; mostly internal, not longitudinally separated (Fig. 7) **(1)**; mostly internal and longitudinally separated (illustrated by Roig-Alsina 1987) **(2)**. Polarity determined with Townsendiellini as the out group.

51. Posterior edge or apex of female S6: entire **(0)**; forming two sclerotized spines (Fig. 7) **(1)**; forming a single sclerotized spine **(2)**.

52. Reduction of male pygidial plate: pygidial plate present, sometimes reduced and confined to distal end of tergum **(0)**; absent **(1)**.

53. Structure of male pygidial plate: pygidial plate simple, reduced or absent **(0)**; well developed and bilobed (illustrated by Roig-Alsina 1987) **(1)**.

54. Loss of anteromedian lobe of male S8: anteromedian lobe short (Fig. 9) (or long) **(0)**; lobe absent (Fig. 12) **(1)**.

55. Elongation of anteromedian lobe of male S8: anteromedian lobe short (or absent) (Fig. 9) **(0)**; elongate **(1)**.

56. Anterolateral lobes of male S8: very small and unmodified or absent (Figs. 9, 12, 69) **(0)**; well developed (Fig. 31) **(1)**.

57. Relative width of posterior region of male S8: narrower than anterior region (Fig. 9) **(0)**; with anterior and posterior regions of more or less equal width (Fig. 96) **(1)**; posterior region wider than anterior region (illustrated by Warncke 1983) **(2)**.

58. Expansion of anterolateral region of male S8: weakly expanded (Fig. 9) **(0)**; strongly expanded (illustrated by Roig-Alsina 1987) **(1)**.

# NOTE

# *Compsobraconoides* (Braconidae: Braconinae), the First Hymenopteran Ectoparasitoid of Adult *Azteca* Ants (Hymenoptera: Formicidae)

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*Azteca* ants (Dolichoderinae) are an important group of plant symbionts in the Neotropics (Davidson & McKey 1993). The ant queens colonize bulb-like domatia in ant-plants (Davidson et al. 1989, Yu & Davidson in press). Work on three species of *Azteca* that colonize the ant-plant *Cordia nodosa* Lam. (Boraginaceae) in the Madre de Dios area of Peru has revealed that the queens of all three species are subject to parasitism by a braconid wasp, which may be important for regulating ant populations (Yu & Pierce in preparation). One of the *Azteca* species has been identified as *A. ulei*, but the other two species are undescribed and are here referred to as *A. depilis*1 and *A. depilis*2. The wasp, a species of *Compsobraconoides* (Braconinae), is a principally solitary, idiobiont ectoparasitoid of *Azteca* queens. The host record has been confirmed by rearing an adult wasp from a larva found feeding on a paralysed *A. depilis*2 queen in a domatium (coll. # DY727.2), and by collections of wasp pupae, larvae, and host remains.

Colonizing *Azteca* queens were collected from both planted and naturally occurring saplings at Cocha Cashu Biological Station in Manu National Park, Madre de Dios, Peru, and from naturally occurring saplings at two other sites in Manu Park; the Tayakome and Yomybato indigenous communities. All three sites are located in lowland, moist-to-seasonal tropical rainforest (annual rainfall = 2100 mm) (Ter-

borgh 1983). Of 46 dead *Azteca* queens collected, eight were found with larvae of *Compsobraconoides*, nine with cocooned pupae and 29 with empty cocoons. The *Compsobraconoides* larvae were found feeding on both the mesosoma and the metasoma of *Azteca* queens. Pupating larvae weave both a cocoon and a protective tent, usually located at the distal end of the domatium. The adult wasp emerges by boring a small hole in the domatium wall. The hole is circular and very smooth, and is located directly below the cocoon/silk tent. This is probably an adaptation to avoiding entering the domatium which by the time of emergence might be colonized by another queen and her brood. The carcasses found with the empty cocoons appear to have been almost completely cleaned out by the wasp larvae: their sclerites were largely separated, and there was very little or no fungus present. Six of the ants collected with larvae were found alone in separate domatia, each with a single larva; the other two ants were found together in a single domatium with two larvae feeding on each of them. Rearing was unsuccessful in the latter case, perhaps due in part to inadequate food for the larvae. This was the only case in which more than a single wasp was associated with a single ant. In addition, seven pupae and one empty cocoon were found without host carcasses but with live *Azteca* queens. It is possible that these

newly colonizing queens had removed the previous queen's remains from the domatia. In another case, an empty cocoon was found with a dead, eaten queen of *Myrmelachista* sp., which also nests in *C. nodosa*, but is exceedingly rare (Yu & Pierce in preparation). However, we cannot conclude that the *Myrmelachista* queen was a host of the wasp. No adult wasps or cocoons were found associated with hosts of any other taxa.

*Azteca* queens lay eggs fairly soon after colonizing a domatium. Unfortunately, we cannot tell whether the parasitized queen had started to produce broods at the time of the attack. Although there was never any brood in the domatium with a parasitized queen, this could either be because the wasp larva had eaten the brood, or because the brood rots quickly when left unattended. It seems likely that wasp attack can take place at any time before workers appear.

The host record is remarkable for three reasons. Firstly, it is the first record of an adult ant being the host of an hymenopteran ectoparasitoid, though neoneurine braconids are probably endoparasitic in worker adults (Shaw & Huddleston 1991, Shaw 1993). Secondly, it is the first record of a member of the Braconinae attacking aculeate Hymenoptera and, thirdly, it is the first record of a braconine attacking any adult insect. Most braconines are idiobiont ectoparasitoids of concealed Coleoptera and Lepidoptera larvae, though a few species attack Diptera and symphytan Hymenoptera larvae (Shaw & Huddleston 1991). Further, this is the first host record for any member of the genus *Compsobraconoides*. The related genera *Compsobracon* and *Cyclaulacidea* have been reared as parasitoids of concealed Lepidoptera and bruchid beetle larvae respectively (Quicke 1989, Quicke & Delobel 1995). *Compsobraconoides* is a moderately large, principally Neotropical genus much in need of revision; the species reported on here is probably undescribed. It seems certain that some other *Compsobraconoides* species attack other hosts since *Azteca* ants are absent from the southern USA (Texas and Florida) where the type species of *Compsobraconoides* occurs (Quicke & Sharkey 1989).

The wasp may play an important role in the ecology of the *Azteca*-*C. nodosa* symbiosis. *C. nodosa* associates not only with the three *Azteca* species but also with *Allomerus* cf. *demerarae* (Myrmicinae) and, more rarely, with *Myrmelachista* sp. (Formicinae). At Cocha Cashu, the most abundant associate is *Allomerus*, inhabiting 77.9% of the plants (1024 plants in total were examined). Workers of *Allomerus* attack and destroy floral buds of their host plants, acting as a castration parasite (Yu & Pierce in preparation). As a result, fruit and pollen production are drastically reduced. The majority of fruit and pollen are apparently produced by the 10.5% percent of the plants inhabited by *Azteca* spp.

As in other ant-plant systems (Yu & Davidson 1997) the identity of the ant symbiont is determined at the colonization stage. The first queen to produce full-size workers is able to take over the plant killing off any other founding queens in the process. *Compsobraconoides* wasps, by preying on colonizing *Azteca* queens, increase the probability of successful establishment by the parasitic *Allomerus* queens.

Thus, the collections of *Compsobraconoides* wasps on *Azteca* ant queens are interesting both for the extreme host-range shift they represent, and also for the ecological problems that the *Compsobraconoides*-*Azteca* interaction poses. What is the role of *Compsobraconoides* in allowing *Allomerus* and *Azteca* species to coexist on the hostplant *C. nodosa*? What prevents *Compsobraconoides* sp. from driving *Azteca* queens and therefore, *C. nodosa*, extinct? That is, how is the host-parasitoid interaction stabilized? And finally, how do the three species of *Azteca* coexist, given that they appear to be engaged in 'apparent

competition' (Holt & Lawton 1993)? Studies of the colonization dynamics of ants and wasps are being undertaken to answer these questions (Yu & Pierce in preparation).

Vouchers of wasps and host carcasses have been deposited at The Natural History Museum, London, and at the Museum of Comparative Zoology at Harvard University.

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## NOTE

# Blue Pan Traps as a Potential Method for Collecting Stephanidae (Hymenoptera)

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Stephanids are usually rare in collections. However, this may be related to the lack of efficient collecting techniques for the group. Sweeping, Malaise traps, and light traps usually yield a low number of stephanids, even in areas where they are known to be abundant (pers. obs. and pers. comm. with collectors). Neither the literature nor the labels of 3000 museum specimens examined by the senior author, have any record of Stephanidae collected with yellow pan traps, an effective trapping method for many Hymenoptera (Masner 1976, Noyes 1989).

During a collection trip to St. Catherines Island (Georgia, USA), September 18–25, 1996, we set 155 yellow pan traps and 39 blue pan traps (Solo® party plates and bowls), on ground level, with water/detergent as a collecting medium. The traps were used for three days, in two sites: (1) an open area (oak savanna) with grassy vegetation, surrounded by oak-pine forest (112 yellow, 15 blue), and (2) a shaded area at the edge of oak-pine forest, with many fallen branches and dead trees scattered around (43 yellow, 24 blue). Site 2 was chosen as a probable habitat for Stephanidae, usually found on or around dead standing and fallen trees (Gauld 1995, and pers. obs.). On the first day, three females of *Megischus bicolor* (Westwood) (Stephanidae) were collected in blue pans on site 2. After that, the 15 blue traps from site 1 were transferred to site 2, resulting in a total of 43 yellow and 39

blue pan traps. No stephanids were caught on the second day, and four more female *M. bicolor* were collected in blue pans on the third day.

The fact that all stephanids were collected only in blue traps strongly suggests a preference of that color to yellow, and that the use of blue pan traps can be an effective trapping technique for these insects. This is in agreement with Kirk's (1984) observation that white or blue pan traps work as well as, or better than yellow in attracting predators and parasitoids not associated with foliage. Preference for white and blue was also observed in Encyrtidae and Pompilidae (Weseloh 1986; Berglind 1993), and in females of *Andrena limnanthis* Timberlake (Andrenidae) (Leong & Thorp 1995).

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# EDITOR'S NOTE

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From **November 1997** to **April 1998** I am requesting that authors send manuscripts directly to the appropriate **Subject Editor** and **not to the Editor**. I will be out of the country part of this time. In order to keep the *Journal of Hymenoptera Research* on schedule, it will be necessary for authors to send their manuscripts as follows:

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