The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization

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Abstract.—The known Cretaceous formicoids are better interpreted from morphological evidence as forming a single subfamily, the Sphecomyrminae, and even a single genus, *Sphecomyrma*, rather than multiple families and genera. The females appear to have been differentiated as queen and worker castes belonging to the same colonial species instead of winged and wingless solitary females belonging to different species. The former conclusion is supported by the fact that the abdomens of workers of modern ant species and extinct Miocene ant species are smaller relative to the rest of the body than is the case for modern wingless solitary wasps. The wingless Cretaceous formicoids conform to the proportions of ant workers rather than to those of wasps (Figs. 1–2) and hence are reasonably interpreted to have lived in colonies.

The Cretaceous formicoids are nevertheless anatomically primitive with reference to modern ants and share some key traits with nonsocial aculeate wasps. They were distributed widely over Laurasia and appear to have been much less abundant than modern ants.

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Introduction

This article attempts to resolve a problem in systematics that bears significantly on the origin and early evolution of the ants and hence the antiquity of advanced social behavior in insects generally. Studies of four mid-Cretaceous amber specimens have established the presence of the ant subfamily Sphecomyrminae across a wide portion of present-day North America: *Sphecomyrma freyi* from New Jersey (Wilson et al. 1967a,b) and *S. canadensis* from Alberta (Wilson 1985a). Dlussky (1975, 1983) has described an important additional collection of ant-like forms from the Upper Cretaceous of the Taymyr Peninsula (extreme north-central Siberia), southern Kazakh S.S.R., and the Magadan region of extreme eastern Siberia. He erected 10 new genera to accommodate this material. In his more recent article, he also created a new family, the Armaniidae, to accommodate some of the genera while elevating the Sphecomyrminae to family rank (hence, Sphecomyrminae) to receive others. This classification is summarized in Table 1.

Dlussky’s taxonomic interpretation, which is based on careful and accurate descriptions of the new material, has sweeping consequences for our conception of the origin of the ants. First, it presents a picture of an extensive radiation of ants or ant-like forms by the early part of the Upper Cretaceous—in other words, by no later than 80 Ma B.P. Second, Dlussky suggested that the Sphecomyrminae are not true ants or even precursors of the Formicidae but a closely related side branch, while the Armaniidae are the true ancestors of the ants. He doubted that either the Sphecomyrminae or the Armaniidae were eusocial; in other words he questioned whether they possessed the most advanced mode of social organization in which distinct queen and worker castes form overlapping adult generations and care for the developing young (see Wilson 1971).

Because of the light that the early fossils can shed on the origin of the ants and their distinctive social systems, which are matters hitherto largely unexplored due to the exclusively eusocial status of modern ant species, I decided to reexamine closely the morphological and biogeographic evidence provided by the Cretaceous material. I have arrived at a wholly different conclusion from that of Dlussky. In essence, the differences among the fossils cannot support the separation of the two new families, the Sphecomyrminae and Armaniidae, from the Formicidae. It is difficult to justify even the recognition of any genus other than *Sphecomyrma* on the
ANALYSIS AND SOCIAL ORGANIZATION OF EARLY ANTS

Table 1. Interpretation by Dlussky (1983) of the Mesozoic (Cretaceous) or antlike forms, classified to genus, with localities and approximate dates. Spelling of formation and estimation of dates follow van Eysinga (1978).

| Taxon                      | Sex  | Locality          | Formation and age before present (million years B.P.) |
|----------------------------|------|-------------------|------------------------------------------------------|
| **Superfamily Formicoidea**|      |                   |                                                      |
| Family Sphecomyrmidae Dlussky 1983 |      |                   |                                                      |
| *Sphecomyrma* Wilson and Brown 1967 | Female (wingless) | New Jersey, U.S.A.; Alberta, Canada | New Jersey: Santonian (80)                           |
| *Cretomyrma* Dlussky 1975 | Female (wingless) | New Jersey: | Santonian (80)                                      |
| *Paleomyrmex* Dlussky 1975 | Male | New Jersey: | Santonian (80)                                      |
| Family Armaniidae Dlussky 1983 |      |                   |                                                      |
| *Archaeopone* Dlussky 1975 | Male | Magadan | Cenomanian (100)                                    |
| *Armania* Dlussky 1983 | Female (winged) | Magadan | Cenomanian (100)                                    |
| *Armilliella* Dlussky 1983 | Female (winged) | Magadan | Cenomanian (100)                                    |
| *Dolichomyrma* Dlussky 1975 | Female (wingless) | Southern Kazakh S.S.R. | Turonian (90)                                          |
| *Poneropterus* Dlussky 1983 | Male | Magadan | Cenomanian (100)                                    |
| *Pseudarmania* Dlussky 1983 | Female (wingless) | Magadan | Cenomanian (100)                                    |
| Incertae Sedis (unplaced to family) |      |                   |                                                      |
| *Cretopone* Dlussky 1975 | Female (wingless?) | Southern Kazakh S.S.R. | Turonian (90)                                          |
| *Petropone* Dlussky 1975 | Female (wingless) | Southern Kazakh S.S.R. | Turonian (90)                                          |

basis of the morphological evidence. The most parsimonious explanation of the data is that the winged females and males from the Soviet deposits are queens and males of eusocial colonies of which the wingless *Sphecomyrma* and wingless Soviet species are the workers.

In proposing this view, I wish to emphasize that the disagreement is not over the facts assembled earlier by Dr. Dlussky and myself. There is only one exception, the supposed divided condition of the hind trochanter in the Armaniidae, to be discussed later. Instead, the disparity is due to a difference of interpretation of the facts with reference to higher classification and phylogeny. This is all to the good. By such contrasts the basic issues can be better clarified and the gathering of new data stimulated.

Materials and Methods

All of the characters known to vary among the Cretaceous species were first broken into character states. Each genus and species was then redescribed character by character in matrix form to allow close comparison of taxa. The holotypes of two of the best preserved and taxonomically most important Soviet species, *Armania robusta* and *Pseudarmania rasnitsyni*, were studied closely in comparison with the descriptions. I also worked with all of the four known specimens of the North American formicoids, placed in *Sphecomyrma* (Wilson 1985a).

In addition, measurements were made of a wide range of contemporary queen and worker ants and the winged and wingless females of other, nonsocial aculeate families deposited in the Museum of Comparative Zoology, in order to detect consistent differences in body proportions between social and nonsocial females. A single representative specimen was taken from the series available in each species, and the species in turn were selected to provide a large amount of phyletic diversity. This information was needed to infer the level of social evolution of the earliest fossils. Further measurements were utilized from the monograph of Miocene ants of North America by Carpenter (1930). All of these fossils belong to extinct species but surviving subfamilies and in some cases surviving genera. They were considered useful because as rock fossils their shapes were likely to have been distorted in the same manner as some of the Soviet specimens, which had been similarly preserved.
Table 2. Character-state analysis of Cretaceous formicoid taxa based on the worker or queen castes.

| Character | Sphecomyrmex freyi | Cretomyrmex arnoldii | Cretomyrmex unicornis | Petropone petiolata | Cretopone magna | Distichomyrmex longipes | Armania robusta | Pseudarma rasmusseni | Pseudarma aberrans | Armaniella curiosa |
|-----------|---------------------|----------------------|-----------------------|--------------------|----------------|-------------------------|----------------|--------------------|----------------|-------------------|
| Mandible shape | Slender, 2-toothed | Slender, 2-toothed | ?                     | ?                  | ?              | ?                       | Slender, 2-toothed | Slender, 2-toothed | ?               | ?                 |
| Head shape | Circular            | ?                    | Circular              | ?                  | ?              | About 1.5x longer than broad | Circular         | Circular          | ?               | ?                 |
| Clypeus form | Broad, simple       | Broad, trapezoidal   | ?                     | ?                  | ?              | Broad, simple          | Broad, simple   | Broad, simple     | ?               | ?                 |
| General antennal form | Scape only 0.3 x as long as funiculus | ? | ? | ? | ? | Scape only 0.3 x as long as funiculus | Scape only 0.2 x as long as funiculus | ? | ? | ? |
| Funiculus Flexible Large | Flexible            | ? | ? | Medium | Large | Large | Flexible | Not applicable | ? | ? |
| Compound eyes | Large               | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Ocelli | 3                   | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Scutum/scutellum | Distinct, convex    | ? | ? | ? | ? | ? | Not applicable | Not applicable | ? | ? |
| Petiole | Node constricted front and rear | Node constricted front and rear | Node constricted front and rear | ? | Node constricted front and rear | Node narrowly constricted in front, weakly constricted in rear | Node narrowly constricted in front, weakly constricted in rear | Node narrowly constricted in front, weakly constricted in rear | ? | ? |
| Gaster | Ovoid, unconstricted | Ovoid, unconstricted | Ovoid, unconstricted | Ovoid, unconstricted | Ovoid, weakly constricted | Ovoid, unconstricted | Ovoid, unconstricted | Ovoid, unconstricted | Ovoid, unconstricted | Ovoid, unconstricted |
| Character            | Worker                      | Queen                        |
|----------------------|-----------------------------|------------------------------|
|                      | Sphecomyrm 
|                      | S. freyi                     | Armania robusta              |
| Sting                | Extrusible                  | Extrusible                   |
| Trochanter           | 1-jointed                   | 1-jointed                    |
| Tarsal claws         | Toothed                     | 2-jointed                    |
| Tibial spurs         | 1, 2, 2                     | ?                            |
| Abdominal segment IV | Freely articulated           | ?                            |
| Metapleural gland    | Present                     | Apparantly present           |
| General comments     | (See text)                  | (See text)                   |
| Source of data       | Wilson et al. (1967)         | Dlussky (1983); direct study of holotype |

1 Horn-like protuberance on propodeum of uncertain nature.
2 Indeterminate, could be *Sphecomyrm*. 
In particular, it was important to take into account the possible increase in length of the abdomen, which tends to occur when this softest of body parts is crushed laterally or dorsally.

Head length was adopted as a reliable index of body size as a whole (see Wilson 1971). The size of the abdomen is critical as an indicator of reproductive as opposed to nonreproductive status in females, because it is the main part of the body containing the ovaries, organs that are proportionately large in fully social hymenopterans. The abdomen in turn was defined in two ways for the present study. First, a "functional" definition marks the abdomen as the posteriormost discrete body part, commonly called the gaster by ant specialists—the ovary-bearing portion behind the one or two segments of the waist. In addition, a strictly homologous definition of the abdomen (or, more precisely, posteriormost major body tagma) was used: all of the true abdominal segments from II posteriad, including the one or two segments of the waist in ants and a few aculeate wasps. The first, functional definition marks the abdomen as the posteriormost discrete body part, commonly called the gaster by ant specialists—the ovary-bearing portion behind the one or two segments of the waist. In addition, a strictly homologous definition of the abdomen (or, more precisely, posteriormost major body tagma) was used: all of the true abdominal segments from II posteriad, including the one or two segments of the waist in ants and a few aculeate wasps. The first, functional definition is intuitively the better, because the waist has by definition been reduced to a relatively thin, largely musculated portion that increases the mobility of the gaster. However, both measures were employed in order to evaluate the situation as fully as possible.

The results were evaluated with reference to the following criteria derived from standard systematic practice on modern faunas of insects and other animals. Individual taxa, whether species, genera, or representative of higher taxa, should be distinguished and named only if they differ by character states. The states can be relatively minor in the case of species, but should be more substantial in the case of genera (e.g., in ants they include the number of antennal and palpal segments, presence or absence of clypeal teeth, and presence or absence of antennal scrobes; and they preferably should exist in multiples). Dlussky (1975, 1983) appears to have used lighter criteria of the kind more commonly accepted in paleontology, in which it is recognized that fossils separated by large geographic distances and stretches of geological time are more likely to belong to different genera or higher categories. Add to this the fact that characters are often obscured due to imperfections in fossilization, and reliance is therefore placed on minor character states.

Because of the importance of the evolutionary issues involved, I believe the criteria employed in assessing the early ant fossils must be the stricter ones used in neontology. That is, it is preferable not to recognize taxa unless the character states separating them can be seen and are of approximately the same magnitude used in recognizing contemporary taxa of the same rank.

Results

The results of the character-state analysis for all of the Cretaceous formicoid genera are summarized in Tables 2 and 3. An inspection shows that no single character state or combination of states can be used to separate a distinct family, the Armaniiidae, if neontological standards are applied. Moreover, almost none of the genera can be unambiguously supported from the existing evidence. The only exception is Cretomyrma.

| Character | Paleomyrma zherichini | Archaeopone kazylzharica | Archaeopone taylori | Poneropterus sphecoides |
|-----------|-----------------------|--------------------------|---------------------|------------------------|
| Ratio, length of 3d antennal segment to 2d segment | 2–3 | ? | ? | 3 |
| Genitalia covered by terminal abdominal tergite, or not | Not covered | Not covered | Not covered | Covered |
| Petiole trapezoidal (or nearly cubical) versus tapered anteriorly (delimiting a node) | Trapezoidal | Trapezoidal | Trapezoidal | Tapered |
| Trochanter | 1-jointed | ? | ? | ? |
| Source of data | Dlussky (1975) | Dlussky (1975) | Dlussky (1983) | Dlussky (1983) |
TABLE 4. Higher classification of Mesozoic (Cretaceous) ants proposed in the present analysis.

Superfamily Formicoidea Latreille 1802
Family Formicidae Latreille 1802

Formicidae Latreille 1802, Hist. Nat. Gen. Part., Crust. & Ins. 3:352. Type genus: Formica.

Sphecomyrmidae Dlussky 1983, Paleontol. Zhurn. 1983, no. 3, p. 65. Type genus: Sphecomyrma Wilson and Brown 1967. NEW SYNONYMY.

Armaniidae Dlussky 1983, Paleontol. Zhurn. 1983, no. 3, p. 66. Type genus: Armania Dlussky 1983. NEW SYNONYMY (tentative).

Subfamily Sphecomyrminae Wilson and Brown 1967

Sphecomyrma Wilson and Brown 1967, Psyche 74:8. Type species: S. freyi Wilson and Brown 1967.

Dolichomyrma Dlussky 1975, Trans. Paleontol. Inst. 147:121. Type species: D. longiceps Dlussky. NEW SYNONYMY (tentative).

Paleomyrmex Dlussky 1975, Trans. Paleontol. Inst. 147:118. Type species: P. zherichini Dlussky. NEW SYNONYMY (tentative).

Archaeopone Dlussky 1983, Trans. Paleontol. Inst. 147:120. Type species: A. robusta Dlussky. NEW SYNONYMY (tentative).

Pseudarmania Dlussky 1983, Trans. Paleontol. Inst. 147:119. Type species: P. rasnitsyni Dlussky. NEW SYNONYMY (tentative).

Armaniella Dlussky 1983, Trans. Paleontol. Inst. 147:71. Type species: A. curiosa Dlussky. NEW SYNONYMY (tentative).

Poneropterus Dlussky 1983, Trans. Paleontol. Inst. 147:73. Type species: P. sphecoides Dlussky. NEW SYNONYMY (tentative).

Cretomyrma Dlussky 1975

Cretomyrma Dlussky 1975, Trans. Paleontol. Inst. 147:115. Type species: C. arnoldii Dlussky.

Incertae Sedis

Petropone Dlussky 1975, Trans. Paleontol. Inst. 147:119. Type species: P. petiolata Dlussky.

Cretopone Dlussky 1975, Trans. Paleontol. Inst. 147:119. Type species: C. magna Dlussky.

possessing a hornlike protuberance on the propodeum (in C. unicornis), more compact gaster, and proportionately longer legs; a second, weaker possibility is Dolichomyrma, with an elongate head and slight constriction of the gaster (Dlussky 1975, 1983, and new details provided the author in litt.). It cannot be denied that still other genera might be represented by the Soviet fossils; we are only sure that few can be defined by neontological standards with existing data. Hence the synonymy suggested in Table 4 is for the moment the appropriate nomenclatural arrangement.

Figures 1 and 2 show that the measurable, relatively undistorted wingless females among the North American and Soviet fossils, in other words Sphecomyrma freyi and Dolichomyrma longiceps, have small abdomens in proportion to the remainder of the body, by both the functional and strictly homologous definitions of the abdomen. In this respect they resemble the worker caste of modern ants more than they do the wingless females of modern nonsocial aculeate wasps. Moreover, the winged female type of Pseudarmania rasnitsyni, a relatively undistorted specimen, is within the range of the queens of modern ants (as well as the females of nonsocial aculeate wasps), as shown in Fig. 3. In sum, the wingless females among the Cretaceous fossils are best interpreted as worker ants rather than wingless reproductive aculeate wasps belonging to solitary...
species, while the winged females are probably the queens.

Several additional observations support this conclusion. In his description, Dlussky (1983) states that a diagnostic trait of the Armaniidae is the approximately equal length of the first and third antennal segments, that is, of the scape and second funicular segments. Although this is quite correct, another and more revealing way of putting the matter is to say that the scape is quite short relative to the funiculus, while the second funicular segment is long relative to the first and third funicular segments. It turns out that these are precisely the same distinctive traits used to define the Sphecomyrminae. Hence both the winged and wingless Cretaceous females share the same unusual character state in antennal form, another reason for associating them closely.

Dlussky (1983) gives as another diagnostic trait of the Armaniidae the possession of a second, free trochanter on the middle and hind legs. This condition is weakly indicated in the drawing of *Pseudarmania aberrans*, but it is wholly lacking in the drawings of all of the other arminiids, and by direct examination I confirmed that it is indeed absent in the holotypes of *Armania robusta* (the type genus and species of the family) and *Pseudarmania rasnitsyni*.

In the winged females of the Armaniidae the petioles are more broadly attached posteriorly to the gaster than in the sphecomyrmine wingless females. But this is not a subfamilial or even species-level character. It is a common difference between the queens and workers belonging to the same species among modern ants, and hence it cannot be reliably used as a taxonomic character to separate higher formicoid taxa.

Discussion

The most parsimonious interpretation of the Cretaceous formicoid fossils, nearly joining the facts we know, is that they all belong to the subfamily Sphecomyrminae of the family Formicidae, or true ants. Furthermore, so long as contrary evidence is lacking, the Cretaceous fossils should all be placed provisionally in the gen-
era Sphecomyrma and Cretomyrma. It is entirely possible that other genera, and even taxa in additional subfamilies or still higher categories, existed in Cenomanian to Santonian times and might be represented by the existing fossils, but until supporting evidence emerges, the conservative taxonomic arrangement suggested here (Table 4) is both more accurate and heuristic.

This interpretation means that the three phases represented among the Cretaceous fossils are most reasonably interpreted to be queen, worker, and male formicoids, respectively, in other words, what we would call ants as opposed to wasps. This hypothesis is more clearly depicted by juxtaposing the best preserved representatives of the three phases as though they are members of the same colony (see Fig. 4). The hypothesis receives considerable support from the size differences between the best-preserved winged fossils and the best-preserved wingless ones, consistent with their being queens and workers. It receives additional support from the fact that the proportional size of the abdomen in the Cretaceous ants is closer to modern ants than to modern aculeate wasps (Figs. 1, 2).

Dlussky (1983) made two inferences connecting anatomy to behavior inclining him to the hypothesis that the Cretaceous formicoids were not eusocial. The first is that the tips of antennal funiculi are too far removed from the mandibles to allow the precise coordination required for social behavior: "The antennae in these insects did not permit them to control the manipulation of small objects, so that they could not have transported their brood or entered into trophallaxis with their larvae—that is, they could not have been true social insects." This supposition is surely incorrect. The eusocial vespid wasps have similarly proportioned antennae yet experience no difficulty in transporting all prey objects and placing them on the larvae. They also engage in trophallaxis, or liquid food exchange. The flexibility of the funiculi contribute to these skills, and the twists and curves of the Cretaceous ant antennae suggest that their funiculi were likewise flexible. To this may be added the fact that some modern ants, such as the primitive Amblyopone pallipes (Traniello 1982) and more advanced Pogonomyrmex badius (Wilson 1971) do not engage in trophallaxis. Hence this form of food exchange was not essential for the evolution of eusocial behavior in ants.

Dlussky also inferred that the short, wasplike mandibles of the Cretaceous formicoids "indicates that these insects did not build true nests, and could have used only pre-existing hollows." But this overlooks the fact that some primitively eusocial wasps and bees use similar mandibles to build quite elaborate nests, mostly from cotton and wax. A few, such as the halictid bees, excavate soil in a very antlike fashion.

To summarize, nothing in the observable anatomy of the Cretaceous formicoids precludes their having possessed a eusocial organization, characterized by brood care, overlap of adult

![Figure 4](image-url)
generations, and division of labor between re-
productive and nonreproductive castes. Al-
though direct evidence either way is lacking on
the matter, these insects could also have con-
structed nests in the soil, rotting wood, or ar-
boreal cavities.

The low accumulation rate of Cretaceous for­
micoids to date indicates that they occurred in
low densities compared with modern ants. Only
two individuals (Specomyrmna canadensis) have
been found so far among thousands of insects in
amber from Alberta Province, Canada (Carpenter
et al. 1939; J. F. McAlpine, pers. comm.). For­
micoids constituted just 13 of the 1,200 in­
sect impressions in the Magadan collection and
5 of the 526 impressions in the Kazakhstan col­
collection, in other words about 1% in both cases
(Dlussky 1983). These figures contrast sharply with
Oligocene and Miocene deposits. In the Florissant
and other shales of North America (Carpenter 1930), as well as the Baltic amber of northern Europe (Wheeler 1914) and amber of the Dominican Republic (Wilson 1985b), the ants are among the most abundant insects, mak­
ning up a large minority of all insect specimens.
Thus the adaptive radiation that took place in
the late Cretaceous or early Tertiary, yielding at
least three of the dominant modern subfamilies
(Myrmicinae, Dolichoderinae, Formicinae) by
mid-Eocene times (Wilson 1985a), was accom­
pained by a marked increase in abundance.

The ants are seen to have paralleled the mam­
mals by achieving dramatic increases in diversity
and abundance around the close of the Mesozoic
Era. How they accomplished this breakthrough
and managed to sustain a dominant position in
the insect world to the present time is a matter
of unusual interest, which additional paleontol­
ogical studies should help to illuminate.

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Appendix

Miocene and modern species used in the measurements of Figs. 1-3 are listed here. All ants, fossil and living, are members of the family Formicinae. The families of the aculeate wasp species are listed individually.

MOIÈEANT WORKERS. Aphaenogaster mayri, Archiponera wheeleri,
Hypoclinea antiqua, Protactesta quadrata.

MOIÈNEANT QUEENS. Formica robusta, Hypoclinea rubieri, Simeomyrmyn
impacts, Pseudomyrmyn extinctus.

MODERNANT WORKERS. Acanthomyrmyn dentata, Amblyopone australis,
Aneuretus simoni, Anillidris bruchi, Aranomyrmyn tenor, Aphaenogaster longiceps,
Bolbomyrmyn flavus, Brachymyrmyn obscurus, Crematogaster parahabita, Dia-
tica conger, Dorymyrmyn planidenti, Entomomyrmyn acutus, Eremhonryrmyn arichi, Forbicula
andinus, Fregattaster kerby, Gignantioponera destructor, Heteronera flavus, Hypoclinea
abrupta, Irudomyrmyn tangitets, Laaxis alienus, Lepismyrmyn fragilis, Lepismyrmyn
apiculatum, Merostropheclenia tricornis, Moromerum cyanae, Myrmecia dicipholia,
Myrmecia dispar, Myrmica incipiens, Neivamyrmyn apicostatus, Neofrelina tus-
manus, Neothyrmymyn macropyla, Notoncus ectatommoides, Odontomachyn opaci-
rentis, Oecophylla maragdina, Pheidole cephalica, Pogonomyrmyn desertorum, Pratina
biteti, Pseudomyrmyn gracilis, Semonius schultzei, Sericomyrmyn sp., Solenopsis
niten, Tapinoma melanocephalum, Typhlomyrmyn albitarsus, Thaumatomyrmyn se-
tekii, Typhlomyrmyn rongehoferi, Zatiponoma sp.

MODERNANT QUEENS. Amblyopone australis, Aneuratus simoni, Ameu-
retus simoni, Amblyopone longiceps, Brachymyrmyn obscurus, Calomyrmyn alber-
tisii, Caenopsis noronhoausensis, Ectius dulcis, Eremhonryrmyn arichi, Formica sub-
peltata, Gignantioponera destructor, Camponopyrmyrm caenicola, Heteronera flavus, Irudomyrmyn
sanguinea, Laaxis alienus, Lepismyrmyn fragilis, Lepismyrmyn apiculatum, Myr-
mycina dicipholia, Myrmica dispar, Myrmica incipiens, Neivamyrmyn apicostatus, Neofrelina tus-
manus, Neivamyrmyn macropyla, Notoncus ectatommoides, Odontomachyn opaci-
rentis, Oecophylla maragdina, Pheidole cephalica, Pogonomyrmyn desertorum, Pratina
biteti, Pseudomyrmyn gracilis, Semonius schultzei, Sericomyrmyn sp., Solenopsis
niten, Tapinoma melanocephalum, Thaumatomyrmyn setekii, Typhlomyrmyn rongehoferi.

ACULEAT WASP FEMALES (WINGED). Alpheidmyrmyn bocauinana (Dryi-
nide), Anteon gaulei (Dryinide), Aphelopus variicornis (Dryinide), Ceroples
breethi (Pompilide), Clistopteryna longiventris (Scolythebiidee), Hypodynyn
exsurgentia (Vespidae), Eusolenops sanguineus (Vespidae), Pseudonactrus
chalcinod (Bethylide), Pseudosolfina mangana (Pompilide), Solythebiides
madecassus (Scolythebiidee), Sphaerorrhyna auripilis (Mulllidide), Vespula evansi
(Scolythebiidee).
ACULEATE WASP FEMALES (WINGLESS). *Acrodontochelys cubensis* (Dryinidae), *Aelurus gayi* (Tiphiidae), *Aegyptiacres sareha* (Tiphiidae), *Apenema browni* (Bethylidae), *Arhipron syphoides* (Tiphiidae), *Braccisula formicaria* (Tiphiidae), *Chyphotes attenuatus* (Mutillidae), *Dasyrastella arenicola* (Mutillidae), *Dremopompilis* sp. (Pompilidae; a brachypterous rather than completely apterous species), *Elaphroptera* sp. (Tiphiidae), *Embolus minutus* (Embolomorphae), *Ephuta* sp. (Mutillidae), *Euryemyris furcata* (Tiphiidae), *Glyptacris angustior* (Tiphiidae), *Glyptometopa americana* (Tiphiidae), *Gonatopus frequens* (Dryinidae), *Hemiscabrus* sp. (Tiphiidae), *Leucopilomatilla cerbera* (Mutillidae), *Metiocha californica* (Tiphiidae), *Myrmica anisola* (Tiphiidae), *Myrmicaria parvula* (Tiphiidae), *Naelaps hankoi* (Rhopalosomatidae), *Olixon* sp. (Rhopalosomatidae; an extremely brachypterous species), *Photopsis zenobia* (Mutillidae), *Plamonias* sp. (Plumariidae), *Prassinocera cockerelli* (Bethylidae), *Pseudometoca ocella* (Mutillidae), *Redemutilla* sp. (Mutillidae), *Rhagigaster laevigatus* (Tiphiidae), *Thynnoides* sp. (Tiphiidae), *Timella leona* (Mutillidae), *Typhoctes peculiaris* (Mutillidae), *Probolurus* sp. (Sclerogibbidae), unidentified sp. no. 3 (Tiphiidae).