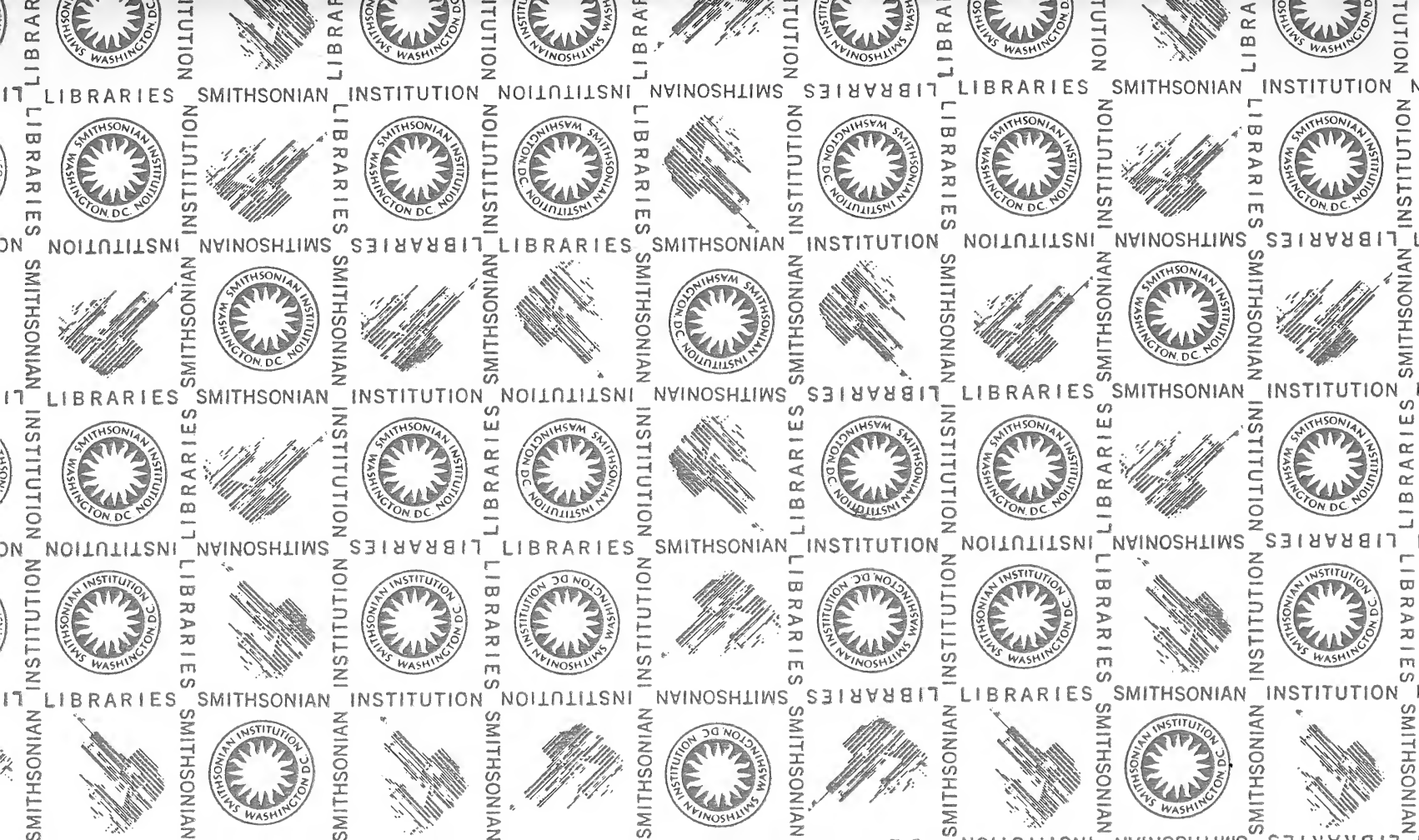
SMITHSONIAN INSTITUTION LIBRARIES


SMITHSONIAN INSTITUTION LIBRARIES

QL
461
P974
Ent.

SMITHSONIAN
DEC 17 1986
LIBRARIES

ISSN 0033 2615

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 93 1986 Nos. 1–2

CONTENTS

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1985–1986

President ..... NORMAN C. CARLIN
Vice-President ..... JAMES M. CARPENTER
Secretary ..... KATHRYN HOY
Treasurer ..... FRANK M. CARPENTER
Executive Committee ..... WAYNE MADDISON
HEATHER HERMANN

EDITORIAL BOARD OF PSYCHE

F. M. CARPENTER, (Editor), *Fisher Professor of Natural History*, Emeritus, *Harvard University*

W. L. BROWN, JR., *Professor of Entomology, Cornell University and Associate in Entomology, Museum of Comparative Zoology*

B. K. HÖLLDOBLER, *Professor of Biology, Harvard University*

H. W. LEVI, *Alexander Agassiz Professor of Zoology, Harvard University*

M. D. BOWERS, *Assistant Professor of Biology, Harvard University*

ALFRED F. NEWTON, JR., *Curatorial Associate in Entomology, Harvard University*

E. O. WILSON, *Baird Professor of Science, Harvard University*

J. M. CARPENTER, *Assistant Professor of Biology, Harvard University*

PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: $15.00, domestic and foreign. Single copies, $4.00

Checks and remittances should be addressed to Treasurer, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138.

Orders for missing numbers, notices of change of address, etc., should be sent to the Editorial Office of Psyche, 16 Divinity Avenue, Cambridge, Mass. 02138. For previous volumes, see notice on inside back cover.

IMPORTANT NOTICE TO CONTRIBUTORS

Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

Authors are required to bear part of the printing costs, at the rate of $29.00 per printed page. The actual cost of preparing cuts for all illustrations must be borne by contributors: the cost for full page plates from line drawings is ordinarily $10.00 each, and for full page half-tones, $12.00 each; smaller sizes in proportion. There is ordinarily no additional charge for setting tables of less than six columns; for tables of six or more columns the cost is $25.00 per page.

Psyche, vol. 92, no. 4, for 1985, was mailed April 27, 1986

The Lexington Press, Inc., Lexington, Massachusetts

PSYCHE

Vol. 93 1986 Nos. 1-2

FUNCTIONAL QUEENS IN THE AUSTRALIAN GREENHEAD ANT, *RHYTIDOPONERA METALLICA* (HYMENOPTERA: FORMICIDAE)*

By Philip S. Ward

Department of Entomology,
University of California,
Davis, CA 95616, U.S.A.

Introduction

In most species of the Indo-Australian ant genus, *Rhytidoponera,* deciduously winged queens are rare or absent, their place being taken by reproductively functional workers (Whelden, 1957, 1960; Haskins & Welden, 1965; Ward, 1981, 1984; Pamilo *et al.,* 1985). A polygynous colony structure, with several mated workers in lieu of a queen, is the normal mode of colony organization in the common Australian greenhead ant, *Rhytidoponera metallica* F. Smith (Whelden, 1960; Haskins & Whelden, 1965; Haskins & Haskins, 1983), and queenright colonies of this species have not been reported. A few alate or dealate females are known in collections, and Haskins & Whelden (1965) noted the sporadic production of alate queens in laboratory colonies of *R. metallica.* However behavioral observations by these authors suggested that the queens had lost the ability to found colonies. In this paper I document the occurrence of functional queens in *R. metallica,* describe colony foundation and growth under laboratory conditions, and discuss the significance of occasional queen production in this species.

**Manuscript received by the editor February 26, 1986.*

Methods

Field observations were made at several Queensland localities in August–September, 1983, of which the following sites are discussed below: (1) 10 km SE Kenilworth (26°40′S, 152°47′E), 340 m, dense *Eucalyptus* forest; (2) Mt. Coot-tha, near Brisbane (27°29′S, 152°58′E), 160 m, mixed wet sclerophyll forest; and (3) St. Lucia, Brisbane (27°30′S, 153°01′E), 15 m, urban parkland on the University of Queensland campus. Voucher specimens of *Rhytidoponera metallica* from these localities have been deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra and the Museum of Comparative Zoology (MCZ), Harvard University. Evidence suggests that *R. "metallica"* is composed of a complex of sibling species (Crozier, 1981; cf. Brown, 1958), and the southeastern Queensland populations may not be conspecific with *R. metallica* sens. str. (type locality: Adelaide, South Australia).

Field-collected queens of *Rhytidoponera* from St. Lucia were maintained in the laboratory in moist plaster-of-Paris nests. Each nest consisted of a glass-covered chamber with the dimensions 40 × 25 × 5 mm, in a block of plaster measuring 85 × 55 × 10 mm. A single exit, 4 mm wide, led to a foraging arena 85 × 110 mm in area. After a colony size of approximately 50 workers was attained, colonies were provided with larger nests. Colonies were fed small arthropods (mostly *Drosophila*) on a daily basis and droplets of honey about once a week. A small quantity of clean sand was provided to allow construction of a cocoon-spinning matrix for the first larvae. Censuses of brood and adults were taken every 3 weeks for the first 9 weeks of colony development, and at weekly intervals thereafter for the first year of growth.

Results

Field observations

While conducting field work in eastern Queensland in August–September, 1983 I frequently encountered foraging workers of *Rhytidoponera metallica* (s.l.), and I dissected several typical, worker-reproductive colonies, i.e. colonies with workers and (sometimes) males, but no queens. At three locations in southeastern Queensland I unexpectedly encounted alate queens of *R. metallica*:

(1) While collecting for a period of one hour in *Eucalyptus* forest 10 km SE Kenilworth (25 August, 1983), I located a single *Rhyti-*

doponera metallica colony under a rotten log; a partial excavation (about two-thirds of the colony) yielded 157 workers, 17 alate queens, and numerous larvae. No males or dealate females were seen.

(2) During several hours of field work in wet sclerophyll forest on Mt. Coot-tha (1 September, 1983), devoted primarily to the task of locating colonies of the very timid species, *R. anceps* Emery, I noted more than a dozen, scattered, individual alates of *R. metallica* resting on low vegetation (leaves, grass stalks, tree roots, etc.), apparently in the aftermath of one or more mating flights. About half of these alates were females (five queens were collected and preserved).

(3) On the University of Queensland campus, St. Lucia, between 28–31 August, 1983, there was considerable flight activity of *R. metallica* alates. Most of these alates were males: they were observed in moderate numbers (30–40 males at any given time) around *R. metallica* nest entrances on a campus lawn at mid-day. Most individuals were dispersing skyward, but a few males were observed approaching nests in a low, cruising flight, 20–50 cm above the ground. Four alate females of *R. metallica* were also noted: three of these were running on campus sidewalks, the fourth was resting on a grass stalk. The alate queens were observed between noon and 3:00 p.m., and none was associated with a specific nest. Three of the *R. metallica* queens were collected; one died within 5 days, and subsequent dissection showed that she was uninseminated. The two remaining queens (acc. nos. 6280 and 6281) were kept in vials with a small quantity of earth and leaf litter. They shed their wings, excavated crude cells, and began laying fertile eggs. On September 17, 1983 the queens were relocated in plaster-of-Paris nest chambers. I also collected a single dealate queen of *R. chalybaea* Emery on 1 September, 1983 in a University of Queensland lecture hall (acc. no. 6297). This queen was treated in the same manner as the *R. metallica* queens, and provided a convenient standard for colony growth and development, since colony-founding queens are a normal occurrence in this species (Ward, 1983).

Development of queenright colonies: incipient stages

The preceding observations established that the early stages of colony-founding behavior have been retained in *R. metallica* queens, i.e. they can mate, disperse, undergo dealation, and exca-

vate nests. Laboratory observations demonstrated that this can be followed by normal haplometrotic colony development.

Both the *R. metallica* and *R. chalybaea* queens readily accepted the plaster-of-Paris nests, and began raising worker brood. The queens of both species foraged in their arenas for food, and accepted both honey and fresh arthropods. Struggling *Drosophila* adults (held in the foraging arena with a pair of fine forceps) were approached with outstretched mandibles, captured, stung, and returned to the nest.

The *R. metallica* queens appeared to be no less dexterous than the *R. chalybaea* queen in capturing and handling prey, or in caring for larval brood. As the larvae matured, queens of both species used sand grains to construct cocoon-spinning matrices for the larvae. Initially the development of brood proceeded at a similar rate in all three colonies, with eggs, larvae, and cocoons present by the tenth week (late November, 1983; Table 1).

Some behavioral differences were noted between the two species: the *R. metallica* queens were observed foraging more frequently during daytime hours than the *R. chalybaea* queen; the *R. metallica* queens established their middens in the nest entrance, thus partially closing it, whereas the *R. chalybaea* queen scattered most of her refuse just outside the nest entrance; and the *R. metallica* queens defecated widely (frequently in the foraging arena) whereas the *R. chalybaea* queen concentrated her fecal deposits at one location (c. 25 mm^2) inside the nest chamber. These minor (and perhaps idiosyncratic) differences hardly diminish the overriding similarity between the two species in early colony development.

After about twelve weeks, and just prior to the eclosion of workers, colonies of the two species of *Rhytidoponera* began to diverge in their patterns of development. The first *R. metallica* workers appeared to have difficulty eclosing from their cocoons—possibly because of inept assistance on the part of the queens—and there was appreciable early worker mortality both as pharate adults in cocoons and as eclosed adults. No such difficulties were evident in the *R. chalybaea* colony, whose worker population increased at considerably faster rate than that of the two *R. metallica* colonies (Table 1). Moreover the *R. chalybaea* colony displayed regular (although increasingly dampened) cycles of brood development, with bouts of egg-laying followed by pulses of larval growth, cocoon formation, and adult eclosion, whereas such cycles appeared to be

Table 1. Development of incipient queenright colonies of *Rhytidoponera* under laboratory conditions. Under columns E, L, C, and W are given the numbers of eggs (approximate), larvae, worker cocoons, and adult workers observed, respectively, at each census period.

	chalybaea 6297				*metallica* 6280				*metallica* 6281			
Date	E	L	C	W	E	L	C	W	E	L	C	W
12.x.83	18	—	—	—	20	1	—	—	20	1	—	—
2.xi.83	5	11	2	—	20	12	—	—	8	20	—	—
22.xi.83	3	10	8	—	5	17	6	—	0	10	6	—
29.xi.83	3	7	9	—	5	21	7	—	5	14	8	—
6.xii.83	7	6	11	—	5	18	8	—	8	14	8	—
13.xii.83	18	4	13	—	0	18	10	—	7	14	8	—
20.xii.83	25	4	13	1	1	15	11	—	9	12	9	—
27.xii.83	29	3	12	4	3	14	13	—	8	10	10	—
3.i.84	25	6	12	5	0	13	12	—	5	6	12	—
10.i.84	25	8	8	7	0	15	13	—	5	9	9	1
17.i.84	25	10	6	9	4	10	14	—	5	9	10	1
24.i.84	23	17	5	9	10	8	10	—	10	8	9	1
31.i.84	20	26	3	13	11	5	10	—	14	7	8	—
7.ii.84	10	27	5	13	12	4	8	—	14	5	11	—
14.ii.84	10	22	11	13	18	3	8	1	17	4	9	2
21.ii.84	15	24	17	13	20	5	8	—	15	4	7	3
28.ii.84	20	15	24	14	22	7	8	—	18	6	7	3
6.iii.84	27	15	32	15	12	9	7	1	20	12	6	4
13.iii.84	32	15	34	18	10	16	6	4	17	14	5	5
20.iii.84	40	17	33	22	4	26	5	5	18	14	6	7

disrupted in the *R. metallica* colonies (compare respective columns of Table 1).

Because of the delay in successful emergence of workers, the *R. metallica* queens continued to forage for about two months after the *R. chalybaea* queen ceased such activity. In both species the foraging activity of the queen declined gradually, over a period of several weeks after the first successful eclosion of workers. For three weeks after her first daughter appeared the *R. chalybaea* queen continued (with decreasing frequency) to capture and sting prey (*Drosophila* adults) held at, or near, the nest entrance. During the equivalent transition period, the *R. metallica* queens continued to make forays into the foraging arena and to capture prey. The sequence of events in colony #6280 is summarized in Table 2; similar observations were made on colony #6281.

Table 2. Observations on foraging activity of the queen and first eclosing workers in *R. metallica* colony #6280. Day #1 (3.iii.1984) is the day of first successful eclosion of a worker.

Day #	No. of adult workers in colony	Foraging activity of queen and workers
1–2	1 (callow)	Queen foraging. Worker confined to nest.
7	2 (1 callow)	Queen foraging. Workers confined to nest.
10	4	Queen took prey (*Drosophila*) at nest entrance.
11–12	4	Queen foraging. Workers confined to nest.
13	4	Worker foraging in arena (first time), captured a subdued *Drosophila* adult; queen removed prey from worker at nest entrance, then proceeded to forage in arena herself.
14–17	4–5	Queen and one worker in foraging arena.
22–27	6–8	Queen and several workers foraging and taking prey, the workers more active than the queen.
28	8	Last observation of queen in foraging arena (thereafter queen confined to nest, and all foraging conducted by workers).

Subsequent growth and development of queenright colonies

The growth rates of the *R. metallica* colonies were rather slow and uneven, relative to that of *R. chalybaea* (Figure 1). One year after colony initiation, the two *R. metallica* colonies had worker populations of 41 and 27 individuals, respectively, while the *R. chalybaea* colony had a worker population exceeding 200. Since the colonies were fed *ad libitum,* food availability is not likely to have been a limiting factor in the slower growth of the *R. metallica* colonies. In fact, all three colonies grew at a rate faster than that inferred for incipient queenright colonies of *R. chalybaea* (and a related species, *R. confusa* Ward) in the field (Ward, 1981).

The *R. metallica* colonies appeared to function similarly during the first year of development. Then a marked divergence took place, apparently due to queen infertility in colony #6280. In mid-October, 1984 (week 56) this colony stopped producing eggs, and the amount of brood began declining. By mid-January, 1985 (week 66), with a population of 50 workers (and one male of unknown parentage), this colony contained no eggs or larvae, and only one cocoon (worker). On January 22, the queen was observed in a sexual calling posture (gaster raised, head and mesosoma lowered) inside the nest;

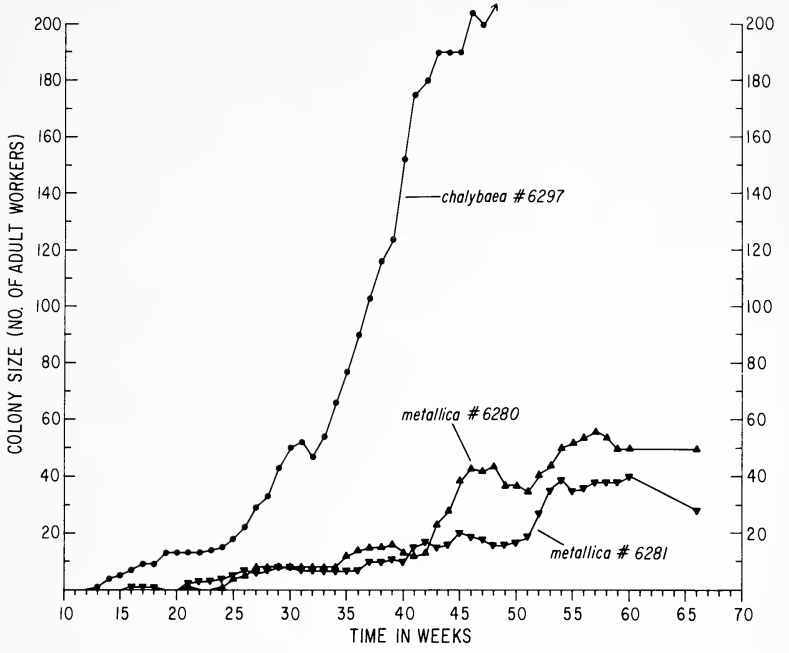


Figure 1. Colony size (number of adult workers) of developing, queenright colonies of *R. metallica* and *R. chalybaea,* as a function of time in weeks since colony initiation.

at the same time she was being spread-eagled by two workers who were tugging on opposite legs. Ten minutes later the queen was dragged and bitten on the tip of her gaster by a worker. The following day the queen was still being molested by workers, who bit her on the legs and gaster. On January 24, the queen was found dead inside the nest. A few days later her disarticulated body had been dumped in a midden pile in one corner of the foraging arena. In the meantime there began a spate of intersibling rivalry among a group of 15–20 workers inside the nest who repeatedly "boxed" one another with their antennae. These rapid antennation movements were very similar to those which occur among mated workers in polygynous, worker-reproductive colonies of the *R. impressa* group (Ward, 1983, p. 293).

One week after the death of the queen in colony #6280, workers began "calling" for males in the characteristic sex pheromone-

releasing posture (Hölldobler & Haskins, 1977). As many as six workers were observed calling simultaneously, both inside and outside the nest. Workers calling inside the nest were subject to repeated rapid antennation of the gaster, sides of body, and head, by other workers. When antennated in front, the calling worker would reciprocate the gesture, while maintaining the calling posture. Workers calling in the foraging arena outside the nest were not the object of rapid antennation by other workers.

The sexual calling behavior of workers continued, with increasing intermittency, for the next six months. During this time, two additional adult males were produced, but no workers. There was no indication that sib mating occurred—males showed no apparent interest in their calling nestmates. The colony continued to decline in size, no additional workers were produced, and, at time of writing (January, 1986), it consisted of 35 workers, 1 male, 2 larvae and several eggs.

By contrast, colony #6281 remained a viable queenright colony. The queen continued to produce fertile eggs, and was not molested by her daughters. There was no obvious conflict among workers (i.e. no spate of antennal boxing or other forms of aggression), and workers did not exhibit sexual calling behavior. At time of writing, the colony was continuing to grow and comprised the queen, about 120 workers, and abundant brood.

Discussion

These findings demonstrate that the deciduously winged females of *Rhytidoponera metallica* have not lost the potential to function as queens, despite their sporadic occurrence in nature. Under laboratory conditions the two *R. metallica* colonies remained queenright for at least a year, and the queens and workers adopted conventional roles of egg-layer and forager, respectively. On the other hand the *R. metallica* colonies grew more slowly than the incipient queenright colony of *R. chalybaea,* and the colony-founding foraging phase of the queens was correspondingly extended. Hence there remains some uncertainty about the efficacy of colony foundation by *R. metallica* queens in nature.

One of the *R. metallica* colonies experienced death of the queen, apparently a case of matricide triggered by queen infertility. Since the workers began calling for males soon after the queen's death,

and continued to do so for six months, it seems likely that, under natural conditions, replacement of the queen by mated workers would be readily accomplished. Ward (1983) alluded to the possibility that some worker-reproductive (Type B) colonies in the *Rhytidoponera impressa* group are derived from orphaned queenright (Type A) colonies, and the present observations provide direct evidence that such a transition can occur in *R. metallica.* Moreover they suggest that reproductive activity on the part of the queen, rather than her mere presence, is necessary for the suppression of hostile takeover attempts by her daughters.

The reverse process, production of colony-founding queens by worker-reproductive colonies, seems certain to have occurred. No mated dealate queen was found in the queen-producing colony from 10 km SE of Kenilworth, and indeed no functional queenright colonies of *R. metallica* have been reported in the field, even though this species is one of the commonest Australian ants.[1] Haskins & Whelden (1965) reported the occasional production of female alates in worker-reproductive colonies of *R. metallica* which had been maintained in the laboratory for several years. These females failed to function as queens but this could have been due to the absence of favorable conditions for mating and dispersal.

Queen production might be viewed as an infrequent, alternate dispersal strategy employed by worker-reproductive *R. metallica* colonies in response to environmental conditions which favor long-range dispersal over short-range movement (colony fission). The unusually large production of queens in Queensland in August–September, 1983 occurred after a period of drought associated with the 1982–83 El Niño. Alate queens appeared in one of Haskins' laboratory colonies after a shift in diet (C. P. Haskins, pers. comm.). The

[1]Among the limited number of *R. metallica* queens in collections, the majority of specimens are alates; the dealate specimens which I have examined contain no information about their reproductive status. During a five year period of collecting ants in eastern Australia (1974–78; 1980) I encountered (and subsequently dissected) *R. metallica* queens only twice. One of these was a mated dealate female wandering on the ground by herself (colony-founding?) in open *Eucalyptus* woodland, 14 km E Grenfell, New South Wales (29. X. 1975, P. S. Ward #1406); the other was a single uninseminated (spermatheca empty, ovaries poorly developed) dealate female in a colony with 173 workers and brood, under a stone in dry sclerophyll forest, at Bathurst, N.S.W. (18. X. 1975, P. S. Ward #1374).

extreme rarity of mature queenright colonies in nature could be attributed to a frequent transition to the worker-reproductive (Type B) colony structure, coupled with the sporadic production of queens in the first place. That *R. metallica* queens still function as dispersal units is suggested by the widespread retention of queen production. Among material in the ANIC and MCZ, there are alate or dealate females of *R. metallica* (s.l.) from Western Australia, South Australia, New South Wales, and Queensland, i.e. throughout the range of this species (or species complex). Queens have also been collected throughout most of the geographical distribution of *R. victoriae* André, another species whose mature colonies are predominantly or entirely worker-reproductive.

It is worth reiterating that queens are entirely unknown in the majority of *Rhytidoponera* species (including the large, robust-bodied forms found primarily in xeric habitats), and in such species aerial dispersal of females is impossible. If queens *are* effective aerial dispersers in *R. metallica* and other occasional queen-producers (including *R. clarki* Donisthorpe, *R. inornata* Crawley, *R. tasmaniensis* Emery, and *R. victoriae*), then this should result in differential patterns of habitat island and offshore island occupancy by the two groups of *Rhytidoponera.* There are not sufficient data available to test this prediction—and the test would be complicated by differing habitat preferences of members of the two groups—but records in the ANIC do show that *R. metallica* and related species are found on a variety of small islands off the coasts of Western Australia, New South Wales and Queensland.

Summary

In colonies of the Australian greenhead ant, *Rhytidoponera metallica* (s.l.), female reproductive activities are almost invariably assumed by workers. Queens (deciduously winged females) are rarely produced, and were heretofore considered non-functional. Field observations in southeastern Queensland in August and September, 1983 revealed an unusually high frequency of alate queens in several localities. Two of three alate queens, collected while dispersing in the vicinity of male mating flights, proved to be inseminated. In the laboratory these mated queens both established functional queenright colonies under non-claustral, haplometrotic conditions. The *R. metallica* colonies grew more slowly than an

incipient, queenright colony of *R. chalybaea* (a species in which functional queens are common), but a clear division of labor developed between the egg-laying queen and foraging workers.

One *R. metallica* colony suffered death of the queen in its second year of development. This was followed by a spate of intersibling rivalry and frequent sexual calling behavior on the part of the workers. The other colony continued to function as a viable queenright colony, and showed no signs of intracolony strife or reproductive attempts by workers.

These observations show that *R. metallica* queens have retained their colony-founding and reproductive potential, despite their sporadic occurrence in nature. This suggests that long-range dispersal via winged queens remains an occasional viable option for worker-reproductive colonies of *R. metallica.*

Acknowledgements

The University of California provided financial support for this work. I thank Ross Crozier, Caryl Haskins and Christian Peeters for comments on the manuscript.

References

Brown, W. L. 1958. Contributions toward a reclassification of the Formicidae II. Tribe Ectatommini (Hymenoptera). Bull. Mus. Comp. Zool. Harvard, **118**: 175–362.

Crozier, R. H. 1981. Genetic aspects of ant evolution. *In* Atchley, W. R. and D. Woodruff (Eds.). Evolution and speciation. Essays in honor of M. J. D. White. Cambridge: Cambridge Univ. Press, pp. 356–370.

Haskins, C. P. and W. M. Whelden. 1965. "Queenlessness", worker sibship, and colony versus population structure in the formicid genus *Rhytidoponera.* Psyche, **72**: 87–112.

Haskins, C. P. and E. F. Haskins. 1983. Situation and location-specific factors in the compatibility response in *Rhytidoponera metallica.* Psyche, **90**: 163–174.

Hölldobler, B. and C. P. Haskins. 1977. Sexual calling behavior in primitive ants. Science, **195**: 793–794.

Pamilo, P., R. H. Crozier, and J. Fraser. 1985. Inter-nest interactions, nest autonomy, and reproductive specialization in an Australian arid-zone ant, *Rhytidoponera* sp. 12. Psyche, **92**: 217–236.

Ward, P. S. 1981. Ecology and life history of the *Rhytidoponera impressa* group II. Colony origin, seasonal cycles, and reproduction. Psyche, **88**: 109–126.

Ward, P. S. 1983. Genetic relatedness and colony organization in a species complex of ponerine ants. I. Phenotypic and genotypic composition of colonies. Behav. Ecol. Sociobiol., **12**: 285–299.

WARD, P. S. 1984. A revision of the ant genus *Rhytidoponera* in New Caledonia. Aust. J. Zool., **32**: 131–175.

WHELDEN, R. M. 1957. Anatomy of *Rhytidoponera convexa*. Ann. Ent. Soc. Amer., **50**: 271–282.

WHELDEN, R. M. 1960. Anatomy of *Rhytidoponera metallica*. Ann. Ent. Soc. Amer., **53**: 793–808.

SOUTH AMERICAN AND FLORIDIAN DISJUNCTS IN THE SONORAN GENUS *COMPSOCRYPTUS* (HYMENOPTERA: ICHNEUMONIDAE).

By Charles C. Porter[1]
Department of Biological Sciences, Fordham University
Bronx, NY 10458

Introduction

Taxonomy

Most *Compsocryptus* may be recognized at a glance by their elegantly yellow banded brown or black wings, large and anteriorly wide areolet, short and weak notauli, axillus intermediate in position between the anal margin of the hind wing and the submediella, strong ventro-lateral carina on postpetiole, and long, upcurved ovipositor.

My concept of this genus agrees, as to species included, with Townes' most recent definition (1969:203–4). Several of Townes' diagnostic features, however, do not apply to the *Compsocryptus* I have examined *(C. fasciipennis, C. fuscofasciatus, C. melanostigma, C. texensis,* and *C. xanthostigma).* All *Compsocryptus* I have seen possess a sharp and strong subvertical groove externo-ventrally near the base of the hind coxa, while Townes describes the hind coxa as "without a groove" (1969:203). All *Compsocryptus* examined by me have, in the female only, a prominent crescentic to subtriangular baso-lateral flange at the base of the petiole, while Townes maintains that the petiole is "without a lateral tooth at the base" (1969:203). *Compsocryptus* forms a compact genus whose species, despite their far-flung and discontinuous distribution, seem unusually homogeneous in color and structure. I thus suspect that all members of the genus will turn out to have a basal first gastric projection in the female and a strong hind coxal groove.

---

[1]Research Associate, Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, P.O. Box 1269, Gainesville FL 32602.

Manuscript received by the editor May 28, 1985

Relationships

Compsocryptus displays close affinity to *Trachysphyrus, Aeliopotes, Joppidium,* and *Lanugo.* Superficially, in color, size, habitus, and many details of geographic distribution, *Lanugo* especially parallels *Compsocryptus.* However, the phylogenetic connection seems distant, since *Lanugo* has only a weak groove at the base of the hind coxa, the axillus vein closer to the hind margin of the wing than to the submediella, and the ovipositor straight and shorter than in *Compsocryptus.* The South American *Trachysphyrus* [now regarded as including only the *Imperialis* group, as defined by Porter (1967:275–319)] seems directly associated with *Compsocryptus.* Important characters that separate *Trachysphyrus* include: dark but never pale banded wings; body color usually metallic blue, green, or purple; female flagellum scarcely flattened below; notauli usually (not always) extending beyond the middle of the mesoscutum; surface of mesoscutum shining, never extensively mat; 1st gastric tergite without a baso-lateral expansion; and 2nd gastric tergite in many species smooth and polished (in numerous others mat). *Aeliopotes paitensis* (Porter, 1986) in some ways (especially the petiolar tooth) seems annectant between *Compsocryptus* and *Trachysphyrus* but in other features (epomial development) is aberrant and deserves generic status. Finally, *Joppidium* seems to be a direct offshoot of *Compsocryptus. Joppidium* is more slender than *Compsocryptus* (postpetiole at least 1.5 as long as wide), lacks a ventro-lateral carina on the 1st gastric tergite, and has the female flagellum more strongly flattened below toward apex. Some of its species have a baso-lateral tooth on the petiole and yellow banded wings, as in *Compsocryptus. Joppidium* also parallels its relative in distribution, with numerous Sonoran species, several which extend (but not disjunctly) into the southeastern United States, and with an isolated species group in subtropical Brasil and north Argentina (no representatives in the Peruvian Coastal Desert).

Biogeography and Ecology

Compsocryptus belongs to the Sonoran Biogeographic category (Porter 1980:25–7). Possibly the genus evolved during the last half

of the Tertiary somewhere in southwestern North America. Certainly, its xerophilous species would have adapted well to the increasingly drier climates of post-Oligocene times and to the microphyll and sclerophyll Madro-Tertiary Geoflora which then overspread the ever-rising Sierra Madre and Rocky Mountains. On the other hand, *Compsocryptus* may have originated in western and southern South America, where so many of its relatives are centered today. Here, the Miocene climate paralleled that of the Sonoran region. By the end of the Miocene the Argentine pampas had become well developed, composites and other dry-adapted plants of open habitats were radiating vigorously, and long dry seasons began to characterize the middle latitudes as a result of the reduced rainfall and "the ever-increasing rain-shadow effect of the rising Andes" (Solbrig 1976:22–3). Thus arose the Chaco, an austral Sonora.

Whatever may have been its genesis, *Compsocryptus* today is centered in the western United States and northern México (15 species). It also has 3 remarkable disjuncts: *C. fasciipennis* in tropical Florida and Cuba, *C. fuscofasciatus* in the Peruvian Coastal Desert, and *C. melanostigma* in north Argentina and nearby areas in Paraguay and Brazil.

Even the most geographically remote species of *Compsocryptus* differ only in apparently minor features of color and sculpture. This fact may suggest that the disjunctions noted above arose in comparatively recent times. Both the increasing aridity of the later Tertiary and xerothermic episodes within the Pleistocene probably allowed semiarid communities (Thorn Scrub, Subtropical Deciduous Forest, etc.) to range almost uninterruptedly from the southeastern United States to Argentina. Wet periods during the Pleistocene (glacial maxima at higher latitudes) would have favored the expansion of forests and probably caused the fragmented distribution that is observed among modern *Compsocryptus* species.

For example, "during a past period of low rainfall a prairie type flora, such as is found today in Texas and Arizona, was able to extend its range into the eastern United States, and remnants of this flora reflecting dry conditions still exist on parts of the west coast of Florida and on Big Pine Key" and other lower Florida Keys (Spencer and Stegmaier 1973:13). Such dry periods occurred both in the Pleistocene and in the climatically unsettled late Tertiary. They

allowed eastward expansion by a whole complex of Sonoran Biota, from *Opuntia, Cereus, Acacia* and other xerophytes, to insects like *Compsocryptus fasciipennis,* several species of *Joppidium, Lanugo retentor, Derocentrus longicaudis, Eiphosoma dentator* (all Ichneumonidae), *Eumenes smithii* (Eumenidae), *Stictiella* (Sphecidae) and even to vertebrates, such as the reptiles *Crotalus, Sistrurus, Pituophis, Sceloporus,* and *Gopherus.*

Concurrently, similar physio-climatic events could have produced the plausibly vicariant differentiation of *Compsocryptus fuscofasciatus* and *C. melanostigma* in South America. As discussed under *C. melanostigma,* the common ancestor of these two species may have ranged in Chaco vegetation from Argentina to coastal Perú at a time before the Andes were high enough at this latitude to impede east-west exchange of lowland biota.

As intimated throughout the above discussion, *Compsocryptus* prefers semiarid or arid environments, but also may be abundant in open, degraded subtropical humid forests. *Compsocryptus melanostigma,* for example, has been cited from the very wet Selva Tucumano-Boliviana and Selva Misionera in Argentina. However, the majority of these forest records are from ecotones between forest and Chaco or from sites in the first stages of secondary succession (logging roads, clearings, windfalls, etc.). This fact demonstrates how precarious is the present-day equilibrium between forest and scrub (Selva and Chaco). Almost all modern forests are surrounded by drier environments, whose aggressive biota tends to encroach with the slightest ecological perturbation. *Compsocryptus melanostigma* in Argentina and *C. fasciipennis* in south Florida are among the many indicator species of these often anthropogenic and usually disastrous environmental changes, from forest to scrub and finally to desert.

Hosts

Compsocryptus are among the most common, conspicuous, and frequently collected of New World Ichneumonidae. Nonetheless, practically nothing is known about their host relationships. Only *Compsocryptus melanostigma* has been reared. It parasitizes noctuid moths of the genera *Alabama* and *Pseudaletia. Alabama* larvae feed on cotton and pupate in rolled leaves. *Pseudaletia* larvae feed at night on many kinds of grains and grasses, hiding by day under

clods of earth or in other slightly subsurface shelters. *Pseudaletia* pupae are made in the ground. These data explain why females of *C. melanostigma* most often are collected on the ground or from low vegetation. Other *Compsocryptus* species occur in similar microhabitats and probably parasitize comparable hosts.

Collections

Listed below in alphabetic order are the collections in which material from this study has been or is to be deposited. Institutional collections are designated by the name of the city where they are located. Individual collections are referred to by the surnames of their owners.

CAMBRIDGE. Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

COLLEGE STATION. Department of Entomology, Texas A & M University, College Station, TX 77843

GAINESVILLE. Florida State Collection of Arthropods, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P. O. Box 1269, 1911 SW 34th Street, Gainesville, FL 32602.

LAWRENCE. Department of Entomology, Snow Entomological Museum, The University of Kansas, Lawrence, KS 66045.

PORTER. Collection of Charles C. Porter, 301 North 39th Street, McAllen, TX 78501.

TOWNES. American Entomological Institute, c/o Dr. Virendra Gupta, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, FL 32602.

Genus *COMPSOCRYPTUS*

Cryptoideus Ashmead, 1900. Proc. U. S. Natl. Mus. **23:** 42. Type: *Cryptus purpuripennis* Cresson.

Compsocryptus Ashmead, 1900. Proc. U. S. Natl. Mus. **23:** 43. Type: *Cryptus calipterus* Say.

Callicryptus Ashmead, 1900. Proc. U. S. Natl. Mus. **23:** 43. Type: *(Cryptus "fasciatus"* Brullé) = *fasciipennis* Brullé.

Stictocryptus Cameron, 1908. Trans. Amer. Ent. Soc. **34:** 243. Type: (*Cryptus "fasciatipennis"* Brullé) = *fasciipennis* Brullé.

Sophocryptus Mallo, 1961. Idia **165:** 17. *Nomen nudum.*

Fore wing 7.2–13.0 mm long. Wings usually dark with yellow transverse bands. Female flagellum somewhat widened and flattened below on apical 0.3. Male flagellum with linear tyloids on many intermediate segments. Mandible usually moderately broad with lower tooth slightly shorter than upper tooth (rarely long and slender with lower tooth much shorter than upper). Clypeus rather large, gently convex in profile; its apical margin always edentate and straight to weakly convex. Occipital carina sharp and narrow. Malar space about 1.0 as long as basal width of mandible. Pronotum with epomia well defined but not extending much dorsad or ventrad of scrobe. Mesoscutum with notaulus faint, traceable less than half its length; surface mat, dully shining, or sometimes polished and with numerous, small to medium sized, crowded to well separated punctures (punctures sparser in males). Mesopleuron without a ridge on prepectus below. Hind coxa with a sharp and strong subvertical groove externo-ventrally near base. Wing venation: areolet large, symmetrically to asymmetrically pentagonal, intercubiti slightly to definitely convergent dorsad, front side of areolet (2nd abscissa of radius) 0.9 to more than 1.0 as long as 1st intercubitus (mesal side of areolet); discocubitus gently arched, without a ramellus; mediella nearly straight; axillus long, diverging from anal margin of wing, as close to submediella as to anal margin. Propodeum: spiracle elongate; apical trans-carina varying from strong throughout, to strong laterad but obsolete mesad, to almost completely absent; cristae usually defined and subcrescentic to bluntly triangular (cristae often obsolete in males). First gastric tergite in female with a prominent crescentic to subtriangular baso-lateral flange and with the postpetiole strongly expanded but in male without a baso-lateral expansion and with the postpetiole slender; ventral longitudinal carina usually sharp throughout, dorso-lateral and dorsal carinae less well developed, weakest in males. Second gastric tergite mat with very fine and dense punctures (sparser in males) which sometimes become more widely spaced mesad and with short, recumbant, mostly overlapping setae. Ovipositor: long, sheathed portion 0.5–1.4 as long as fore wing, gently upcurved, cylindro-compressed, its tip elongate (0.10–0.25 as high at nodus as long from nodus to apex), nodus low and without a notch, ventral valve on tip with sharp and inclivously oblique ridges.

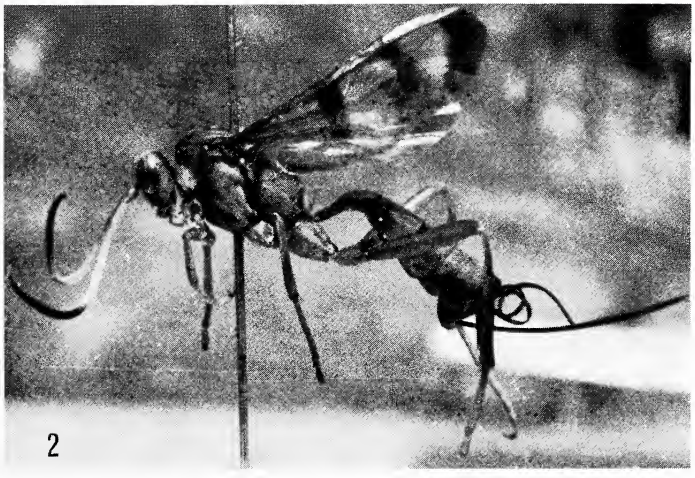


Fig. 1. *Compsocryptus melanostigma,* ♀. Photograph of whole insect in lateral view. Fig. 2. *Compsocryptus fuscofasciatus,* ♀. Photograph of whole insect in lateral view.

KEY TO THE SOUTH AMERICAN SPECIES OF *COMPSOCRYPTUS*

1. Fore wing yellow with 2 narrow brown cross bands and with brown on apex; 2nd abscissa of radius 0.9–1.0 as long as 1st intercubitus; female mesopleuron usually with some strong longitudinal wrinkling ..... 1. *C. fuscofasciatus* (Brullé)

1′. Fore wing dark brown with a broad median yellow cross band and a large subapical yellow blotch; 2nd abscissa of radius 1.2–1.5 as long as 1st intercubitus; female mesopleuron without any longitudinal wrinkling, almost uniformly punctoreticulate ..... 2. *C. melanostigma* (Brullé)

1. *Compsocryptus fuscofasciatus* (Brullé) (Fig. 2, 3, 4)

Cryptus fusco-fasciatus Brullé, 1846. *In* Lepeletier: Histoire naturelle des insectes. Hyménoptères **4:**194. Holotype ♀: Perú, Lima (lost).

Callicryptus ornatipennis Cameron, 1902. Trans. Amer. Ent. Soc. **28:**372. Holotype ♀: Perú, Callao (London).

FEMALE. *Color:* antenna ferruginous on scape and pedicel, yellowish ferruginous on 1st (sometimes also 2nd and 3rd) flagellomere, mostly yellow on flagellomeres 2, 3 or 4–9, brown and yellow on flagellomeres 10–11 or 12, and black or brownish black beyond 12th or 13th flagellomere; head ferruginous with black on apex of mandible; palpi dull ferruginous; mesosoma ferruginous with inconspicuous dusky staining on some margins and sutures or sometimes with rather extensive black markings (as described for male); gaster dull ferruginous with faint dusky staining on 2nd and following tergites or occasionally with better defined black areas toward base on 2nd and 3rd tergites; legs ferruginous, duller on tarsi, with dusky staining on apical tarsomeres, narrowly on apex of hind trochantellus and base of hind femur, and with blackish on much of hind tibia except toward its paler (sometimes contrastingly flavoferruginous) base; fore wing light yellow with three brown areas as follows: a broad transverse band on most of apical 0.3 of median cell, on base of discocubital cell, on apical 0.3 of submedian cell, on basal 0.3 of 1st brachial cell, and on adjoining region of anal cell; a second brown cross-band covering basal 0.3 of radial cell, apical 0.3

of discocubital cell, areolet, apical 0.5 of 2nd discoidal cell, and expanding below to cover all but basal 0.3 (or less) of 2nd brachial cell; as well as with a third brown area on apical 0.5 of 3rd cubital cell and apical 0.5 of 3rd discoidal cell and confluent below with dark area of 2nd brachial cell; hind wing pale yellow with apical 0.3 dusky and with dusky staining prolonged more narrowly far basad on its hind margin, as well as sometimes with an irregular transverse dusky area at level of nervellus.

Length of fore wing: 10.5–12.5 mm. *Flagellum:* 1st segment 3.2–3.5 as long as deep at apex; apical segments averaging 0.7–0.8 as long as wide. *Malar space:* 1.0 as long as basal width of mandible. *Mesoscutum:* dully shining with abundant, dense, sharp, tiny punctures which emit inconspicuous, short and mostly close-packed setae. *Mesopleuron:* surface with delicate to strong, trans-biased puncto-reticulation and, at least ventrad, usually with some strong longitudinal wrinkling. *Wing venation:* radial cell 3.6–4.1 as long as wide; areolet about as high as broad, symmetrically pentagonal, intercubiti weakly to moderately convergent above, 2nd abscissa of radius 0.9–1.0 as long as 1st intercubitus. *Hind femur:* 5.6–6.0 as long as deep. *Hind tibia:* below and laterally on apical 0.5 with a few, scattered enlarged setae. *Propodeum:* apical face discrete from the gently arched basal face and almost vertical; basal trans-carina traceable throughout, uniformly fine and sharp or sometimes partly weak and irregular. *First gastric tergite:* dorso-lateral carinae percurrent but faint; dorsal carinae well defined, but not sharp, on apex of petiole and basal 0.5 of postpetiole; surface of postpetiole mat, sometimes dully shining toward apex, with fine micro-reticulation and with tiny, sparse, shallow punctures that are best developed apico-laterad (where their short setae partially overlap). *Ovipositor:* sheathed portion 0.69–0.81 as long as fore wing; tip 0.15–0.17 as high at nodus as long from nodus to apex.

Male. Differs from female as follows: *Color:* pedicel sometimes marked with black; flagellomeres 1–5 (sometimes up to 9) ferruginous to yellowish with dusky staining, mostly above; at least flagellomeres 10–13 yellow with some ferruginous staining; rest of flagellum black; head ferruginous with yellowish on base of mandible, much of face laterally, and narrowly on lower 0.6 of frontal orbit as well as with black on apex of mandible, broadly above and between antennal sockets (sometimes reaching and including stem-

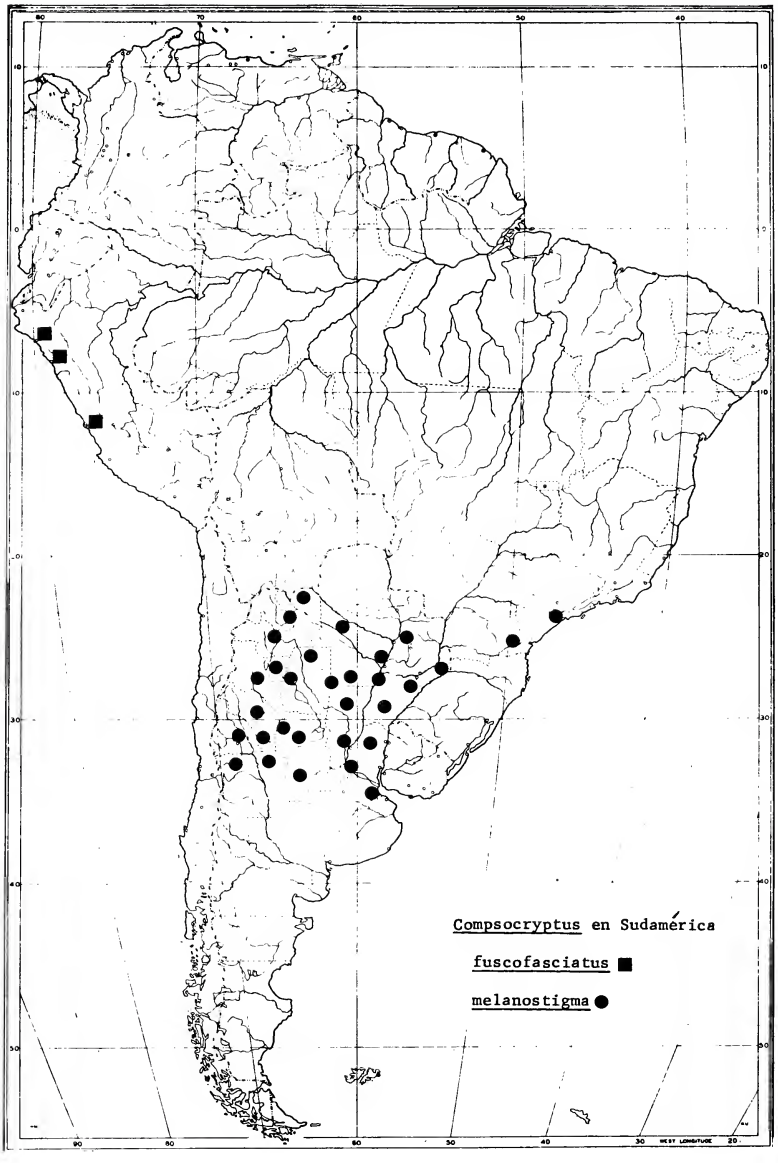


Fig. 3. Map showing geographical distribution of *Compsocryptus fuscofasciatus* and *C. melanostigma*.

maticum) and on most of postocciput; mesosoma ferruginous with black markings usually better developed than in female and including areas on propleuron anteriorly, pronotal collar, spot on epomia (sometimes contiguous with black on collar), broad band on hind margin of pronotum, prescutellar groove, much of meso and metanotal axillary troughs, groove at base of propodeum, all of prepectus, mesosternal sulcus, hind face of mesosternum, broad band on hind margin of mesopleuron—prolonged dorsad along upper mesopleural margin to subalarum, broadly on all but dorsal margin of lower metapleuron, and irregularly on hind margin of propodeum; gaster dull to bright ferruginous with a little black at base of 1st tergite and with succeeding tergites sometimes only with irregular dusky staining and sometimes with well defined black areas toward base of tergites 2 and 3; fore and mid tibiae and tarsi more yellowish than in female; mid femur with some blackish staining dorsad and apicad; hind tibia black with basal 0.15 contrastingly pale yellow; hind tarsus blackish with light yellow at least near base of 1st segment and sometimes almost throughout on both segments 1 and 2.

Length of fore wing: 8.5–9.6 mm. *Flagellum:* linear, largely percurrent tyloids present on segments 11 or 12 to 19 or 20; 1st segment 2.5–2.7 as long as deep. *Malar space:* 0.77–0.90 as long as basal width of mandible. *Mesoscutum:* shining with abundant, moderately small, sharp punctures that are separated by 1.0–2.0 their diameters and which emit dense, erect, moderately long setae. *Mesopleuron:* more shining than in female, with medium sized, sharp, dense, subadjacent to reticulately confluent punctures and some longitudinally biased reticulation. *Hind femur:* 6.3–7.4 as long as deep. *Hind tibia:* with enlarged setae more abundant and conspicuous than in female. *Propodeum:* rather elongately convex in profile; apical face not discrete from basal; apical trans-carina weaker than in female, forming low and subcrescentic cristae or sometimes with cristae obsolete. *First gastric tergite:* ventro-lateral carina obsolete on petiole but sometimes becoming sharp toward apex of postpetiole; dorso-lateral and dorsal carinae in great part obsolete; surface of postpetiole smooth and shining with abundant but well separated tiny punctures that emit long and uniformly overlapping setae.

Specimens Examined. 15 ♀ and 47 ♂: PERÚ, Lambayeque Province, 33 km E. Olmos, Ruta a Jaén, 23-VII-1975, C. Porter, L. Stange; 1 km S. Lambayeque, 24-27-VII-1975, C. Porter, L. Stange; La Libertad Province, Laredo nr. Trujillo, 7-8-VII-1974, C. Porter, L. Stange; Simbal nr. Trujillo, 4-7-VII-1974, C. Porter, L. Stange; Lima Province, Cupiche, 10 km E. Chosica, 25-VI-2-VII-1974, C. Porter, L. Stange; Palle nr. Chosica, 17-VII-1974, C. Porter, L. Stange; San Gerónimo nr. Chosica, 28-VI-5-VII-1976, C. Porter, C. Calmbacher; nr. Surco on Carretera Central at km 59, 30-VI-1976, C. Porter, C. Calmbacher.

Relationships. This Peruvian Coastal Desert endemic differs only in minor chromatic and structural features from the other South and North American *Compsocryptus.* It seems closely related to the Argentine *C. melanostigma* (Brullé) but may be distinguished by the following characters: (1). Fore wing yellow with two narrow brown cross bands and with brown on apex (vs. dark brown with a broad median yellow cross band and a large subapical yellow blotch), 2. Second abscissa of radius 0.9–1.0 as long as 1st intercubitus (vs. 1.2–1.5 as long), 3. Female mesopleuron usually with some strong longitudinal wrinkling (vs. puncto-reticulate), 4. Male mesoscutum with punctures mostly separated by 1.0–2.0 their diameters (vs. 2.0 or more their diameters) and 5. Male flagellum with tyloids extending to segments 19–20 (vs. 21–23).

Field Notes. *Compsocryptus fuscofasciatus* has been reported only from the northern and central Peruvian Coastal Desert between Lima and Piura. Here, it frequents most well watered habitats between sealevel and 1500 m. I have collected it along rivers and irrigation ditches in arid country as well as in orchards and degraded cloud forest. Like other *Compsocryptus,* this species most often occurs near or on the ground in exposed, disturbed, weedy or grassy places.

2. *Compsocryptus melanostigma* (Brullé)
(Fig. 1, 3, 5)

Cryptus melanostigma Brullé, 1846. *In* Lepeletier: Histoire naturelle des insectes. Hyménoptères **4:**191. Lectotype ♀: Brasil: "Prov. de Misiones" (Paris Museum).

Cryptus opaco-rufus Taschenberg, 1876. Ztschr. f. die Gesam. Natuw. Halle **48:**64. Lectotype ♀: (Brasil): Paraná (Halle).

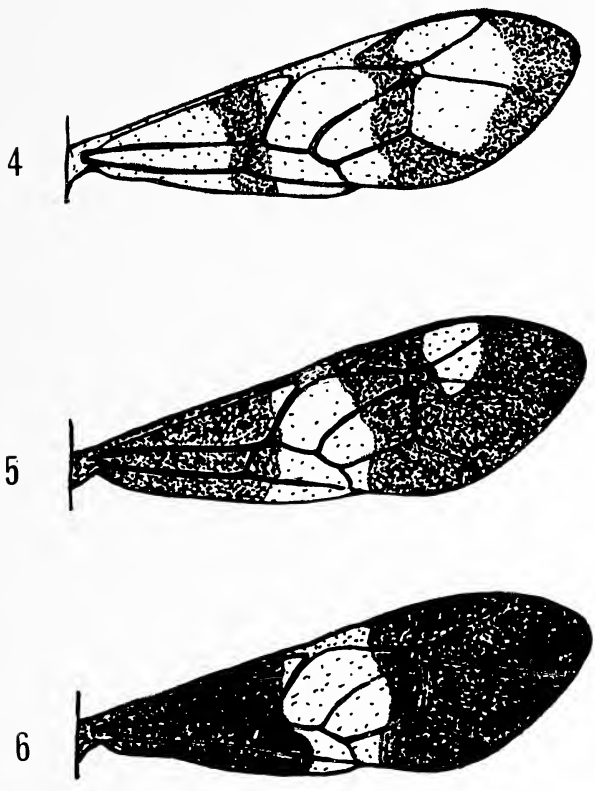


Fig. 4. *Compsocryptus fuscofasciatus,* ♀. Fore wing, showing color pattern. Fig. 5. *Compsocryptus melanostigma,* ♀. Fore wing, showing color pattern. Fig. 6. *Compsocryptus fasciipennis,* ♀. Fore wing, showing color pattern.

Cryptus lateritus Taschenberg, 1876. Ztschr. f. die Gesam. Naturw. Halle **48:**65. Lectotype ♂: (Brasil): Paraná (Halle).
Callicryptus pulchrifasciatus Cameron, 1909. Trans. Amer. Ent. Soc. **35:**437. Lectotype ♀: Argentina: Mendoza (London).
Sophocryptus bisulcatus Mallo, 1961. Idia **165:**17. *Nomen nudum.*

FEMALE. *Color:* antenna with scape brownish ferruginous, pedicel dusky ferruginous with apex paler, and flagellum black with

a yellowish white annulus on segments 4 (near apex) –9; head brownish ferruginous with black on mandibular teeth; mesosoma brownish ferruginous; gaster dull brownish ferruginous with vague but often widespread dusky staining; legs brownish ferruginous with dusky on fore tibia and tarsus, mid femur dusky dorso-apicad, mid tibia extensively blackish or dusky, mid tarsus blackish brown, some dusky staining on hind trochantellus, much blackish brown (especially apicad) on hind femur, and black almost throughout on hind tibia and tarsus; wings dark brown; fore wing with a broad transverse median yellow band that covers dorso-apical corner of median cell, basal 0.6 of discocubital cell, basal 0.5 of 2nd discoidal cell, all but base of 1st brachial cell, basal 0.2 of 2nd brachial cell, and anal cell beneath 1st and 2nd brachial cells, as well as with a rounded yellow blotch covering most of apical 0.5 of radial cell, a little of areolet, and basal 0.3 of 3rd cubital cell; hind wing with a very broad yellow transverse band on its postmedian 0.25, contiguous with median yellow band of fore wing.

Length of fore wing: 10.0–12.3 mm. *Flagellum:* 1st segment 3.4–3.5 as long as deep at apex; apical segments 0.6–0.8 as long as wide. *Malar space:* 1.0–1.1 as long as basal width of mandible. *Mesopleuron:* with extensive comparatively fine puncto-reticulation and without any strong longitudinal wrinkling. *Wing venation:* radial cell 3.8–4.5 as long as wide; areolet a little broader than high, intercubiti weakly convergent above, 2nd abscissa of radius 1.2–1.5 as long as 1st intercubitus. *Hind femur:* 6.0–7.0 as long as deep. *Hind tibia:* on apical 0.5 with numerous but widely spaced enlarged setae. *First gastric tergite:* dorso-lateral carinae often sharp on petiole; dorsal carinae varying from obsolete to weak; surface of postpetiole uniformly mat with finely granular micro-reticulation, practically glabrous, even apico-laterad. *Ovipositor:* sheathed portion 0.76–0.83 as long as fore wing; tip 0.14–0.16 as high at nodus as long from nodus to apex.

MALE. Differs from female as follows: *Color:* scape yellow and ferruginous, pedicel brown with some yellowish apicad, flagellum with a yellowish white annulus on segments 9 or 10–12 or 13; face rather pale ferruginous with some yellowish staining or with yellow on facial orbits and less extensively also on frontal orbits; front becoming dark brown to black between and above antennal sockets; postocciput partly to mostly black; mesosoma with some black on

propleuron, sometimes with a pair of black spots on pronotum dorsally behind collar, sometimes narrowly black on anterio-lateral margin of pronotum, sometimes narrowly black on much of hind margin of pronotum, vaguely to extensively blackish on prepectus, sometimes tinged with black in meso and metanotal axillary troughs, sometimes blackish behind subalarum, sometimes black stained in mesosternal sulcus, and sometimes blackish on margins of lower metapleuron; gaster with slight to conspicuous blackish staining, often irregularly on 2nd tergite and always rather broadly on tergites 5–7; fore tibia and tarsus yellowish with tarsus comparatively dark and dusky on last segment; mid leg with blackish in part on trochanter and trochantellus, femur pale yellow on apical 0.2 and otherwise blackish to brownish, tibia pale yellow, and tarsus dusky with dirty yellow on basal 0.5 of first segment; hind leg with black and brown staining on trochanter and trochantellus, femur black or dark brown, and tibia black with a broad, dull yellowish-white prebasal band covering about 0.25 of segment.

Length of fore wing: 8.6–10.3 mm. *Flagellum:* linear, largely percurrent tyloids present on segments 11 or 12–21, 22, or 23; 1st segment 2.6–3.1 as long as deep. *Malar space:* 0.82–0.93 as long as basal width of mandible. *Mesoscutum:* shining with abundant, small, sharp punctures that generally are separated by more than 2.0 their diameters. *Mesopleuron:* similar to female but with coarser, longitudinally biased wrinkling and larger intercalated punctures. *Hind femur:* 5.5–7.2 as long as deep. *First gastric tergite:* postpetiole smooth and shining with abundant but well separated tiny punctures whose setae mostly overlap laterad but become somewhat sparser toward the meson.

Specimens Examined. 31♀ and 24♂: ARGENTINA, Formosa Province, Arroyo Eh Eh Grande, 76 km N Formosa, Rta. 11, 14-VIII-1977, C. Porter, L. Stange, P. Fidalgo, Arroyo San Hilario, 15 km S. Formosa, Rta. 11, 11-12-VIII-1977, C. Porter, L. Stange, P. Fidalgo, Riacho Pilagá, 27 km N. Formosa, Rta. 11, 12-VIII-1977, C. Porter, L. Stange, P. Fidalgo; Salta Province, Dique Itiyuro, 70 km N. Tartagal, 30-VII-1977, C. Porter, L. Stange, P. Fidalgo, Tartagal, 11-18-VIII-1973, C. Porter, 10 km N. Vespucio, 12-VIII-1976, C. Porter, L. Stange, Rosario de la Frontera, 19-VI-1972, C. Porter; Tucumán Province, Río Nio, 30-XI-1964, C. Porter, San Pedro de Colalao, 19-XII-1964, C. Porter, Villa Nougués, 26-27-XI-1964, 6-7-XII-1964, C. Porter; Santiago del Estero Pro-

vince, Termas de Río Hondo, Dique Frontal, 3-V-1972, 2-VIII-1973, C. Porter; La Rioja Province, Villa Unión, 22-IV-1972, C. Porter; Córdoba Province, La Lejanía ca. Nono, 23-25-X-1984, C. Porter, T. O'Neill.

RELATIONSHIPS. As discussed under that species, *Compsocryptus melanostigma* much resembles *C. fuscofasciatus* of the Peruvian Coastal Desert. The two species may have originated from a common ancestor that once ranged across what is now subtropical South America from north Argentina to the Pacific coast. Warm, seasonally dry conditions, of a type preferred by most modern *Compsocryptus,* apparently prevailed across this area during the early Tertiary (Solbrig 1976:42). Subsequent Andean uplift would have split early *Compsocryptus,* populations into eastern and western isolates, setting the stage for differentiation of the modern *C. melanostigma* in Argentina and *C. fuscofasciatus* in coastal Perú.

FIELD NOTES. This conspicuous species occurs throughout northern Argentina below 1500 m and ranges into adjoining parts of Brasil and Paraguay. It occupies many forest, thorn scrub, and desert biomes, including Southeast Brasilian Wet Forest, subtropical Andean Cloud Forest, Chaco Forest, Wet Chaco, Dry Chaco, Montane Chaco, and Subandean Desert. In wooded areas, *C. melanostigma* prefers disturbed situations in full sun along trails or at the forest edge. In all habitats, it flies mostly near the ground among grasses, forbs, or low shrubs.

Compsocryptus melanostigma often is very common during fall and winter but may be collected in most habitats at any time of the year.

This is the only *Compsocryptus* for which host information has been obtained. It has been reared from the noctuid moths *Alabama argillacea* and *Pseudaletia unipunctata* (Townes 1966:77).

3. *Compsocryptus fasciipennis* (Brullé)
(Fig. 6)

Cryptus fasciipennis Brullé, 1846. *In* Lepeletier: Histoire naturelle des insectes. Hymenopteres 4:191. Lectotype ♀ (labeled by H. K. Townes Townes): Cuba (Paris).

This elegant species was well characterized by Townes (1962: 282–3). It differs from other *Compsocryptus* by its bluish black

ground color; black wings with a single yellow cross band on fore wing; coarsely punctate to (medially) reticulo-punctate mesopleuron; very densely setose 2nd gastric tergite; and sheathed portion of ovipositor averaging only 0.67 as long as fore wing.

Like the South American *Compsocryptus, C. fasciipennis* is isolated by more than 1000 km from its nearest congeners. It occurs only on the Keys and in the Everglades region of tropical Florida as well as on Cuba. Other North American *Compsocryptus* range both northwest and southwest from near Houston in east Texas.

Current research has added some new information on the ecology and geographic distribution of *C. fasciipennis.* These data are summarized below.

New Specimens Examined: 13♀ and 33♂: UNITED STATES, Florida, Monroe County, Bahia Honda Key State Park 11-X-1981, C. Porter, L. Stange; Big Pine Key, 16-18-V-1982, 25-X-1982, C. Porter; Fleming Key, V-1979 to V-1980, Malaise Trap, H. V. Weems, Jr.; North Key Largo, 15-V-1982, 12-X-1981, C. Porter, L. Stange; Stock Island, 18-V-1982, C. Porter, L. Stange.

Field Notes. Like other *Compsocryptus,* this species usually occurs flying close to or crawling on the ground in early secondary successional habitats at the edge of mature forests. In October of 1981 I netted 12 males from *Bidens pilosa* growing on the center strip of a parking lot on Bahia Honda Key. My Key Largo specimens also were taken from stands of *Bidens.* On Big Pine Key, I swept several *C. fasciipennis* amid herbaceous undergrowth on a sand ridge along a trail through a Tropical Hardwood Hammock.

Townes (1960:283) cites 75 males and 44 females of *C. fasciipennis* from south Florida (Miami and Everglades National Park to Key West) and indicates that the yearly activity period for this species in Florida spans "December 28 to April 12" with 1 record for 5 December. My new records show that the species begins to fly as early as 11 October and continues at least until 18 May. It is scarce in May but often becomes abundant in October (e.g., 12♂ from Bahia Honda Key on 11-X-1981).

The Malaise Trap records from Fleming Key elicit interest for several reasons. They are the first annual survey of *Compsocryptus* (and other ichneumonid) abundance done on the Florida Keys. They also provide an idea of ichneumonid species composition and density in a highly disturbed part of the Keys. Fleming Key is an artificial appendage of Key West, mainly given over to a U. S. D. A.

animal quarantine facility and with little vegetation other than mangroves, pioneering stage herbs, and introduced ornamental trees, such as *Casuarina.* Such environments select for unusually hardy ichneumonids and species of this type should particularly concern the biological control specialist, who is looking for parasites that will thrive in climatically stressed agricultural systems.

The Fleming Key Survey, run between May 1979 and May 1980, with a gap in September and October, amassed 631 ichneumonid specimens belonging to 37 species. Only 9 of these species accounted for about 89% (561 specimens) of all Ichneumonidae trapped. *Diadegma* sp. (22 specimens) was the least abundant of the "common" group, followed by *Compsocryptus fasciipennis* (23), *Labena grallator* (36), *Mallochia agenioides* (41), *Anomalon* sp. (43), *Temelucha* sp. (68), *Paraditremops albipectus* (103), *Calliephialtes ferrugineus* (107), and *Eiphosoma dentator* (118, Porter 1983).

Table 1 summarizes monthly phaenology for *Compsocryptus fasciipennis* and the eight other common ichneumonid species of the depauperate Fleming Key Fauna, as sampled by Malaise traps. *Compsocryptus fasciipennis* is active from fall to late spring with maxima in March and October (as shown by Malaise and hand collected specimens). This seasonal phaenology coincides approximately with that of the Argentine *C. melanostigma* and agrees even more closely with the pattern shown by *C. texensis* in the Lower Río Grande Valley (present from January to May and again in December with greatest abundance in December, as documented by Porter, 1977:82).

Compsocryptus fasciipennis follows a cool-season phaenologic cycle not unlike that of many other ichneumonids which inhabit subtropical communities from Florida and Texas to Argentina. Among the abundant Ichneumonidae at Fleming Key, 4 species have autumn to early spring maxima and roughly parallel *C. fasciipennis* (*Calliephialtes ferrugineus, Paraditremops albipectus, Temelucha* sp., and *Diadegma* sp.), 2 peak in May (*Labena grallator, Anomalon* sp.), and the other 2 become most abundant during July and August (*Eiphosoma dentator, Mallochia agenioides*). Nonetheless January to March seem the best overall months for ichneumonids at this locality. All 9 species occur during this trimester and 230

Table 1. Monthly phaenology for nine common ichneumonoid species of the depauperate Fleming Key Fauna. For details, see text.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	NOV	DEC	PEAK MONTH
1. *E. dentator*	7	7	10	2	11	15	28	27	5	6	JULY
2. *C. ferrugineus*	26	17	16	1	11	9	5	2	2	18	JANUARY
3. *P. albipectus*	14	16	23	2	1	3	4	—	(29)[1]	12	MARCH (OCT.)
4. *Temelucha* sp.	6	8	12	3	8	6	4	4	2	13	DECEMBER
5. *Anomalon* sp.	2	2	8	—	18	8	5	—	—	—	MAY
6. *M. agenioides*	2	2	4	1	6	7	9	9	—	1	JULY, AUGUST
7. *L. grallator*	4	3	4	2	11	2	2	—	6	2	MAY
8. *C. fasciipennis*	3	4	8	3	3	—	—	—	2	—	MARCH
9. *Diadegma* sp.	7	6	9	—	—	—	—	—	—	—	MARCH
Total spp/month	9	9	9	7	8	7	7	4	5	6	
Total specimens/ month	71	65	94	14	69	50	57	42	17	52	

[1]Hand collected specimens, 24-X-1982, Key West, between Smather's Beach and Airport; swarming in Mangrove Swamp around aerial roots and herbs; C. Porter, L. Stange.

of the 561 specimens were collected then. These data agree closely with my earlier studies on south Texas mesostenine Ichneumonidae (Porter 1977), which reported peak diversity (20/34 species) and maximum abundance (138/679 specimens) for December and only slightly less impressive statistics for January (18 species and 135 specimens).

Acknowledgments

This research was done principally under my current National Science Foundation Grant (BSR-8313444) and in part was supported by previous NSF awards (DEB-75-22426, GB-6925). Grants from the Committee for Research and Exploration of the National Geographic Society permitted field research in South America during 1973, '74, '75, '79, and '81. Support also came from Faculty Fellowships conferred by Fordham University for the Spring Semester of 1980 and the Fall Term of 1984.

As a Research Associate of the Florida State Department of Agriculture and Consumer Services, I have received generous support from the Division of Plant Industry at Gainesville, among whose personnel special thanks befit Dr. Howard V. Weems, Jr., Dr. Lionel A. Stange, and Mr. Harold A. Denmark. All my collecting in South Florida was facilitated by the Division of Plant Industry.

Material of *Compsocryptus melanostigma* was obtained in Argentina during repeated periods of cooperation with the Instituto Miguel Lillo of the Universidad de Tucumán. I am particularly indebted to Professor Rodolfo Golbach and to Dr. Abraham Willink of this institution.

I also thank Mr. Thomas J. O'Neill of Fordham University for his assistance on fieldtrips to Argentina and Perú.

Summary

Compsocryptus is a mesostenine closely related to *Trachysphyrus*. Its short notauli, long anterior side of areolet, medially situate axillus, long and upcurved ovipositor, and (usually) dark and yellow banded wings distinguish *Compsocryptus* from most other trachysphyroids. There are 15 species centered in the Sonoran region of

western North America and México plus 1 isolated species in Florida and Cuba, another in the Peruvian Coastal Desert, and a 3rd in the Argentine Chaco. *Compsocryptus fuscofasciatus* from Perú has the fore wing yellow with 2 brown bands, while in the Argentine *C. melanostigma* the fore wing is dark with a broad median yellow cross band and a large subapical yellow blotch. Townes (1962) has fully characterized the North American species. *Compsocryptus* inhabits a variety of exposed situations at altitudes below 1500 m, including deserts, Thorn Scrub, Subtropical and Tropical Deciduous forests, and disturbed sites in humid Neotropic forests. The species fly mostly from fall to spring. *Compsocryptus melanostigma* has been reared as a solitary parasite from noctuid moth pupae.

Literature Cited

Porter, C.

1967. A revision of the South American species of *Trachysphyrus*. Mem. Amer. Ent. Inst. **10**:1–386.

1977. Ecology, zoogeography, and taxonomy of the Lower Río Grande Valley Mesostenines. Psyche **84**(1):28–91.

1980. Zoogeografía de las Ichneumonidae latino-americanas. Acta Zool. Lilloana **36**:5–52.

1983. *Eiphosoma dentator* in Florida. Florida Ent. **66**: 353–358.

1986. *Trachysphyrus* and the new genus *Aeliopotes* in the coastal desert of Perú and North Chile. Psyche **92**: 513–545.

Spencer, K. A. and C. E. Stegmaier, Jr.

1973. Agromyzidae of Florida. Arthropods of Florida and neighboring land areas **7**:1–205. Division of Plant Industry, Gainesville.

Solbrig, O.

1976. The origin and floristic affinities of the South American temperate desert and semidesert regions. *In* D. Goodall (ed.), Evolution of desert biota, p. 7–49. University of Texas Press, Austin.

Townes, H. K.

1962. Ichneumon-flies of America north of México: Subfamily Gelinae, Tribe Mesostenini. Bull. U. S. Natl. Mus. **216**(3):1–602.

1966. A catalog and reclassification of the Neotropic Ichneumonidae. Mem. Amer. Ent. Inst. **11**:1–367.

1969. Genera of Ichneumonidae, Part 2: Gelinae. Mem. Amer. Ent. Inst. **12**:1–537.

THE ORB-WEAVER GENUS *WITICA* (ARANEAE: ARANEIDAE).*

By Herbert W. Levi

Museum of Comparative Zoology,
Harvard University, Cambridge, MA. 02138

Two species of neotropical orb-weavers, *"Edricus" crassicauda* and *Witica talis,* have each been known from a single sex, the first from females only, the second from males. The male of *Edricus spinigerus,* suspected by F.P.-Cambridge (1904) to belong with the female *Epeira crassicauda,* has never been collected with it, although Cambridge's suspicion was the reason for placing the female *E. crassicauda* in the genus *Edricus.* While parthenogenesis could account for absence of males in *E. crassicauda,* the absence of females in *Witica* was more perplexing. The large females of *Epeira crassicauda* have a tail with a constriction (Fig. 1), the minute males of *Witica talis* (Fig. 5) have a round, subspherical abdomen bearing a glossy plate. The two placed in different subfamilies did not appear to be likely mates.

Surveying our collections, I found males of *Witica* to have been collected in Cuba, Puerto Rico, Central and northern South America, roughly the same distribution as the female specimens named *"Edricus" crassicauda.* Both are fairly common on Barro Colorado Island in Gatun Lake of Panama, from which large collections are available.

Unexpected evidence for existence of males in *E. crassicauda* turned up: a male palpal part was found in the microscope slide preparation of the seminal receptacles. When expanding the palpus of *Witica talis,* I noticed that the structure first considered to be the conductor, and which is sometimes missing from specimens, is actually an appendage of the embolus. Further, its structure is remarkable, including a hand with many fine teeth, presumably functioning as a hold-fast inside the female genital duct (Fig. 11). Subsequently,

*This is the third of a series of revisions of neotropical noncribellate orb-weaving spiders.

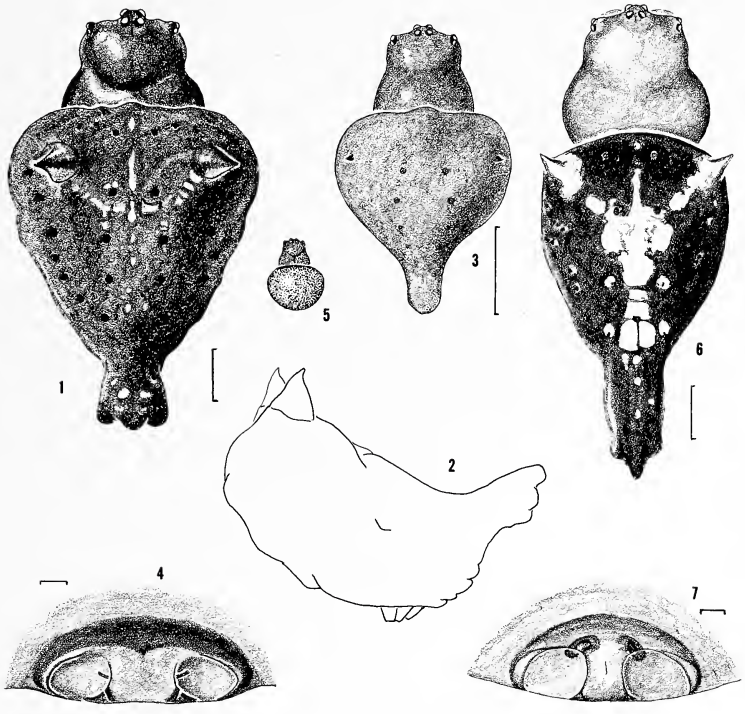
Manuscript received by the editor March 17, 1986.

I examined a female epigynum in ventral view with the pigmented integument carefully removed. The mystery suddenly resolved itself when I found the same structure embedded in the female genital duct (Fig. 8), proving that *Witica talis,* placed in the group Witicae close to *Hypognatha* and Cyrtarachneae by Simon (1895) and Roewer (1942), is in fact the male of *"Edricus" crassicauda,* placed in Cycloseae by the same two authors.

In examining all available males, I noted certain differences in the appendage of the embolus in males from Trinidad and some South American localities (Fig. 14). This different structure was found in females (Fig. 13) from the same areas, further proof that *Witica* males belong with females of *"Edricus,"* and also providing evidence that there are two species, the females of which look quite similar except for the contents of the genital duct.

Only one embolus tip was found on each side in each female duct, never two. Are they there to protect a male's sperm and prevent further mating by the female? Or might they be spermatophores with sperm inside the tips? Or do they just function to block the ducts? Only one or two males with broken emboli were in collections suggesting that males do not survive mating. Males with broken tips could not be determined to species.

The relationship and placement of the two species of *Witica* is uncertain. The male palpus lacks a median apophysis and terminal apophysis, but I expect this to be a secondary loss rather than a primitive absence, perhaps correlated with the minute size of the males. The female genitalia are unusual in being lightly sclerotized and lacking a scape and other projections; the epigynum resembles the epigynum of *Pronous.* The enormous difference in size of the sexes, the total length of females being more than 4.5 times that of the male, is found in some other orb-weaver genera, such as *Gasteracantha* and *Nephila* (the latter probably belonging to the family Tetragnathidae). Also, males of *Arachnura* are dwarf. The females of *Arachnura* have a tail, perhaps a synapomorphy. A male *Arachnura logio* Yaginuma from Japan examined also has a spherical abdomen with a sclerotized dorsal plate, but has a median apophysis and terminal apophysis in the palpus. The anterior median eyes of males and females of *Arachnura* are more projecting than those of *Witica.*



Figures 1–5. *Witica crassicauda* (Keyserling). 1. Female, legs removed. 2. Female abdomen from side. 3. Immature female. 4. Epigynum. 5. Male in same magnification as female.

Figures 6–7. *W. cayana* (Taczanowski). 6. Female. 7. Epigynum.

Size indicators: 1.0 mm, except Figures 4, 7, 0.1 mm.

Witica O.P.-Cambridge

Salassia Gétaz, 1893: 105. Type species by monotypy *S. tricuspis* Gétaz. (Name preoccupied by *Salassia* Folin, 1871, a mollusk.)

Witica O.P.-Cambridge, 1895: 160. Type species by monotypy *Witica talis* O.P.-Cambridge, 1895. NEW SYNONYMY.

Salassina Simon, 1895: 784. Type species by original designation and monotypy *S. crassicauda* Keyserling, 1865.

Physiola Simon, 1895: 875. Type species by original designation and monotypy. *P. nigrans* Simon, 1895. Synonymized with *Witica* by Simon, 1903.

Bion O.P.-Cambridge, 1898: 244, pl. 30. Type species by monotypy *B. brevis* O.P.-Cambridge, 1898. First synonymized with *Witica* by Simon, 1903.

SYNONYMY. Simon (1903: 1003) synonymized his *Physiola* published in 1895 with *Witica* published the same year, as an objective synonym. I do not know the month of the publications; Simon presumably did and *Witica* was published earlier. Thus since *Salassina* was published at the same time as *Physiola* it must also have been published after *Witica.*

F.P.-Cambridge (1904: 500) placed *Epeira crassicauda* described from a female into the genus *Edricus. Edricus* O.P.-Cambridge, 1890, has as type species *Edricus spinigerus,* 1890. *Edricus spinigerus* was described from a large male similar and perhaps congeneric with *Wagneriana tauricornis* F.P.-Cambridge, 1904. F.P.-Cambridge thought that *Edricus spinigerus* might be the unknown male of *Epeira crassicauda.* This proved to be an error.

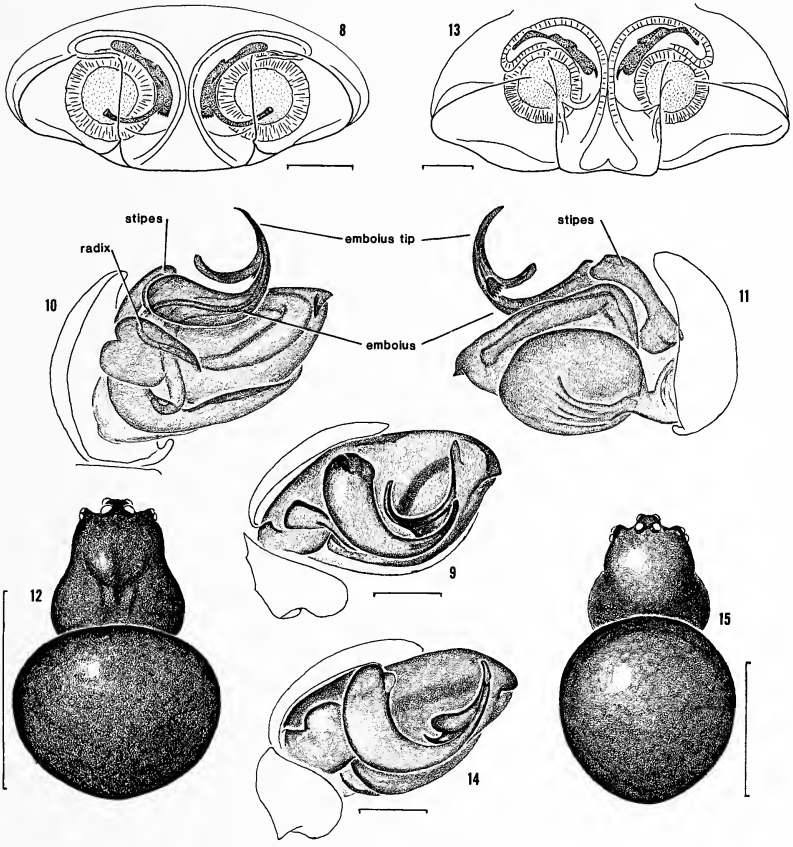
Diagnosis. Unlike the females of most Araneidae, the abdomen has a tail usually constricted at its base (Figs. 1, 6) and the epigynum is flat, lightly sclerotized, with a pair of depressions, (Figs. 4, 7). The male is separated from other Araneidae by the minute size, 1.5–1.9 mm (Fig. 5), sclerotized abdomen (Figs. 12, 15) and lacking a median apophysis and conductor of the palpus and having a large embolus tip which is transferred and plugs the female's ducts (Figs. 9, 14).

Description. Female. Carapace, sternum dark brown. Legs light with contrasting dark rings. Dorsum of abdomen black with variable white patches, venter black with a pair of small, white spots. Eyes subequal in size. Chelicerae with three teeth on anterior, three on posterior margin. First legs longer than fourth, second and fourth subequal, third shortest. Abdomen with a pair of anterior blunt spines and a tail of variable shape (Figs. 1, 6). The tail is constricted at its base and distally has three lobes.

Male. Carapace shiny brown, sternum, legs dark brown. Dorsum of abdomen shiny brown, venter black. Eyes subequal in size. Median eyes their diameter apart. Cheliceral teeth as in female, leg proportions as in female. Endites without tooth, palpal femora without tooth, first coxae without hook. Abdomen with round convex dorsal shield, sometimes wider than long or longer than wide.

Genitalia. Female epigynum has openings on each side of a flat septum in a depression (Figs. 4, 7), short connecting ducts lead into seminal receptacles (Figs. 8, 13).

The male palpus has a radix, embolus and, between them, a stipes. Median apophysis and conductor have been lost, probably secondarily (Figs. 10, 11). The embolus is large and has a distal



Figures 8–12. *Witica crassicauda* (Keyserling). 8. Epigynum cleared showing embolus tip. 9. Left male palpus. 10, 11. Male palpus expanded. 10. Mesal. 11. Lateral. 12. Male.

Figures 13–15. *W. cayana* (Taczanowski). 13. Epigynum cleared showing embolus tip. 14. Male palpus. 15. Male.

Size indicators: 0.1 mm, except Figures 12, 15, 1.0 mm.

curved tip which breaks off in mating and remains in the female connecting duct. Whether it serves only as a plug or perhaps is a spermatophore is not known.

Almost all females had one tip on each side in the epigynum, none were seen with two. Females appear to mate only once. Very few males with a missing tip are in collections. Apparently they do not survive mating.

Variation. Dorsal coloration of the abdomen of females of both species is quite variable, sometimes all white (in alcohol). The tail of the female abdomen may be shortened or blunt or long and is at times turned up.

Habits. The web of *Witica crassicauda* was found to be fairly common in a coffee plantation at about 1000 m altitude in Puerto Rico. It is built between trees about 1.5 meters apart, the hub 1.5 meters above the ground, the orb 30 to 35 cm horizontal diameter. The hub is open. There is a short vertical stabilimentum and the frame threads below the orb have whitish decorations, flattened threads as seen under a magnifying lens. The spider hangs in the hub, head down (Figure 17); there is no retreat. In Panama and Costa Rica the spider is common in low elevation forests; it does not make a stabilimentum, nor decorations on lines. The egg-sac, made in a vial, was fluffy, yellowish white, the size of the spider and contained about 200–250 lemon-yellow eggs.

Key to species

1 Females 2
_ Males 3

2(1) Median septum of epigynum as wide or wider than depression on each side (Figs. 4, 8); mated females show tubes, the ends of embolus tip on sides of septum (Figs. 4, 8); West Indies, Mexico to South America (Map)..... *crassicauda.*
Median septum of epigynum narrower than depressions (Figs. 7, 13); tip of embolus never visible in depressions. Trinidad, South America (Map) ..... *cayana.*

3(1) Base of tip of palpal embolus swollen and with spur (Fig. 14); Trinidad, South America (Map) ..... *cayana.*
___ Base of tip of palpal embolus a curved tube (Fig. 9); West Indies, Mexico to South America (Map) ..... *crassicauda.*

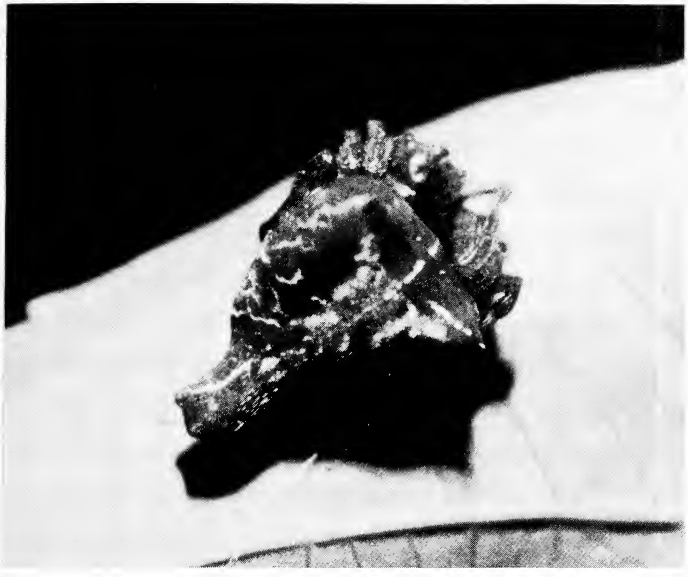


Figure 16. *Witica crassicauda.* Female on a leaf from Panama.

Witica crassicauda (Keyserling)
Figures 1–5, 8–12, 16, 17; Map

Epeira crassicauda Keyserling, 1865; 806, pl. 18, fig. 3, 4, ♀. Female specimen from New Granada (BMNH) examined.

Cyclosa crassicauda:—Keyserling, 1893: 270, pl. 14, fig. 200, ♀.

Witica talis O.P.-Cambridge, 1895: 160, pl. 16, fig. 13, ♂. Male lectotype from Teapa, Tabasco, Mexico (BMNH) here designated. Simon, 1903: 1003. Petrunkevitch, 1930: 337, figs. 225, 226, ♂. Roewer, 1942: 894. NEW SYNONYMY.

Salassia tricuspis Gétaz, 1893: 105. Female holotype from Uruca, Costa Rica (P. Biolley), lost. NEW SYNONYMY.

Salassina crassicauda:—Simon, 1895: 784, fig. 853, ♀.

Salassina tricuspis:—Simon, 1895: 784.

Physiola nigrans Simon, 1895: 876, figs. 938, 939, ♂. Lectotype male, two males, one immature and fragments of immatures paralectotypes from forest San Esteban, Venezuela (MNHN), here designated. First synonymized with *Witica* by Simon, 1903.

Bion brevis O.P.-Cambridge, 1898: 244, pl. 30, fig. 5, ♂. Male from Teapa, Tabasco, Mexico (BMNH), not examined. First synonymized with *Witica* by Simon, 1903.

Edricus crassicauda:—F.P.-Cambridge, 1904: 500, pl. 47, fig. 21, ♀. Roewer, 1942: 762

Edricus tricuspis:—F.P.-Cambridge, 1904: 500. Roewer, 1942: 762.

SYNONYMY. *Salassia tricuspis* is synonymized with *crassicauda* since the description fits the latter species with which Gétaz compares it. Also only one species is known from Costa Rica. The immature *Physiola nigrans* were thought by Simon to be adult females.

Female. Total length, 7.8 mm. Carapace, 3.2 mm long, 2.7 wide. First femur, 3.5 mm; patella and tibia, 3.7; metatarsus, 2.1; tarsus, 0.9. Second patella and tibia, 3.3 mm; third, 2.0; fourth, 3.3.

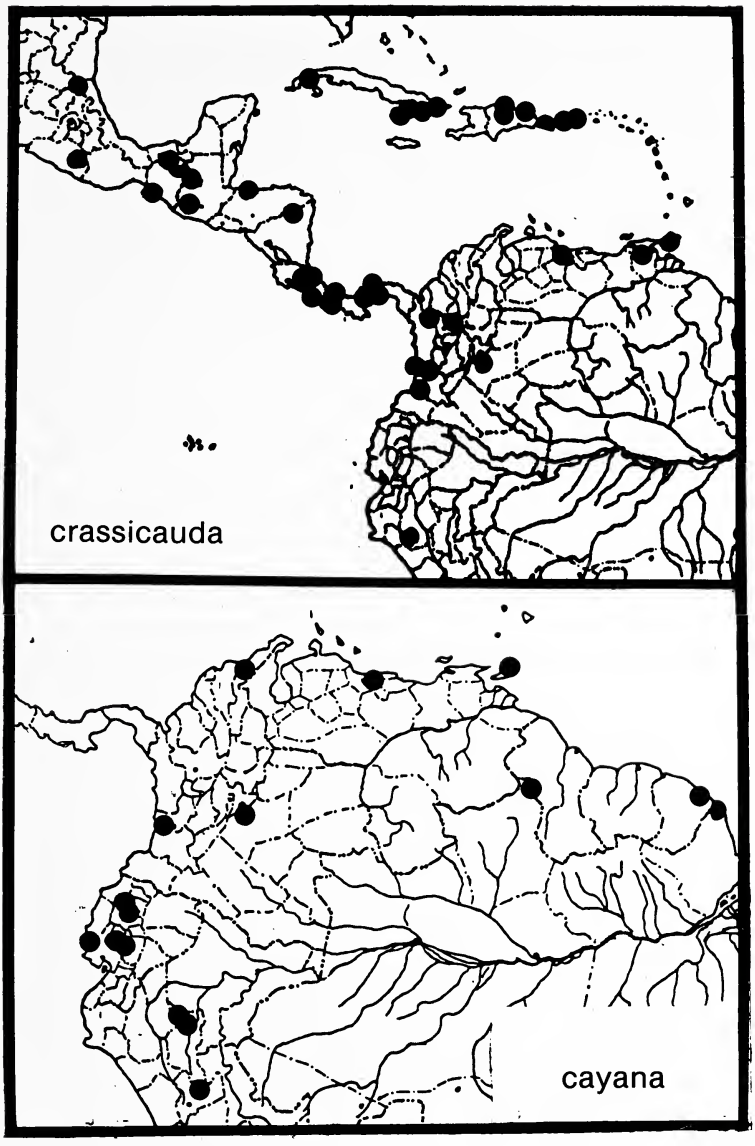
Male. Total length, 1.4 mm. Carapace, 0.9 mm long, 0.7 wide. First femur, 0.8 mm; patella and tibia, 0.8; metatarsus, 0.4; tarsus, 0.3. Second patella and tibia, 0.7 mm; third, 0.4; fourth, 0.6.

Diagnosis. The median septum of the epigynum is as wide or wider than the depressions on each side (Fig. 4); the male has a curved tube on the base of the embolus tip (Fig. 9).

Variation. Dorsal color, pattern and shape of abdomen of females are variable. Total length of female 6.5 to 12.0 mm, males, 1.4 to 1.7.

Habits and Distribution. Forests from Mexico to Venezuela and Peru, Greater Antilles (Map).

RECORDS. MEXICO *San Luis Potosí:* Huichihuayán, June 1941, immat. (H. Dybas, AMNH). *Guerrero:* S of Acahuizotla, 17 Nov. 1946, ♀(E. S. Ross, CAS). *Tabasco:* Teapa, 16 July 1947, ♂ (C. M. Goodnight, AMNH). *Chiapas:* San Quintín, Feb. 1966, ♀ (G. Ball, D. R. Whitehead, RL); Palenque ruins, 28 May 1980, ♀ (J. Coddington, MCZ). GUATEMALA Moca, 31 Aug. 1947, ♀ (C. P. Vaurie, AMNH). HONDURAS *Atlantida:* Lancetilla, July, 1929, ♀ (A. M. Chickering, MCZ). NICARAGUA Musawas, Waspuc Riv., Sept. 1955, ♀ (B. Malkin, AMNH). COSTA RICA *Heredia:* La Selva, 4 ♂ (MCZ). *Puntarenas:* Corcovado Natl. Park, 2 ♀ (MCZ). *Limón:* Río Reventazón, imm. (AMNH). *San José*: San José, 3 ♂ (AMNH). *Cartago:* Turrialba, dense jungle, ♀ (EPC). PANAMA *Bocas del Toro:* Río Changuinola, 2 ♀ (AMNH). *Chiriquí:* ♀ (AMNH). *Panamá*: Canal area, very common (MIUP, MCZ, CAS, AMNH).



Map. Distribution of *Witica* species.

CUBA. *Pinar del Río.* common (MCZ). *Oriente:* common (MCZ, AMNH). DOMINICAN REPUBLIC. Sánchez; Puerto Plata, S of Santiago (all MCZ). MONA ISL. (MCZ). PUERTO RICO. very common (MCZ, AMNH, JC)

TRINIDAD. ♀ (MCZ). VENEZUELA. *Monagas:* Caripito, Aug. 1942, ♀ (AMNH). *Carabobo:* San Esteban, 21 Jan. 1940, ♀ (CUC). COLOMBIA *Antioquia:* Mutatá, Dec. 1963, ♀ (MCZ); Remedios, 20 Dec. 1984; ♀ (MCZ). *Meta:* Caño Grande, Sept. 1944, ♀ (AMNH). *Valle:* Río Jamundi, 1000 m; Anchicayá; E. of Buenaventura, 3 ♀ (all MCZ). *Cauca:* Guapi, Aug. 1975, ♀ (W. Eberhard, MCZ). PERU. *Cajamarca:* Nanchoc, Caserío Bolívar, 30 April 1967, ♀ (C. Mazabel, AMNH).

Witica cayana (Taczanowski), new combination
Figures 6, 7, 13–15; Map.

Epeira cayana Taczanowski, 1873: 135, pl. 5, fig. 15, ♀. Female holotype from Cayenne, French Guiana (PAN). Specimens examined came from Uassa (Uaça, Amapa, Brazil) in the Taczanowski collection, PAN.

Female. Total length, 9.0 mm. Carapace, 3.1 mm long, 2.8 wide. First femur, 3.6 mm; patella and tibia, 4.0; metatarsus, 2.4; tarsus, 1.0. Second patella and tibia, 3.5 mm; third, 2.0; fourth, 3.6.

Male. Total length, 1.6 mm. Carapace, 1.0 mm long, 1.0 wide. First femur, 1.1 mm; patella and tibia, 1.1; metatarsus; 0.6; tarsus, 0.4. Second patella and tibia, 0.9 mm; third, 0.5; fourth, 0.8.

Diagnosis. The median septum of the epigynum is narrower than the depression on each side (Fig. 7). Base of embolus tip is a lobe (Fig. 14).

Variation. The color, pattern, and shape of the female abdomen are variable. Females vary 6.8 to 10.5 mm total length, males 1.4 to 1.6.

Habits and Distribution. Probably from forest, Trinidad and Venezuela to Peru (Map).

RECORDS. TRINIDAD 16 km from Arima, 27 Feb. 1959, ♂; Arima Rd, 29 Dec. 1945, ♂ (both A. M. Nadler, AMNH); Tucuche, 12 Nov. 1944, ♀ (R. H. Montgomery, AMNH). VENEZUELA *Aragua:* Rancho Grande, 1945, 1946, 4 ♀ (W. Beebe, AMNH). BRAZIL *Roraima:* Rio Irene, Aug. 1911, ♀ (AMNH). COLOMBIA *Magdalena:* San Pedro, 8 Feb. 1974, ♀ (J. A. Kochalka, IBNA). *Meta:* Villavicencio, 11 March 1955, 2 ♀ (E. I. Schlinger, E. S. Ross, CAS).

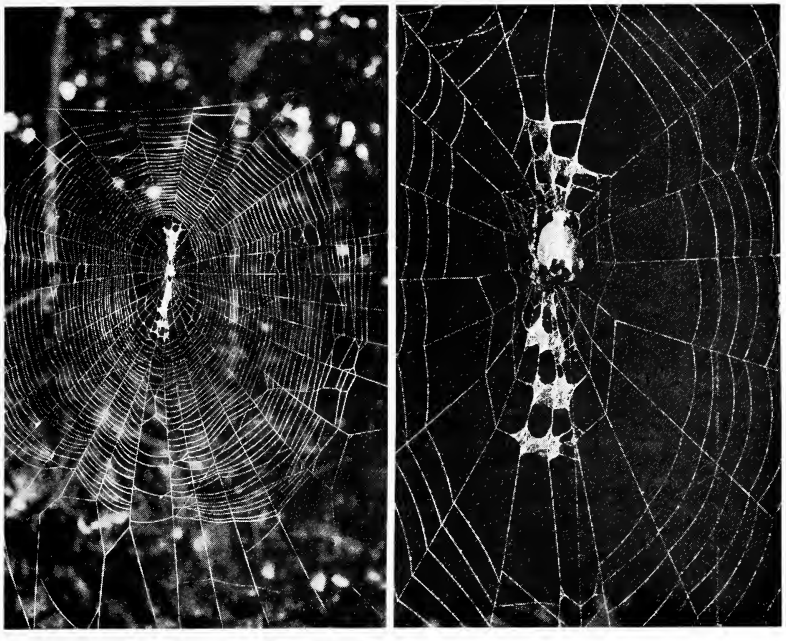


Figure 17. *Witica crassicauda.* Left: web of female in Puerto Rico, orb 32 cm horizontal diameter. Right: hub of another web with female. Webs dusted with corn starch.

ECUADOR *Pichincha:* Via Pto. Quito, km 113, 1984, 1985, 4 ♀ (L. Avilés, MECN); 16 km SE San Domingo Tinalandia, June, 1975, ♀, ♂ (S. and J. Peck, MCZ). *Guayas.* 16 km N Manglaralto, 30 Jan. 1955, 3 ♀ (E. I. Schlinger, E. S. Ross, CAS). *Los Ríos:* Juan Montalvo, March 1938, 3 ♀ (W. Clarke-Macintyre, AMNH). *Bolívar:* Balzapamba, 1938, 1939, 3 ♀, ♂ (W. Clarke-Macintyre, AMNH, MCZ). PERU *San Martín:* 20 km NE Moyobamba; SE Moyobamba; Ekin, E. of Tarapoto, 1947, 6 ♀ (all F. Woytkowski, AMNH). *Huánuco:* Monson Valley, Tingo María, 18 Dec 1954, ♀ (E. I. Schlinger, E. S. Ross, CAS).

Acknowledgements

National Science Foundation grant BSR 8312772 made the research and publication possible. L. R. Levi and W. P. Maddison have read the paper and made suggestions. Most specimens came

from the collections of the Museum of Comparative Zoology (MCZ); other collections used were those of the American Museum of Natural History (AMNH), Cornell University Collection (CUC) N. Platnick, curator; British Museum (Natural History), P. Hillyard (BMNH), California Academy of Sciences, W. J. Pulawski (CAS), Exline-Peck Collection, W. Peck (EPC), Museo Ecuatoriano de Ciencias Naturales, Quito, L. Avilés (MECN), Muséum National d'Histoire Naturelle, Paris, J. Heurtault, J. Kovoor (MNHN), J. Carico (JC), R. Leech (RL), Polska Akademia Nauk, Warszawa, W. Starega, A. Riedel, J. Proszynski (PAN), Inventario Biologico Nacional, Asunción, J. A. Kochalka (IBNA), Museo de Invertebrados, Universita de Panamá, D. Quintero A. (MIUP). T. Yaginuma loaned a male *Arachnura.*

Literature Cited

Cambridge, O. P.- 1890. Arachnida, Araneidea. **1**: 57–72 in Biologia Centrali-Americana. Zoologia, London.

_____. 1895. Arachnida, Araneidea. **1**: 145–160 in Biologia Centrali-Americana. Zoologia, London.

_____. 1898. Arachnida, Araneidea. **1**: 233–288 in Biologia Centrali-Americana. Zoologia, London.

Cambridge, F. P.- 1904. Arachnida, Araneidea. **2**: 465–545 in Biologia Centrali-Americana. Zoologia, London.

Gétaz, A. 1893. Fauna Arachnologica de Costa Rica. An. Inst. fis.- geogr. nac. Costa Rica **4**: 103–106.

Keyserling, E. 1865. Beiträge zur Kenntnis der Orbitelae. Verhandl. zool.-bot. Gesellsch. Wien, **15:** 799–856.

_____. 1893. Die Spinnen Amerikas, Nurnberg. **4**: 209–377.

Petrunkevitch, A. 1930. The spiders of Porto Rico. Trans. Connecticut Acad. Sci. **30**: 159–355.

Roewer, C. Fr. 1942. Katalog der Araneae, Bremen, vol. 1.

Simon, E. 1895. Histoire Naturelle des Araignées, Paris, **1**: 761–1084.

_____. 1903. Histoire Naturelle des Araignées, Paris. **2**: 669–1080.

Taczanowski, L. 1873. Les Aranéides de la Guyane française. Horae Soc. Entom. Rossicae **9**: 64–150.

AN EYELESS SUBTERRANEAN BEETLE (*PSEUDANOPHTHALMUS*) FROM A KENTUCKY COAL MINE (COLEOPTERA: CARABIDAE: TRECHINAE)*

By Thomas C. Barr, Jr.

School of Biological Sciences,
University of Kentucky
Lexington, Kentucky 40506

The trechine genus *Pseudanophthalmus* includes approximately 240 species from caves of the Appalachian valley, Mississippian plateaus, and Bluegrass and Central Basin regions of eastern United States. Although the model of cave trechine speciation which I have developed for this fauna (Barr, 1967a, 1968, 1981, 1985) requires a two-step process of 1) local diversification in deep soil and 2) subsequent isolation in nearby caves, the first stage was postulated on the basis of an abundant edaphobitic trechine fauna in Europe and elsewhere (see Jeannel, 1926–1930, for example). In eastern United States a single species of *Pseudanophthalmus* has been described from a non-cave habitat: *P. sylvaticus* occurs deep in the soil under large stones in mountain forests near Marlinton, West Virginia (Barr, 1967b).

Existing distributions of cave *Pseudanophthalmus* species strongly suggest an ancestral Pleistocene refugium in the mixed mesophytic forests of the Allegheny plateau (Barr, 1981, 1985). The distinctly different lineages occupying caves of the Appalachian valley to the east of the plateau and those of the Interior Low Plateaus to the west of the Alleghenies indicate substantial local differentiation prior to cave colonization (Barr, 1981); the geographic clustering of related species suggests vicariance among cave descendants of these locally differentiated edaphobites (Barr, 1965, 1981, 1985).

An integrated phylogeny of *Pseudanophthalmus* has thus far proven elusive, as though key pieces of a jigsaw puzzle were missing. Preliminary track analysis at the species group level thus shows a

Manuscript received by the editor December 15, 1985

void in the Allegheny plateau, with only the *gracilis* (east) and *inexpectatus* (west) groups clearly related by synapomorphic characters. The *engelhardti* group (s. str., see Barr, 1981) does track through the Allegheny plateau, but only via the Tennessee River gorge west of Chattanooga. The large, pubescent, riparian species of the *tenuis* group (IN, IL, KY) are superficially and ecologically similar to the species of the *grandis* group (chiefly eastern WV), but there are insufficient synapomorphies to provide substantive support to an hypothesis of taxonomic affinity (Barr, 1985). It is tempting to speculate that transitional species or species groups occupied the non-limestone terranes of the interior of the Allegheny plateau. If these transitional forms are extinct, no sound phylogeny of *Pseudanophthalmus* may be possible. No caves occur in the thick sequences of clastic rocks—sandstones, conglomerates, coals, and shales—in this region. But if ancestral edaphobitic beetles are hypothetically invoked throughout the Pleistocene to supply the caves on either side of the Alleghenies, why should they suddenly become extinct after Wisconsinan glaciation? Could some of these obligate soil inhabitants still survive in deep, forest floor soil of this region? The discovery of *P. sylvaticus* suggested that this could indeed be the case, but two decades have elapsed without further edaphobitic trechines being found.

Juberthie et al. (1980) demonstrated that "troglobitic" arthropods exist in the "milieu souterrain superficiel" of non-karst regions in southern France. At the interface between the soil mantle and the bedrock there are air-filled pockets—microcaverns—from which these authors have trapped several species of millipedes and beetles (including trechines) that are for all intents and purposes "troglobites," even in non-calcareous terranes. However, attempts to trap such organisms in eastern United States have met with failure. Suitable sites for trap insertion in France or Japan are in areas of fractured rock (C. Juberthie and S.-I. Uéno, pers. comm.), unlike the majority of karst regions in eastern United States. The traps are baited pitfall traps containing Galt's solution or equivalent; they are placed about 1 m below the surface, buried, and checked at intervals of 2–4 weeks.

On October 18, 1985, J. R. MacGregor and H. D. Bryan collected 2 female *Pseudanophthalmus* specimens in an abandoned coal mine

in Floyd County, eastern Kentucky. The mine portal, designated "D-104" in MacGregor's notes, is located at Bosco (= Hueysville), about 22 km SSW Prestonsburg. The beetles were found in a muddy spot on the mine floor under rocks.

These two females are identical with females of *Pseudanophthalmus hypolithos* (Barr, 1981: 83, figs. 28, 34), a species previously known only from Old Quarry Cave, in Pine Mountain, near Ashcamp, Pike County, Kentucky, 45 km SE of the Bosco mine. The *hypolithos* group, which includes 4 species from Pine Mountain, KY, and a single species (*P. praetermissus*) near the base of Cumberland Mountain in Scott County, VA, belongs to the *engelhardti* complex, a group of 55 largely Appalachian valley species arranged in 7 species groups (Barr, 1981). *Pseudanophthalmus hypolithos,* itself, is distinguished from other species of the group by quite deep elytral striae and convex elytral intervals, greatly reduced pubescence limited chiefly to sparse and very short rows on each elytral interval, and falciform aedeagal apex. The aedeagal character could not be checked, but based on my experience with species of the genus, the absence of non-genitalic differences is decisive; only 2/240 species are determined solely on male genitalic characters.

Previously I had considered Pine Mountain as a "karst island" within the Allegheny plateau; it is a fault block about 125 km long, extending from Elkhorn City, Kentucky, southwest to Campbell County, Tennessee, with a band of Newman limestone (Mississippian) exposed on its northwest face. To the extent that "troglobitic" *Pseudanophthalmus* species are collectable within the caves of Pine Mountain, this is still true after a fashion, but the discovery of *P. hypolithos* in a coal mine indicates that "caves" are a somewhat artificial concept in terranes where highly fractured rocks (shales, coals, conglomerates) exist, and that "troglobitic" trechines may occur over a wider area than is strictly delimited by karst terrane. The Bosco mine offers another sort of entry into the deep soil community, and the discovery of *P. hypolithos* there is a strong impetus to search for other edaphobitic trechines within the interior of the Allegheny plateau.

Acknowledgements

I thank John R. MacGregor for making these specimens available for study. This paper was supported in part by NSF DEB-8202339.

Literature Cited

Barr, Thomas C., Jr.

1965. The *Pseudanophthalmus* of the Appalachian valley (Coleoptera: Carabidae: Trechini). Amer. Midl. Nat. **73**: 41–72.

1967a. Observations on the ecology of caves. Amer. Nat. **101**: 475–492.

1967b. A new *Pseudanophthalmus* from an epigean environment in West Virginia (Coleoptera: Carabidae). Psyche **74**: 166–174.

1968. Cave ecology and the evolution of troglobites. Evolutionary Biology **2**: 45–102. Appleton-Century-Crofts, New York.

1981. *Pseudanophthalmus* from Appalachian caves (Coleoptera: Carabidae): the *engelhardti* complex. Brimleyana, no. **5**: 37–94.

1985. Pattern and process in speciation of trechine beetles in eastern North America (Coleoptera: Carabidae: Trechinae). *IN* G. E. Ball, ed., *Taxonomy, Phylogeny, and Zoogeography of Beetles and Ants.* Dordrecht, Netherlands: Dr. W. Junk Publishers.

Jeannel, René

1926–1930. Monographie des Trechinae: Morphologie comparée et distribution d'un groupe de Coléoptères. L'Abeille **32**: 221–550; **33**: 1–592; **34**: 59–122; **35**: 1–808.

Juberthie, C., B. Delay, and M. Bouillon

1980. Extension du milieu souterrain en zone non-calcaire: déscription d'un nouveau milieu et de son peuplement par les Coléoptères troglobies. Mém. Biospéol. **7**: 19–52.

BICONUS IN PERÚ, WITH NOTICE OF AN ENDEMIC SPECIES FROM THE COASTAL DESERT (HYMENOPTERA: ICHNEUMONIDAE).

By Charles C. Porter[1]
Department of Biological Sciences, Fordham University
Bronx, NY 10458

Introduction

Taxonomy and Relationships

Townes (1969:178–9) places *Biconus* in his Subtribe Ischnina *(Ischnus, Trachysphyrus* and allied mesostenine genera), where he considers it related to *Chromocryptus*[2], *Cryptopteryx,* and *Trachysphyrus. Biconus,* however, shows some features unapproached or rarely approximated by members of the preceding genera. These characters include absence of tyloids on the male flagellum, medially bituberculate clypeus, profoundly cleft female 4th tarsomere, and tendency for loss or reduction of the brachiella vein. I remain uncertain as to the affinities of *Biconus.* Comparative analysis of mesostenine genera in all parts of the world probably will be necessary to clarify this problem.

Collections

Specimens of *Biconus* have been or are to be deposited in the following institutional and personal collections.

CAMBRIDGE. Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

GAINESVILLE. Florida State Collection of Arthropods, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, P. O. Box 1269, 1911 SW 34th Street, Gainesville, FL 32602.

---

[1]Research Associate, Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, P.O. Box 1269, Gainesville FL 32602.

Manuscript received by the editor May 24, 1985

[2]Townes' concept of *Chromocryptus* includes the species of *Trachysphyrus (sensu* Porter 1967) in which the axillus vein is close to the anal margin of the hind wing.

LAWRENCE. Department of Entomology, Snow Entomological Museum, The University of Kansas, Lawrence, KS 66045.

PORTER. Collection of Charles C. Porter, 301 North 39th Street, McAllen, TX 78501.

TOWNES. American Entomological Institute, c/o Dr. Virendra Gupta, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, FL 32602.

Genus *BICONUS*

Biconus Townes, 1969. Mem. Amer. Ent. Inst. **12:** 178–9.
Type: *Biconus atroruber* Townes.

Fore wing 4.1–10.2mm long. Wings hyaline with dark brown blotches. Female flagellum long and slender, not flattened below apicad. Male flagellum without tyloids. Mandible moderately long with lower tooth almost as long as upper. Clypeus 1.5–2.0 as wide as long, moderately and asymmetrically convex or weakly and symmetrically convex in profile; its apical margin subtruncate to a little convex and usually with a pair of often inconspicuous median preapical tubercles or swellings. Malar space: 0.72–1.0 as long as basal width of mandible. Pronotum with epomia sharp but not prolonged much dorsad or ventrad of scrobe. Mesoscutum with notaulus sharp but fine, reaching more than 0.6 the length of mesoscutum; surface mat with delicate puncto-reticulation and very dense, short setae. Mesopleuron has no ridge on prepectus below. Hind coxa with a strong and polished subvertical groove externoventrally near base. Female tarsus with 4th segment very deeply bilobed at apex. Wing venation: areolet large, symmetrically pentagonal, intercubiti gently to moderately convergent dorsad, 2nd abscissa of radius 1.0–1.1 as long as 1st intercubitus; discocubitus broadly angled, ramellus well developed to vestigial; mediella definitely arched; axillus close to and paralleling anal margin of hind wing; brachiella sometimes short or absent. Propodeum with spiracle round to short-oval and with its apical trans-carina represented only by conspicuous ligulo-cuneate, ligulate, ligulo-conic or even conical cristae. First gastric tergite without a baso-lateral expansion; ventral longitudinal carina traceable but often weak or obsolete on postpetiole and sometimes faint also on petiole; dorsal carinae more or less suggested toward apex of petiole and on base of

postpetiole, sometimes absent. Second tergite mat, usually with fine and dense micro-reticulation but lacking discrete punctures and almost without setae, but sometimes with fine and dense short setae that originate in very tiny, inconspicuous punctures. Ovipositor 0.30–0.45 as long as fore wing; straight, moderately slender to rather stout; nodus weak but with a minute notch; ventral valve on tip with sharp, well spaced inclivously oblique ridges.

Biconus occurs at moderate elevations in the Andes of tropical South America from Ecuador to Bolivia. Many species inhabit montane wet forests. They are most often collected by sweeping undergrowth in areas with a flora characterized by tree ferns, a woody arborescent element rich in Myrtaceae and Lauraceae, and by strikingly diverse epiphytic bromeliads and orchids.

Biconus apoecus Porter (n. sp.) is the only species that frequents relatively arid habitats. It is found in semihumid valleys of the west Andean foothills along the Peruvian coast from near Lima north at least as far as Trujillo. These valleys doubtless were much wetter only 10,000 years ago during the most recent glacial maximum and even today support a relict cloud forest vegitation.

Key to Peruvian Species of *Biconus*

1. Flagellum uniformly dark; fore wing with a median and an apical brown area; mesosoma and gaster ferruginous with black on mesoscutum, tegula, and most of scutellum; mesopleuron mostly with delicate and irregular wrinkling; 2nd recurrent 0.7–0.8 as long as 1st abscissa of cubitus; male 1st flagellomere with many but sparse and inconspicuous linear whitish sensilla ..... *B. apoecus* n. sp.

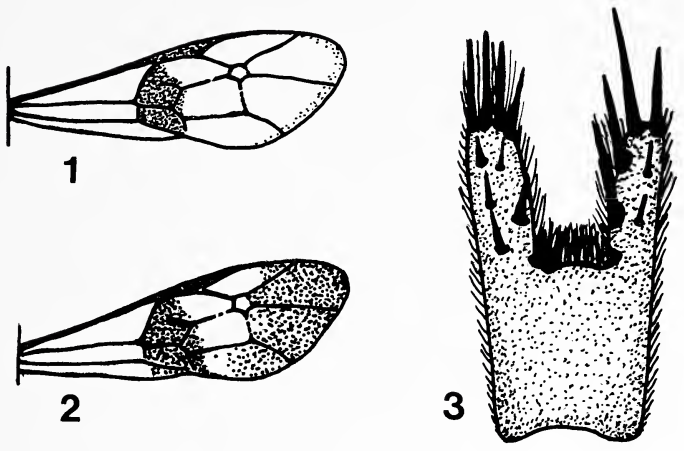
1.′ Flagellum with a white band; fore wing with a single median brown blotch; mesosoma and gaster brownish yellow to orange; mesopleuron with much sharp, horizontal wrinkling; 2nd recurrent 0.4–0.5 as long as 1st abscissa of cubitus; male 1st flagellomere with prominent and rather crowded linear white sensilla ..... 2. *B. subflavus* n. sp.

1. **Biconus apoecus** Porter, new species
(Fig. 2, cf. Fig. 4)

Female. *Color:* antenna black with some pale brown on scape; head black; mandible black except for dull brown subapically and

brownish white on dorsal margin; palpi light dusky brown; mesoscutum ferruginous with black on mesoscutum, tegula, and on most of scutellum; gaster ferruginous with weak dusky staining on last tergite; wings hyaline with a broad transverse median band occupying upper hind corner of median cell, basal 0.5 of discocubital cell, 2nd discoidal cell basad of ramellus, 1st brachial cell, base of 2nd brachial cell, and (more faintly) apex of anal cell as well as with a light brownish blotch that covers apical 0.3 of radial cell plus most of 3rd cubital cell, 3rd discoidal cell, and (more faintly) part of apical 0.2 of 2nd brachial cell; coxae ferruginous with blackish staining apicad or sometimes more extensively; trochantelli black with ferruginous staining, especially below; front femur black above and dull ferruginous below; mid femur black with dull ferruginous throughout, or at least in part, dorso-anteriorly; hind femur black with dull ferruginous staining basad, especially above; fore tibia dusky ferruginous; mid and hind tibiae black; tarsi black.

Length of fore wing: 7.8–9.3 mm. *First flagellomere:* 8.0 as long as deep at apex. *Clypeus:* with a pair of weak median preapical tubercles but only slightly convex on apical margin beneath tubercles; lateral margin broad and reflexed. *Malar space:* 0.94–1.0 as long as basal width of mandible. *Mesopleuron:* in large part with delicate and irregular wrinkling. *Wing venation:* radial cell 3.2–3.6 as long as wide; 2nd abscissa of radius 1.0 as long as 1st intercubitus; ramellus inserted at basal 0.4 of discocubitus; bulla of 1st abscissa of cubitus 0.2–0.3 as long as entire vein; 2nd recurrent 0.7–0.8 as long as 1st abscissa of cubitus; brachiella reaches 0.4–0.6 the distance to wing margin. *Propodeum:* rather short and high; basal face steeply declivous, 0.9 as long as the almost vertical apical face; cristae large, stout, conspicuously projecting, broadly ligulate, about 0.3 as long as apical face of propodeum; surface on basal face distad of basal trans-carina with at least some strong and oblique wrinkles laterad but mesad more or less extensively more finely sculptured and on apical face strongly trans-rugose laterad but mesad often less strongly wrinkled or mostly smooth and shining. *First gastric tergite:* postpetiole short and weakly expanded apicad, 1.4–1.7 as wide apically as long from spiracle to apex; ventro-lateral carina traceable throughout, sharp apicad on petiole and on postpetiole; dorso-lateral carina sharp on postpetiole but gradually becoming weaker basad on petiole; dorsal carinae traceable (not sharp) toward apex



Figs. 1–3. *Biconus.* Fig. 1, *Biconus subflavus.* Paratype. Fore wing, showing color pattern. Fig. 2, *Biconus apoecus.* Paratype. Fore wing, showing color pattern. Fig. 3, *Biconus subflavus.* Paratype. Hind tarsomere 4, showing very deep median apical emargination.

of petiole and on base of postpetiole; surface of postpetiole shining with delicate microreticulation that is strongest laterad and fades out toward apex. *Gaster:* stout fusiform. *Ovipositor:* sheathed portion 0.35–0.44 as long as fore wing; tip 0.25–0.32 as high at notch as long from notch to apex.

MALE. differs from female as follows: *Color:* scape brownish white below and laterally; mandible more broadly pale brown to whitish; palpi dull white; tegula partly reddish; front femur ferruginous with dusky staining above; mid femur extensively ferruginous with irregular dusky staining below and apico-dorsally; hind femur ferruginous on much of basal 0.3 (especially above) and mostly black apically.

Length of fore wing: 9.8–10.2 mm. *First flagellomere:* 5.5–5.7 as long as deep at apex; on apical 0.6 with numerous but inconspicuous and well separated whitish linear sensilla. *Clypeus:* median preapical tubercles stronger than in female; apical margin gently

bisinuate beneath tubercles; profile weakly convex with highest point near middle. *Malar space:* 0.72–0.77 as long as basal width of mandible. *Wing venation:* brachiella sometimes reaches less than 0.5 the distance to wing margin. *Propodeum:* much as in female but a little more elongate: basal face about 1.2 as long as the steeply sloping apical face; cristae a little broader and stouter than in female, ligulo-cuneate, very prominent; surface apicad of basal trans-carina duller than in female with delicate reticulation and more or less extensive moderately strong oblique wrinkling. *First gastric tergite:* postpetiole elongate, parallel-sided, 1.0–1.2 as wide apically as long from spiracle to apex; dorsal carinae obsolete. *Gaster:* rather strongly depressed.

Type Material. Holotype ♀: PERÚ, Lima Province, San Gerónimo, nr. Chosica, 1–5–VII-1976, C. Porter, C. Calmbacher. Paratypes: 5♀, 2♂, same date as holotype. Holotype in Florida State Collection of Arthropods. Paratypes in Florida State Collection of Arthropods (1♀, 1♂), Collection of Henry K. Townes (1♀), Museum of Comparative Zoology (1♀), University of Kansas Collection (1♀), Collection of Charles C. Porter (1♀, 1♂).

Relationships. This species appears closely related to the Ecuadorian *Biconus atroruber* (Townes 1969:178–79), with which it agrees in being ferruginous with black markings and in having a median and an apical dark area on the fore wing. It differs from *B. atroruber* by its entirely dark (instead of white banded) flagellum; in having the mesosomatic black markings restricted to the mesoscutum, tegula, and scutellum (instead of extending also onto the pronotum, subalarum, mesosternum, upper metapleuron, and propodeum); in its mostly ferruginous (instead of mostly black) coxae; by its strongly (instead of finely) wrinkled apical propodeal face; and in having the female propodeal cristae ligulate (instead of subconic and decurved slightly at apex) and the male cristae ligulocuneate (instead of high and cone-like).

Biconus apoecus may be distinguished from the central Peruvian *B. subflavus* Porter by characters given in the key, as well as by its shorter first flagellomere, more weakly tuberculate and apically less convex clypeus, longer female malar space, shorter and higher propodeum, and less definitely micro-reticulate postpetiole.

Field notes. San Gerónimo, Perú, the type locality, is on the lower west Andean slopes in the valley of the Santa Eulalia River

not far from Chosica and Lima. The valley is well watered and enjoys a warm microclimate because of its sheltered situation at an altitude just above the point normally reached by nightly Pacific coastal fogs during the coolest months of the year. Natural vegetation at San Gerónimo includes *Acacia, Salix, Schinus, Baccharis, Tessaria* and many other Andean, Chaqueñan, and Holarctic genera. Much of the valley is covered by orchards of chirimoyas, citrus, apples, pears, and bananas. Irrigation ditches that traverse the orchards permit growth of a lush herbaceous understory from which *Biconus apoecus* and other ichneumonids may be swept.

SPECIFIC NAME. From the Greek adjective *apoecus,* "away from home, abroad".

2. **Biconus subflavus** Porter, new species
(Fig. 1, 3).

FEMALE. *Color:* antenna black with some dark brown on scape and with a white annulus (extensively brown to black stained below) on flagellomeres 3 (near apex) or 4–9 or 10 (basally); head black with dark brown on clypeus and lighter brown on mandibular condyle; mandible blackish with much brown to pale brown, especially subapicad and dorsad; palpi dull white; mesosoma pale brownish yellow, a little darker and more orangish dorsally; gaster pale brownish to orangish yellow; wings hyaline with a single brown blotch that covers basal 0.4 of discocubital cell, extends a little into base of 2nd discoidal cell, and reaches below across most of 1st brachial cell; legs pale brownish yellow with some darker staining, especially on apices of trochantelli and bases of femora, as well as with 4th and 5th tarsomeres largely dark brown.

Length of fore wing: 8.1–10.1 mm. *First flagellomere:* 9.3–9.7 as long as deep at apex. *Clypeus:* with a pair of broad but weak median subapical swellings, apical margin moderately convex medially beneath swellings, lateral margin not reflexed. *Malar space:* 0.80–0.87 as long as basal width of mandible. *Mesopleuron:* largely with fine but sharp horizontally biased wrinkling. *Lower metapleuron:* with strong, obliquely biased wrinkling. *Wing venation:* radial cell 3.4–4.1 as long as wide; 2nd abscissa of radius 1.0–1.1 as long as 1st intercubitus; ramellus inserted near basal 0.3 of discocubitus;

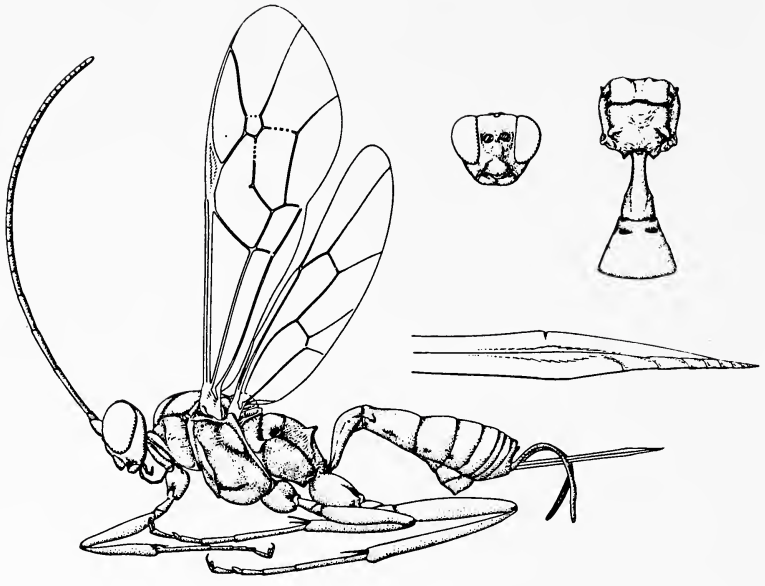


Fig. 4. *Biconus atroruber.* Female in lateral view, head in anterior view, propodeum and first 2 gastric tergites in dorsal view, and ovipositor tip in lateral view. (From Townes, 1969:431).

bulla of 1st abscissa of cubitus 0.1–0.2 as long as entire vein; 2nd recurrent 0.4–0.5 as long as 1st abscissa of cubitus; brachiella reaches 0.4 or less the distance to wing margin (sometimes almost absent). *Propodeum:* moderately elongate; basal face gently declivous, 0.70–0.85 as long as the almost vertical apical face; cristae stout, conspicuously projecting, conico-ligulate; surface on basal face distad of basal trans-carina mat with uniformly strong reticulate wrinkling and on apical face with even stronger wrinkling. *First gastric tergite:* postpetiole short but rather strongly expanded apicad, 1.3–1.5 as wide apically as long from spiracle to apex; ventral longitudinal carina sometimes obsolete on petiole; dorsal carinae weakly suggested above spiracles; surface of postpetiole strongly shining with faint microreticulation. *Gaster:* moderately elongate fusiform. *Ovipositor:* sheathed portion 0.35–0.41 as long as

fore wing; tip 0.23–0.26 as high at notch as long from notch to apex.

MALE. differs from female as follows: *Color:* white flagellar annulus reaches from apex of 8th to base of 13th segment.

Length of fore wing: 9.6 mm. *First flagellomere:* 6.0 as long as deep at apex; except near base with numerous and prominent, rather crowded, linear white sensilla. *Clypeus:* tubercles more distinct and apical margin more strongly convex than in female; profile rather strongly convex with highest point a little distad of middle. *Malar space:* 0.82 as long as basal width of mandible. *Wing venation:* radial cell 3.1 as long as wide; brachiella absent. *Propodeum:* basal face long but more strongly declivous than in female, 0.85 as long as the almost vertical apical face; cristae a little stouter and more conical than in female; surface distad of basal trans-carina more coarsely and regularly wrinkled than in female. *First gastric tergite:* postpetiole slender and parallel-sided, 0.91 as wide apically as long from spiracle to apex. *Gaster:* cylindric, not depressed.

TYPE MATERIAL. Holotype ♀: PERÚ, Cuzco Province, Machu Picchu, 1900 m, 4–19–IX-1964, C. Porter. Paratypes: 2♀, 1♂, same data as holotype. Holotype in Florida State Collection of Arthropods. Paratypes in Florida State Collection of Arthropods (1♀, 1♂), and Collection of Charles C. Porter (1♀).

RELATIONSHIPS. As indicated previously, this species differs substantially in many points of color and structure from the other described *Biconus*. It may be recognized at a glance by its orangish ground color and unifasciate fore wing.

FIELD NOTES. The type locality is in cool tropical cloud forest. Specimens of *Biconus subflavus* were swept from lush undergrowth at the forest edge along the railway tracks which parallel the Urubamba River.

SPECIFIC NAME. From the Latin adjective *subflavus,* "somewhat yellow".

ACKNOWLEDGMENTS

This research was done under my National Science Foundation Grants BSR-8313444 and DEB-75-22426. It was also subsidized in 1974, '75, and '79 by grants from the Committee for Research and Exploration of the National Geographic Society, which made possible fieldwork in the Peruvian Coastal Desert.

I am also indebted to the Florida State Department of Agriculture and Consumer Services, from whose Division of Plant Industry I have received generous support mediated primarily by Dr. Howard V. Weems, Jr, Dr. Lionel A. Stange, and Mr. Harold A. Denmark.

Summary

Biconus is a "trachysphyroid" mesostenine found in Andean wet forests and in the Coastal Desert of Perú. It is recognizable by its brown blotched wings; lack of tyloids on male flagellum; mat mesoscutum; arched mediella; anally situate axillus; sharply grooved hind coxal base; deeply cleft female 4th tarsomere; nearly round propodeal spiracle; unarmed petiolar base; and subligulate to conical, prominent (but never spiniform) propodeal cristae. There are 3 species: *B. atroruber* Townes from Ecuador (white band on flagellum, body ferruginous and black, fore wing with 2 brown areas); *B. apoecus* n. sp. from the Peruvian Coastal Desert (similar to *B. atroruber* but without a white flagellar band); and *B. subflavus* from Peruvian montane forest (mesosoma and gaster orangish, fore wing with 1 brown blotch).

Literature Cited

Porter, C.

1967. A revision of the South American species of *Trachysphyrus*. Mem. Amer. Ent. Inst. **10:** 1–386.

Townes, H. K.

1969. Genera of Ichneumonidae, Part 2: Gelinae. Mem. Amer. Ent. Inst. **12:** 1–537.

A SYNONYMIC GENERIC CHECKLIST OF THE EUMENINAE (HYMENOPTERA: VESPIDAE)*

By James M. Carpenter

Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138

The present work is an extension of a similar list in Carpenter (1983), and arose from preparatory work for a phylogenetic analysis of nearctic potter wasp genera (Carpenter and Cumming, 1985). The most recent available world list of genera is over 80 years old (Dalla Torre, 1904), and fully 57% of the genus-group names currently used in the Eumeninae have been proposed since Bluethgen (1938; for more detail on the history of eumenine taxonomy see Carpenter and Cumming, 1985). The following checklist includes all the currently recognized genera of Eumeninae *sensu* Carpenter (1981), with their synonyms and subgenera. The arrangement is alphabetical based upon most recent usage, and incorporates the decisions pertaining to eumenine generic nomenclature rendered by the International Commission on Zoological Nomenclature (ICZN) in Opinions 747 (1965), 893 (1970) and 1363 (1985). The format is basically that of Krombein *et al.* (1979). The original citations are followed by the type species designation. Synonyms, and subgenera with their citations and synonyms, are listed after this; the nominotypical subgenera are not listed separately. Where two dates are listed, the first is the true date of publication, whereas the date listed in parentheses is that printed on the paper. A misspelling is indicated by (!), and quotation marks are used for incorrect names. No effort has been made to list all misspellings; only those occurring in works considered important. Nomenclatural changes derive from ongoing work on a catalog of neotropical eumeninae (with J. van der Vecht) and a generic reclassification of this group: *Neodiscoelius* Stange is a junior objective synonym of *Protodiscoelius* Dalla Torre (new synonymy); *Cephalastor* Soika is raised to genus (new status), and its type species, *Hypalastoroides depressus* Soika, synonymized with *Odynerus relativus* Fox. In addition, type species are designated for

Manuscript received by the editor July 14, 1985

Stenolabus Schulthess (junior subjective synonym of *Ischnocoelia* Perkins) and *Nesodynerus* Perkins. These designations conform to standard generic concepts. Two *nomina dubia* and four *nomina nuda* not otherwise placed are listed separately at the end of this paper.

It is not to be inferred that I agree with this classification, but considering the current confusion in eumenine taxonomy, a catalog of the available names and their status is a prerequisite for rectifying the situation.

Abispa Mitchell, 1838, Three. Exped. Interior Eastern Australia 1:104 (as subgenus of *Vespa* L.). Type species *Abispa australiana* Mitchell, 1838. Monotypic.

Abisba (!) Ashmead, 1902, Can. Ent. **34**: 208 (gives as type *Vespa ephippium* Fabricius, 1775, originally not included).

Monerebia Saussure, 1852, Ét. Fam. Vesp. **1**: 98. Type species *Odynerus splendidus* Guerin, 1838. Designated by Vecht, 1960, Nova Guinea Zool. **6**: 92.

Monorebia (!) Smith, 1857, Cat. Hym. Brit. Mus. **5**: 42.

Monerobia (!) Bridwell, 1919, Proc. Hawaiian Entomol. Soc. **4**: 120.

subg. **Parabispa** Vecht, 1960, Nova Guinea Zool. **10**(6): 93, 94. Type species *Pterochilus eximius* Smith, 1865. Original designation.

Acanthodynerus Gusenleitner, 1969, Boll. Mus. Civ. Ven. **19**: 13. Type species *Acanthodynerus giordanii* Gusenleitner, 1969. Original designation.

Acarepipona Soika, 1985 (1983), Boll. Mus. Civ. Ven. **34**: 189, 192. Type species *Acarepipona insolita* Soika, 1985. Original designation.

Acarodynerus Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 64, 146. Type species *Odynerus clypeatus* Saussure, 1853. Original designation.

Acarozumia Bequaert, 1921, Rev. Zool. Afr. **9**: 249 (as subgenus of *Montezumia* Saussure). Type species *Nortonia amaliae* Saussure, 1869. Monotypic.

Afrepipona Soika, 1965, Boll. Soc. Entomol. Ital. **95**: 46. Type species *Odynerus macrocephalus* Gribodo, 1894. Original designation.

Afreumenes Bequaert, 1926, Ann. S. Afr. Mus. **23**: 486 (as subgenus of *Eumenes* Latreille). Type species *Eumenes melanosoma* Saussure, 1852. Monotypic.

Afrodynerus Soika, 1934, Ann. Mus. Civ. Genova **57**: 25, 26 (as subgenus of *Odynerus* Latreille). Type species *Odynerus monstruosus* Soika, 1934. Monotypic.

Afroxanthodynerus Soika, 1979, Boll. Mus. Civ. Ven. **30**: 243. Type species *Afroxanthodynerus nigeriensis* Soika, 1979. Original designation.

Alastor Lepeletier, 1841, Hist. Nat. Ins. Hym. **2**: 668. Type species *Alastor atropos* Lepeletier, 1841. Designated by Ashmead, 1902, Can. Ent. 34: 210.

Antalastor Saussure, 1856, Ét. Fam. Vesp. 3: 328 (as division of *Alastor*). Type species *Alastor atropos* Lepeletier, 1841. Designated by ICZN, Opinion 893, 1970: 187.

Eualastor Dalla Torre, 1904, Gen. Ins. **19**: 60. New name.

Belalastor Atanassov, 1967, Izv. Zool. Inst. Sof. **23**: 167 (as subgenus of *Alastor*). Type species *Alastor bulgaricus* Atanassov, 1967 (= *Alastor seidenstueckeri* Bluethgen, 1956). Original designation.

subg. **Parastalor** Bluethgen, 1939, Veroeff. Dts. Kolon. Ueberssee-Mus. Bremen **2**: 264. Type species *Alastor algeriensis* Bluethgen, 1939. Monotypic.

subg. **Megalastor** Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 169. Type species *Alastor savignyi* Saussure, 1852. Original designation.

Alastoroides Saussure, 1856, Ét. Fam. Vesp. 3: 327 (as subgenus of *Alastor* Lepeletier). Type species *Alastor clotho* Lepeletier, 1841. Designated by Ashmead, 1902, Can. Ent. **34**: 210.

Paralastoroides Saussure, 1856, Ét. Fam. Vesp. 3: 328 (as division of subgenus *Alastoroides* Saussure of genus *Alastor* Lepeletier). Type species *Alastor clotho* Lepeletier, 1841. Monotypic. Rejected by ICZN, Opinion 893, 1970: 188, in favor of *Alastoroides.*

Alasteroides (!) Zavattari, 1912, Arch. Naturgesch. **78A**(4): 255.

Alastorynerus Bluethgen, 1938 (1937), Konowia 16: 294. Type species *Odynerus ludendorffi* Dusmet, 1917. Original designation.

Alastodynerus (!) Parker, 1966, Misc. Publ. Entomol. Soc. Am. **5**: 157.

Alfieria Soika, 1934, Bull. Soc. Entomol. Egypte 18: 436. Type species *Eumenes anomalus* Zavattari, 1909. Original designation.

Alferia (!) Neave, 1939, Nomencl. Zool. **1**: 111.

Allodynerus Bluethgen, 1938 (1937), Konowia **16**: 280 (as subgenus Saussure, 1853. Original designation. (as *"Lionotus floricola* Sauss. 1852").

Delphinaloides Moczar, 1937, Folia Ent. Hung. 3: 15. Invalid; no type designated. Made available by Bohart, 1951, *in* Muesebeck *et al.,* Cat. Hym. N. Am.: 888; with type species *Odynerus delphinalis* Giraud, 1866.

Allorhynchium Vecht, 1963, Zool. Verh. (Leiden) **60**: 57, 58. Type species *Vespa argentata* Fabricius, 1804. Original designation.

Alphamenes Vecht, 1977, Proc. K. Ned. Akad. Wet. (C) **80**: 238, 242. Type species *Eumenes campanulatus* Fabricius, 1804. Original designation.

Alphamenes Bertoni, 1934, Rev. Soc. Cient. Paraguary **3**: 109 (as subgenus of *Eumenes* Latreille). Invalid; no type designated.

Ancistroceroides Saussure, 1855, Et. Fam. Vesp. **3**: 221 (as division of subgenus *Ancistrocerus* Wesmael of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187. Type species *Odynerus alastoroides* Saussure, 1853. Designated by ICZN, Opinion 1363, 1985: 353.

Ancistrocerus Wesmael, 1836, Bull. Acad. Sci. Bruxelles **3**: 45 (as subgenus of *Odynerus* Latreille). Type species *Vespa parietum* L., 1758. Designated by Girard, 1879, Traité Élém. Ent. **2**(2): 900.

Aucistrocerus (!) Rudow, 1876, Arch. Ver. Freunde Naturgesch. Mecklenb. **30**: 197.

Ancystrocerus (!) Dalla Torre, 1894, Cat. Hym. **9**: 50 ff.

Euancistrocerus Dalla Torre, 1904, Gen. Ins. **19**: 36. New name.

Antamenes Soika, 1958 (1957), Boll. Mus. Civ. Ven. **10**: 214. Type species *Odynerus flavocinctus* Smith, 1857 (= *Odynerus vernalis* Saussure, 1853). Original designation.

subg. **Australochilus** Soika, 1962 (1961), Boll. Mus. Civ. Ven.

14: 184. Invalid; no type designated. Made available by Soika, 1974 (1973), Boll. Mus. Civ. Ven. **24**: 53; with type species *Odynerus citreocinctus* Saussure, 1867.

Antepipona Saussure, 1855, Et. Fam. Vesp. **3**: 244 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus silaos* Saussure, 1853. Designated by ICZN, Opinion 893, 1970: 187.

Antepiponus Saussure, 1875, Smiths. Misc. Coll. **254**: xxxv, 361. Emendation.

Antepipone (!) Dalla Torre, 1894, Cat. Hym. **9**: 50, 96.

Mehelyella Moczar, 1937, Folia Ent. Hung. 3: 16. Invalid; no type designated. Made available by Bohart, 1951, *in* Muesebeck *et al.,* Cat. Hym. N. Am.: 888; with type species *Odynerus parvulus* Lepeletier, 1841.

Odontodynerus Bluethgen, 1938 (1937), Konowia **16**: 280 (as subgenus of "*Euodynerus* Bluethgen"). Type species *Odynerus orbitalis* Herrich-Schaeffer, 1841. Original designation.

Dichodynerus Bluethgen, 1938. Dts. Entomol. Z.: 444. Type species *Odynerus vagabundus* Dalla Torre, 1889. Original designation (as "*Lionotus vagus* Radoszkowsi (= *vagabundus* Dalla Torre nom. nov.)").

Metastenancistrocerus Bluethgen, 1938, Dts. Entomol. Z.: 460. Error for *Dichodynerus; cf.* Bluethgen, 1939, Veroeff. Dts. Kolon. Uebersee-Mus. Bremen **2**: 246.

Anterhynchium Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève **17**: 205 (as division of *Rhynchium* Spinola). Type species *Rygchium synagroides* Saussure, 1852. Designated by Vecht, 1963, Zool. Verh. (Leiden) **60**: 73.

Anterrhynchium (!) Dalla Torre, 1904, Gen. Ins. **19**: 33.

subg. **Dirhynchium** Vecht, 1963, Zool. Verh. (Leiden) **60**: 74, 77. Type species *Ancistrocerus flavopunctatus* Smith, 1852. Original designation.

Antezumia Saussure, 1875, Smiths. Misc. Coll. **254**: 113 (as division of *Montzumia* Saussure). Type species *Montezumia chalybea* Saussure, 1855. Designated by Bequaert, 1921, Rev. Zool. Afric. **9**: 240.

Pinta Zavattari, 1912, Arch. Naturgesch. **78A**(4): 6, 151. Type species *Montezumia chalybea* Saussure, 1855. Original designation.

Antodynerus Saussure, 1855, Ét. Fam. Vesp. **3**: 242, 287 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Vespa flavescens* Fabricius, 1775 ("*Odynerus punctum* (Fabricius)" *sensu* Saussure, 1853). Designated by ICZN, Opinion 893, 1970: 187.

Kalliepipona Soika, 1952 (1951), Riv. Biol. Colon. **11**: 81 (as subgenus of *Pseudepipona* Saussure). Type species *Rhynchium radiale* Saussure, 1855 (as *"Odynerus radialis"*). Original designation.

Pseudokalliepipona Soika, 1955, Ann. Mus. R. Congo Belge Tervuren, Zool. **36**: 366 (as subgenus of *Pseudepipona* Saussure, 1853. Type species *Odynerus bellatulus* Saussure, 1853. Original designation.

Parepipona Soika, 1957, Brit. Mus. (Nat. Hist.) Exped. S. W. Arabia **1**(31): 477 (as subgenus of *Pseudepipona* Saussure). Type species *Rhynchium radiale* Saussure, 1855 (as *"Odynerus radialis"*). Original designation.

Anthodynerus (!) Soika, 1961, South Afr. Anim. Life **8**: 445.

Araucodynerus Willink, 1968 (1967), Acta Zool. Lilloana **22**: 143, 152. Type species *Odynerus tuberculatus* Saussure, 1853. Original designation.

Argentozethus Stange, 1979, Acta Zool. Lilloana **35**: 729. Type species *Argentozethus willinki* Stange, 1979. Original designation.

Asiodynerus Kurzenko, 1977, Ins. Mongolia **5**: 557. Type species *Odynerus lucifer* Kostylev, 1937. Original designation.

Astalor Schulthess, 1925, Konowia **4**: 59, 207 (as subgenus of *Alastor* Lepeletier). Type species *Astalor maidli* Schulthess, 1925. Monotypic.

Astator (!) Schulthess, 1925, Konowia **4**: 208.

Australodynerus Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 65, 114. Type species *Odynerus pusillus* Saussure, 1856. Original designation.

Australozethus Soika, 1969, Boll. Mus. Civ. Ven. **19**: 27, 29. Type species *Australozethus tasmaniensis* Soika, 1969. Original designation.

Bidentodynerus Soika, 1977 (1976), Mem. Soc. Entomol. Ital. **55**: 177. Type species *Odynerus bicolor* Saussure, 1855. Original designation.

Brachymenes Soika, 1961, Verh. XI Int. Kongr. Entomol. Wien: 243. Type species *Eumenes wagnerianus* Saussure, 1875. Original designation.

Brachyodynerus Bluethgen, 1938, Dts. Entomol. Z.: 450, 459. Type species *Odynerus magnificus* Morawitz, 1867. Original designation.

Brachypipona Gusenleitner, 1967, Polskie Pismo Ent. **37**: 671. Type species *Pseudepipona schmidti* Gusenleitner, 1967. Original designation.

Desertodynerus Kurzenko, 1977, Zool. Zh. **56**(6): 957. Type species *Desertodynerus gratus* Kurzenko, 1977. Original designation.

Calligaster Saussure, 1852, Ét. Fam. Vesp. **1**: 22. Type species *Calligaster cyanopterus* Saussure, 1852. Designated by Ashmead, 1902, Can. Ent. **34**: 205.

Cephalastor Soika, 1982 (1981), Boll. Mus. Civ. Ven. **32**: 33, 40 (as subgenus of *Hypalastoroides* Saussure); NEW STATUS. Type species *Hypalastoroides depressus* Soika, 1969 (= *Odynerus relativus* Fox, 1902; NEW SYNONYMY). Original designation.

Cephalochilus Bluethgen, 1939, Mitt. Entomol. Ges. Halle **17**: 13. Type species *Pterochilus grandis* Lepeletier, 1841 (= *Vespa labiata* Fabricius 1798). Original designation.

Cephalodynerus Parker, 1965, Ann. Entomol. Soc. Am. **58**: 364. Type species *Cephalodynerus unicornis* Parker, 1965. Original designation.

Chelodynerus Perkins, 1902, Trans. Entomol. Soc. Lond.: 136. Type species *Odynerus chelifer* Perkins, 1899. Monotypic.

Chlorodynerus Bluethgen, 1951, Boll. Soc. Entomol. Ital. **81**: 67, 75 (as subgenus of "*Euodynerus* Bluethgen"). Type species *Odynerus chloroticus* Spinola, 1838. Original designation.

Coeleumenes Vecht, 1963, Zool. Verh. (Leiden) **60**: 16, 45. Type species *Montezumia impavida* Bingham, 1897. Original designation.

Ctenochilus Saussure, 1856, Ét. Fam. Vesp. **3:** 323 (as division of *Pterochilus* (!) Klug). Type species *Epipona pilipalpa* Spinola, 1851. Monotypic.

Cuyodynerus Willink, 1968 (1967), Acta Zool. Lilloana **22**: 143, 151. Type species *Odynerus cuyanus* Brèthes, 1903. Original designation.

Cyphodynerus Vecht, 1971, Entomol. Ber. (Amst.) **31**: 127. Type species *Odynerus dimidiatus* Spinola, 1838 (*non Odynerus dimidiatus* Guérin, 1834; = *Odynerus canaliculatus* Saussure, 1855). Original designation.

Cyphomenes Soika, 1978, Boll. Mus. Civ. Ven. **29**: 13, 210. Type species *Eumenes infernalis* Saussure, 1875. Original designation.

Cyrtolabulus Vecht, 1969, Entomol. Ber. (Amst.) **29**: 1. New name for *Cyrtolabus* Vecht.

Cyrtolabus Vecht, 1963, Zool. Verh. (Leiden) **60**: 11 *non Cyrtolabus* Voss, 1925. Type species *Cyrtolabus suavis* Vecht, 1963. Original designation.

Delta Saussure, 1855, Ét. Fam. Vesp. **3**: 130, 143 (as division of *Eumenes* Latreille). Type species *Vespa maxillosa* DeGeer, 1773 (= *Vespa emarginata* L., 1758). Designated by Bequaert, 1925, Bull. Brook. Entomol. Soc. **20**: 137 (as *"Sphex maxillosus"*).

Phi Saussure, 1855, Ét. Fam. Vesp. **3**: 132 (as division of *Eumenes* Latreille) *non Phi* Saussure, 1854. Type species *Vespa arcuata* Fabricius, 1775. Designated by Bequaert, 1926, Ann. S. Afr. Mus. **23**: 487.

Erinys Zirngiebl, 1953, Mitt. Pollichia (3)**1**: 173 *non Erinys* Rye, 1876. Type species *Vespa unguiculata* Villers, 1789. Monotypic.

Deuterodiscoelius Dalla Torre, 1904, Gen. Ins. **19**: 18 (as division of *Discoelius* Latreille). Type species *Odynerus verrauxii* Saussure, 1852. Monotypic.

Pseudozethus Perkins, 1914, Pr. Zool. Soc. Lond.: 622. Type species *Pseudozethus australensis* Perkins, 1914 (= *Odynerus verrauxii* Saussure, 1852). Monotypic.

Diemodynerus Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 65, 141. Type species *Odynerus diemensis* Saussure, 1853. Original designation.

Discoelius Latreille, 1809, Gen. Crust. Ins. **4**: 140 (as subgenus of *Eumenes* Latreille). Type species *Vespa zonalis* Panzer, 1801. Monotypic.

Discaelius (!) Leach, 1815, Edinburgh Encyc. **9**: 153.

Discaelias (!) Leach, 1815, Edinburgh Encyc. **9**: 166.

Dicoelius (!) Haliday, 1836, Trans. Linn. Soc. Lond. **17**: 325.

Discollius (!) Froggatt, 1892, Proc. Linn. Soc. N.S.W. **2**(7): 226.

Tritodiscoelius Dalla Torre, 1904, Gen. Ins. **19**: 18 (as division of *Discoelius*). Type species *Vespa zonalis* Panzer, 1801.

Designated by Bequaert and Ruiz, 1942 (1940), Rev. Chil. Hist. Nat. **64**: 217.

Dolichodynerus Bohart, 1939, Pan-Pac. Ent. **15:** 97, 101 (as subgenus of *Odynerus* Latreille). Type species *Odynerus turgiceps* Bohart, 1939. Original designation.

Ectopioglossa Perkins, 1912, Ann. Mag. Nat. Hist. (8)**9**: 118. Type species *Ectopioglossa australensis* Perkins, 1912 (*non Eumenes australensis* Meade-Waldo, 1910; = *Ectopioglossa polita australensis* (Meade-Waldo)). Monotypic.

Elimus Saussure, 1852, Ét. Fam. Vesp. **1**: 7. Type species *Elimus australis* Saussure, 1852. Monotypic.

Elisella Soika, 1974 (1972), Boll. Mus. Civ. Ven. **25**: 109, 132. Type species *Ellisella linae* Soika, 1974. Original designation.

Epiodynerus Soika, 1958 (1957), Boll. Mus. Civ. Ven. **10**: 195 (as subgenus of *Pseudepipona* Saussure). Type species *Odynerus alecto* Lepeletier, 1841. Original designation.

Epsilon Saussure, 1855, Ét. Fam. Vesp. **3**: 229 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus dyscherus* Saussure, 1852. Designated by ICZN, Opinion 893, 1970: 187.

Eudiscoelius Friese, 1904, Z. Hym. Dipt. **4**: 16. Type species *Eudiscoelius metallicus* Friese, 1904. Monotypic.

Euchalcomenes Turner, 1908, Trans. Entomol. Soc. Lond.: 90. Type species *Euchalcomenes gilberti* Turner, 1908. Original designation.

Eumenes Latreille, 1802, Hist. Nat. Crust. Ins. **3**: 360. Type species *Vespa coarctata* L., 1758. Designated by Latreille, 1810, Consid. Gén. Crust. Arach. Ins.: 328.

Alpha Saussure, 1855, Ét. Fam. Vesp. **3**: 128, 137 (as division of *Eumenes*) *non Alpha* Saussure, 1854. Type species *Vespa coarctata* L., 1758. Designated by Bequaert, 1926, Ann. S. Afr. Mus. **23**: 435.

Eumenis Kriechbaumer, 1879, Entomol. Nachr. **5**: 57. Emendation.

Eumenidion Schulthess, 1913, Soc. Entomol. **28**: 2 (as subgenus). Type species *Vespa coarctata* L., 1758. Original designation.

Eumenidium (!) Sharp, 1915, Zool. Rec. Ins. 1913: 275.

subg. **Zeteumenoides** Soika, 1972, Boll. Soc. Entomol. Ital.

104: 110 (as genus). Type species *Eumenes filiformis* Saussure, 1855 (= *Eumenes versicolor filiformis*). Original designation.

Eumenidiopsis Soika, 1939 (1938), Mem. Soc. Entomol. Ital. **17**: 87 (as subgenus of *Leptomenes* Soika). Type species *Leptomenes subtilis* Soika, 1939. Original designation.

Eumicrodynerus Gusenleitner, 1972, Nachrbl. Bayer. Ent. **21**: 74 (as subgenus of *Microdynerus* Thomson). Type species *Leptomenes europaeus* Soika, 1942. Original designation.

Euodynerus Dalla Torre, 1904, Gen. Ins. **19**: 38 (as section of subgenus *"Lionotus"* Thomson of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187. Type species *Vespa dantici* Rossi, 1790. Designated by Bluethgen, 1938 (1937), Konowia **16**: 277.

subg. **Pareuodynerus** Bluethgen, 1938 (1937), Konowia **16**: 278 (as subgenus of *"Euodynerus* Bluethgen"). Type species *Vespa notata* Jurine, 1807. Original designation.

Leionotus Saussure, 1851, Ét. Fam. Vesp. **1**: 121 (as subgenus of *Odynerus* Latreille), *non Leionotus* Kirby and Spence, 1828. Type species *Odynerus foraminatus* Saussure, 1853. Designated by Bohart, 1951, *in* Muesebeck *et al.,* Cat. Hym. N. Am.: 887.

Lionotus (!) Thomson, 1874, Opusc. Ent. 2: 85, *non Lionotus* Agassiz, 1846.

Lejonotus (!) Costa, 1882, Atti. R. Acad. Sci. Fis. Mat. Napoli **9**: 37.

Eustenancistrocerus Bluethgen, 1938, Dts. Entomol. Z.: 443, 460 (as subgenus of *"Stenancistrocerus* Saussure" *sensu* Bluethgen, 1938). Type species *Odynerus blanchardianus* Saussure, 1855. Original designation.

subg. **Hemistenancistrocerus** Bluethgen, 1938, Dts. Entomol. Z.: 443, 459 (as subgenus of *"Stenancistrocerus* Saussure" *sensu* Bluethgen, 1938). Type species *Leptochilus parvulus* Saussure, 1853 (*non Odynerus parvulus* Herrich-Schaeffer, 1938; = *Odynerus pharao* Saussure, 1863). Original designation.

subg. **Parastenancistrocerus** Bluethgen, 1938, Dts. Entomol. Z.: 444, 460 (as subgenus of *"Stenancistrocerus* Saussure" *sensu* Bluethgen, 1938). Type species *Odynerus transitorius* Morawitz, 1867. Original designation.

Flammodynerus Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 65, 124. Type species *Odynerus subalaris* Saussure, 1855. Original designation.

Gamma Zavattari, 1912, Arch. Naturgesch. **78A**(4): 85 (as division of *Eumenes* Latreille). Type species *Pachymenes ventricosa* Saussure, 1852. Designated by Bequaert, 1926, Ann. S. Afr. Mus. **23**: 486.

Gastrodynerus Bohart, 1984, Pan-Pac. Ent. **60**: 12. Type species *Stenodynerus vanduzeei* Bohart, 1948. Original designation.

Gioiella Soika, 1985 (1983), Boll. Mus. Civ. Venezia **34**: 30, 155. Type species *Odynerus katonai* Schulthess, 1913. Original designation.

Gribodia Zavattari, 1912, Arch. Naturgesch. **78A**(4): 161. Type species *Monobia cavifrons* Gribodo, 1891 (= *Odynerus confluentus* Smith, 1857). Original designation.

Gymnomerus Bluethgen, 1938 (1937), Konowia **16**: 286 (as subgenus of "*Hoplomerus* (Westwood) Agassiz" *sensu* Bluethgen, 1938). Type species *Odynerus laevipes* Shuckard, 1837. Original designation.

Hemipterochilus Ferton, 1909 (1908), Ann. Soc. Entomol. Fr. **77**: 572 (as subgenus of *Pterocheilus* Klug). Type species *Odynerus terricola* Mocsary, 1883 (= *Hemipterochilus bembeciformis terricola*). Monotypic.

Pseudopterochilus Kostylev, 1940, Bull. Soc. Nat. Moscou, Biol. (N.S.) **49**: 153. Invalid; no type designated. Made available by Vecht, 1972, *in* Vecht and Fischer, Hym. Cat. **8**: 19; with type species *Odynerus bembeciformis* Morawitz, 1867.

Hypalastoroides Saussure, 1856, Ét. Fam. Vesp. **3**: 328 (as division of subgenus *Alastoroides* Saussure of genus *Alastor* Lepeletier; validated by ICZN, Opinion 893, 1970: 187). Type species *Alastor brasiliensis* Saussure, 1856. Monotypic.

Hypalastor Saussure, 1856, Ét. Fam. Vesp. **3**: 328 (as division of subgenus *Alastor* of genus *Alastor* Lepeletier; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus angulicollis* Spinola, 1851. Designated by ICZN, Opinion 893, 1970: 187. Rejected by Soika, 1960 (1958) Boll. Mus. Civ. Ven. **11**: 35, acting as first reviser, in favor of *Hypalastoroides.*

Hypalasteroides (!) Zavattari, 1912, Arch. Naturgesch. **78A**(4): 253.

subg. **Larastoroides** Soika, 1982 (1981), Boll. Mus. Civ. Ven. **32**: 33, 40. Type species *Hypalastoroides costaricensis* Soika, 1960. Original designation.

subg. **Ortalastoroides** Soika, 1982 (1981), Boll. Mus. Civ. Ven. **32**: 34, 56. Type species *Alastor singularis* Saussure, 1852. Original designation.

Ortastoroides (!) Soika, 1982 (1981), Boll. Mus. Civ. Ven. **32:** 57.

Hypancistrocerus Saussure, 1855, Ét. Fam. Vesp. **3**: 222 (as division of subgenus *Ancistrocerus* Wesmael of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus advena* Saussure, 1855. Monotypic.

Hypancistroceroides (!) Saussure, 1856, Ét. Fam. Vesp. 3, Table des Matières: 8.

Hypancystrocerus (!) Dalla Torre, 1894, Cat. Hym. **9**: 50.

Hypodynerus Saussure, 1855, Ét. Fam. Vesp. **3**: 225 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus humeralis* Haliday, 1836. Designated by Bequaert and Ruiz, 1943 (1941), Rev. Chil. Hist. Nat. **45**: 69.

Hypodernus (!) Cameron, 1908, Trans. Am. Entomol. Soc. **34**: 199.

Incodynerus Willink, 1968 (1967), Acta Zool. Lilloana **22**: 143, 148. Type species *Odynerus romandinus* Saussure, 1853. Original designation.

Ischnocoelia Perkins, 1908, Proc. Hawaiian Entomol. Soc. **2**: 28, 32. Type species *Ischnocoelia xanthochroma* Perkins, 1908. Monotypic.

Stenolabus Schulthess, 1910, Dts. Entomol. Z.: 189. Type species *Stenolabus fulvus* Schulthess, 1910. By present designation.

Ischnogasteroides Magretti, 1884 (1883), Boll. Soc. Entomol. Ital. **15:** 251; 1884, Ann. Mus. Civ. Stor. Nat. Genova **21**: 603. Type species *Ischnogasteroides flavus* Magretti, 1884 (= *Ischnogasteroides leptogaster flavus*). Monotypic.

Jucancistrocerus Bluethgen, 1938, Dts. Entomol. Z.: 442, 460 (as subgenus of *"Stenancistrocerus* Saussure" *sensu* Bluethgen, 1938). Type species *Odynerus jucundus* Mocsary, 1883. Original designation.

Iucancistrocerus (!) Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 174.

subg. **Eremodynerus** Bluethgen, 1939, Veroeff. Dts. Kolon. Uebersee-Mus. Bremen **2**: 257 (as genus). Type species *Odynerus saharensis* Soika, 1934. Original designation.

Katamenes Meade-Waldo, 1910, Ann. Mag. Nat. Hist. (8)**5**: 46. Type species *Katamenes watsoni* Meade-Waldo, 1910. Monotypic.

Knemodynerus Bluethgen, 1940, Entomol. Tidskr. **61**:43 (as subgenus of "*Euodynerus* Bluethgen"). Type species *Odynerus excellens* Pérez, 1907. Original designation.

Labochilus Bluethgen, 1939, Mitt. Entomol. Ges. Halle **17**: 12. Type species *Pterochilus linguarius* Saunders, 1905. Monotypic.

Leptopterocheilus Soika, 1953 (1952), Bull. Soc. Sci. Nat. Phys. Maroc. **32**: 262. Type species *Pterochilus linguarius* Saunders, 1905. Original designation.

Labus Saussure, 1867, Zool. Novara 2, Hym.: 3. Type species *Labus spiniger* Saussure, 1867. Designated by Bingham, 1897, Fauna Brit. India Hym. **1**: 348.

Laevimenes Soika, 1978, Boll. Mus. Civ. Ven. **29**: 11, 359. Type species *Eumènes laevigatus* Brèthes, 1906. Original designation.

Leptochiloides Bohart, 1940, Ann. Entomol. Soc. Am. **33**: 165. Type species *Leptochiloides utahensis* Bohart, 1940. Original designation.

Leptochilus Saussure, 1853, Ét. Fam. Vesp. **1**: 233. Type species *Pterochilus mauritanicus* Lepeletier, 1841. Designated by Ashmead, 1902, Can. Ent. **34**: 209 (as "*mauritianus*"!).

Zendalia Robertson, 1928, Flowers and Insects: 12. Type species *Odynerus zendaloides* Robertson, 1928 (= *Leptochilus republicanus* Dalla Torre, 1889). Designated by Bohart, 1951, *in* Muesebeck *et al,* Cat. Hym. N. Am.: 897.

subg. **Euleptochilus** Bluethgen, 1943, *in* Berland, Bull. Mus. Hist. Nat. Paris (2)**15**: 316. Type species *Odynerus oraniensis* Lepeletier, 1841. Original designation.

subg. **Lionotulus** Bluethgen, 1938 (1937), Konowia **16**: 276. Type species *Odynerus alpestris* Saussure, 1855. Original designation.

subg. **Neoleptochilus** Bluethgen, 1961, Abh. Dts. Akad. Wiss.

Berl. (2): 66, 100. Type species "*Leptochilus medanae* (Gribodo i.l.) André" (= *Odynerus medanae* Gribodo, 1886). Original designation.

subg. **Sarochilus** Gusenleitner, 1970, Isr. J. Entomol. **5**: 57. Type species *Leptochilus alterego* Gusenleitner, 1970. Original designation.

Leptodynerus Bluethgen, 1938, Dts. Entomol., Z.: 448, 457. Type species *Leptodynerus biskrensis* Bluethgen, 1938. Original designation.

Leptomenes Soika, 1939 (1938), Mem. Soc. Entomol. Ital. **17**: 87. Type species *Pachymenes congensis* Bequaert, 1918 (= *Odynerus eumenoides* Smith, 1857). Original designation.

Leptomenoides Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 64, 171. Type species *Leptomenoides placidior* Soika, 1962. Original designation.

Leptomicrodynerus Soika, 1985, Lavori Soc. Ven. Sc. Nat. **10**: 37. Type species *Leptomicrodynerus tieshengi* Soika, 1985. Original designation.

Leucodynerus Bohart, 1982, J. Kans. Entomol. Soc. **55**: 442. Type species *Odynerus congressus* Viereck, 1908. Original designation.

Macrocalymma Perkins, 1908, Proc. Hawaiian Entomol. Soc. **2**: 28, 31. Type species *Macrocalymma smithianum* Perkins, 1908. Monotypic.

Maricopodynerus Viereck, 1908, Trans. Am. Entomol. Soc. **33**: 397 (as subgenus of *Odynerus* Latreille). Type species *Odynerus maricoporum* Viereck, 1908. Monotypic.

Micreumenes Ashmead, 1902, Can. Ent. **34**: 208. Type species *Micreumenes currei* Ashmead, 1902 (in key). Monotypic.

Smithia Saussure, 1855, Rev. Mag. Zool. **7**: 371 *non Smithia* Edwards and Haime, 1851. Type species *Smithia natalensis* Saussure, 1855. Monotypic.

Hymenosmithia Dalla Torre, 1904, Gen. Ins. **19**: 61. New name for *Smithia* Saussure.

Microdynerus Thomson, 1874, Hym. Scand. **3**: 58. Type species *Odynerus exilis* Herrich-Schaeffer, 1839. Designated by Jones, 1937, Entomol. Mon. Mag. **73**: 15.

subg. **Pseudomicrodynerus** Bluethgen, 1938 (1937), Konowia 16: 276. Type species *Odynerus parvulus* Herrich-Schaeffer, 1838. Original designation.

Pachymicrodynerus Bluethgen, 1938, Dts. Entomol.: 447, 455 (as subgenus of *Pseudomicrodynerus*). Type species *Pseudomicrodynerus eurasius* Bluethgen, 1938. Original designation.

Pseudomycrodynerus (!) Gusenleitner, 1977, Linz. Biol. Beitr. **9**: 138.

Minixi Soika, 1978, Boll. Mus. Civ. Ven. **29:** 14, 367. Type species *Eumenes mexicanus* Saussure, 1857. Original designation.

Mitrodynerus Vecht, 1981, Proc. K. Ned. Akad. Wet. (C) **84**: 444. Type species *Mitrodynerus vitripennis* Vecht, 1981. Monotypic.

Monobia Saussure, 1852, Ét. Fam. Vesp. **1**: 94. Type species *Vespa quadridens* L., 1763. Designated by Ashmead, 1902, Can. Ent. **34**: 210.

Triarthra Dalla Torre, 1904, Gen. Ins. **19**: 28 (as group of *Monobia*), *non Triarthra* Ehrenberg, 1832. Type species *Odynerus cyanipennis* Guérin, 1830. Designated by Bequaert, 1940, Rev. Entomol. **11**: 822.

Tetrathra Dalla Torre, 1904, Gen. Ins. **19**: 28. Type species *Vespa quadridens* L., 1763. Designated by Bequaert, 1940, Rev. Entomol. **11**: 822.

Tetrarthra (!) Bequaert, 1940, Rev. Entomol. **11**: 822.

Monodynerus Gusenleitner, 1982, Entomofauna **3**: 279. Type species *Monodynerus insimilis* Gusenleitner, 1982. Original designation.

Montezumia Saussure, 1852, Ét. fam. Vesp. **1**: 87. Type species *Montezumia rufidentata* Saussure, 1852 (= *Odynerus azurescens* Spinola, 1851). Designated by Ashmead, 1902, Can. Ent. **34**: 207.

Alpha Saussure, 1855, Ét. Fam. Vesp. **3**: 160 (as division of *Montezumia*), *non Alpha* Saussure, 1854. Type species *Montezumia rufidentata* Saussure, 1952 (= *Odynerus azurescens* Spinola, 1851). Designated by Bohart, 1951, *in* Muesebeck *et al.,* Cat. Hym. N. Am.: 885.

Beta Saussure, 1855, Ét. Fam. Vesp. **3**: 162 (as division of *Montezumia*). Type species *Montezumia morosa* Saussure, 1852. Designated by Bequaert, 1921, Rev. Zool. Afric. **9**: 240.

Metazumia Saussure, 1875, Smiths. Misc. Coll. **254**: 114 (as division of *Montezumia*). Type species *Montezumia huas-*

teca Saussure, 1857. Designated by Bequaert, 1921, Rev. Zool. Afric. **9**: 240.

Eumontezumia Dalla Torre, 1904, Gen. Ins. **19**: 27. New name.

Nesodynerus Perkins, 1901, Entomol. Mon. Mag. **37**: 267. Type species *Odynerus rudolphi* Dalla Torre, 1889. By present designation.

Nortozumia Vecht, 1937, Treubia **16**: 263. Type species *Zethus rufofemoratus* Cameron, 1903. Original designation.

Odynerus Latreille, 1802, Hist. Nat. Crust. Ins. **3**: 362. Type species *Vespa spinipes* L., 1758. Designated by Shuckard, 1837, Mag. Nat. Hist. (N. S.) **1**: 494.

Odynera Illiger, 1807, Magaz. Insektenk. **6**: 196. Emendation.

Epipone Kirby and Spence, 1815, Introd. Entomol. 1: 340, *non* "epipone" Latreille 1802, a vernacular name. Type species *Vespa spinipes* L., 1758. Monotypic.

Oplopus Wesmael, 1836, Bull. Acad. Sci. Bruxelles **3**: 45 (as subgenus of *Odynerus*), *non Oplopus* Laporte, 1832. Type species *Vespa spinipes* L., 1758. Designated by Girard, 1879, Traité Élém. Ent. **2**(2): 902.

Oplomerus Westwood, 1840, Intro. Mod. Classif. Ins. 2(Synopsis): 84. New name for *Oplopus* Wesmael; *non Oplomerus* Dejean, 1833, a *nomen nudum.*

Hoplomerus Agassiz, 1846, Nomencl. Zool. Index Univ.: 185. Emendation of *Oplomerus* Westwood.

Hoplopus Agassiz, 1846, Nomencl. Zool. Index Univ.: 186. Emendation of *Oplopus* Wesmael, *non Hoplopus* D'Orbigny, 1838.

Epiponus Saussure, 1875, Smiths. Misc. Coll. **254**: 360 (as subgenus of *Odynerus* Latreille). Emendation of *"Epipona* Shuckard" *sensu* Saussure, 1855, an incorrect spelling of *Epipone* Kirby and Spence.

Hoplonus (!) Dalla Torre, 1889, Ent. Almanach.: 11.

Euepipona Dalla Torre, 1904, Gen. Ins. 19: 39. New name for *Epiponus* Saussure. Type species *Vespa spinipes* L., 1758. Designated by Richards, 1937, Gen. Names Br. Ins. **5**: 128.

subg. **Allogymnomerus** Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 174 (as subgenus of *Hoplomerus* Westwood). Type species *Odynerus consobrinus* Dufour, 1839. Original designation.

subg. **Monoplomerus** Bluethgen, 1941, Arch Naturgesch. (N. F.) **10**: 308 (as subgenus of *Hoplomerus* Westwood). Type species *Hoplomerus caroli* Morawitz, 1885. Original designation.

subg. **Spinicoxa** Bluethgen, 1938 (1937), Konowia **16**: 285 (as subgenus of "*Hoplomerus* (Westwood) Agassiz" *sensu* Bluethgen, 1938). Type species *Vespa reniformis* Gmelin, 1790. Original designation.

Omicroides Soika, 1935, Ann. Mus. Civ. Genova **57**: 129 (as subgenus of *Eumenes* Latreille). Type species *Eumenes singularis* Smith, 1857. Original designation.

Omicron Saussure, 1855, Ét. Fam. Vesp. **3**: 133, 148 (as division of *Eumenes* Latreille). Type species *Zethus* ? *globicollis* Spinola, 1841. Designated by Bequaert, 1926, Ann. S. Afr. Mus. **23**: 486.

Beta Saussure, 1875, Smiths. Misc. Coll. **254**: 88 (as division of *Eumenes* Latreille) *non Beta* Saussure, 1855. Type species *Eumenes nortonianus* Saussure, 1875. Designated by Bequaert, 1926, Ann. S. Afr. Mus. **23**: 486.

Amphimenes Bertoni, 1923, Rev. Soc. Cient. Paraguay **1**: 53, *non Amphimenes* Bates, 1873. Type species *Eumenes totonacus* Saussure, 1875. Monotypic.

Onychopterocheilus Bluethgen, 1955, Mitt. Muench. Ges. **44/45**: 407 (as subgenus of *Pterocheilus*). Type species *Odynerus daw* Dusmet, 1903. Original designation.

Orancistrocerus Vecht, 1963, Zool. Verh. (Leiden) **60**: 58, 99. Type species *Odynerus drewseni* Saussure, 1857. Original designation.

Oreumenes Bequaert, 1926, Ann. S. Afr. Mus. 23: 488 (as subgenus of *Eumenes* Latreille). Type species *Eumenes harmandi* Pérez, 1905 (= *Eumenes decoratus* Smith, 1852). Original designation.

Oreumenoides Soika, 1961, Verh. XI Int. Kongr. Entomol. Wien: 245. Type species *Eumenes edwardsi* Saussure, 1852. Original designation.

Ovodynerus Soika, 1985 (1983), Boll. Mus. Civ. Ven. **34**: 31, 130. Type species *Odynerus capicola* Meade Waldo, 1915. Original designation.

Pachodynerus Saussure, 1870, Rev. Mag. Zool. **22**: 56 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; vali-

dated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus californicus* Saussure, 1870. Designated by Bohart, 1951, *in* Muesebeck *et al.,* Cat. Hym. N. Am.: 892.

Pachyodynerus (!) Dalla Torre, 1894, Cat. Hym. **9**: 82.

Monobiella Ashmead, 1900, Trans. Entomol. Soc. Lond.: 312 (as genus). Type species *Vespa atrata* Fabricius, 1798. Monotypic.

Pachyodernus (!) Cameron, 1908, Trans. Am. Entomol. Soc. **34**: 199.

Pachycoelius Soika, 1969, Boll. Mus. Civ. Ven. **19**: 28, 54. Type species *Pachycoelius brevicornis* Soika, 1969. Original designation.

Pachymenes Saussure, 1852, Ét. Fam. Vesp. **1:** 73. Type species *Pachymenes sericea* Saussure, 1852. Designated by Ashmead, 1902, Can. Ent. **34**: 208.

Pachimenes (!) Saussure, 1855, Ét. Fam. Vesp. **3**: 153.

Pachyminixi Soika, 1978, Boll. Mus. Civ. Ven. **29**: 14, 387. Type species *Eumenes sumichrasti* Saussure, 1875. Original designation.

Parachilus Soika, 1961 (1960), Atti Soc. Ital. Sci. Nat. **99**: 389, 392. Type species *Pterochilus capensis* Saussure, 1854. Original designation.

Paragymnomerus Bluethgen, 1938 (1937), Konowia **16**: 286 (as subgenus of *"Hoplomerus* (Westwood) Agassiz" *sensu* Bluethgen, 1938). Type species *Odynerus spiricornis* Spinola, 1808. Original designation.

Paralastor Saussure, 1856, Ét. Fam. Vesp. **3:** 328 (as division of subgenus *Alastor* of genus *Alastor* Lepeletier; validated by ICZN Opinion 893, 1970: 187). Type species *Alastor tuberculatus* Saussure, 1853, Designated by ICZN, Opinion 893, 1970: 187.

Paraleptomenes Soika, 1970, Boll. Mus. Civ. Ven. **20/21:** 79. Type species *Paraleptomenes nurseanus* Soika, 1970. Original designation.

Paralionotulus Bluethgen, 1938 (1937), Konowia **16**: 293. Type species *Leptochilus mervensis* Radoszkowski, 1887. Original designation.

Pseudolionotulus (!) Bluethgen, 1938, Dts. Entomol. Z.: 446, 454. Type species *Leptochilus mervensis* Radoszkowski,

1887. Original designation.

Paramischocyttarus Magretti, 1884 (1883) Boll. Soc. Entomol. Ital. **15**: 250; 1884, Ann. Mus. Civ. Genova **21**: 600. Type species *Paramischocyttarus subtilis* Magretti, 1884. Monotypic.

Tanyzethus Cameron, 1910, Wiss. Ergebn. Schwed. Zool. Exped. Kilimandjaro (8)**6**: 195. Type species *Tanyzethus africanus* Cameron, 1910. Monotypic.

Parancistrocerus Bequaert, 1925, Trans. Am. Entomol. Soc. **51**: 64 (as subgenus of *Ancistrocerus* Wesmael). Type species *Odynerus fulvipes* Saussure, 1855. Original designation.

Paranortonia Bequaert, 1940, Ann. Entomol. Soc. Am. **33**: 100 (as subgenus of *Pachymenes* Saussure). Type species *Nortonia tolteca* Saussure, 1875. Original designation.

Paranortonia Bertoni, 1934, Rev. Soc. Cient. Paraguay **3**: 109 (as genus). Invalid; no type designated.

Pararhaphidoglossa Schulthess, 1910, Dts. Entomol. Z.: 187. Type species *Pararhaphidoglossa fulva* Schulthess, 1910. Original designation.

Pararaphidoglossa (!) Zavattari, 1912, Arch. Naturgesch. **78A**(4): 5; Soika, 1941, Boll. Soc. Ven. Stor. Nat. **2**: 227 and 1978, Boll. Mus. Civ. Ven. 29.

Pararrhynchium Saussure, 1855, Ét. Fam. Vesp. **3**: 173 (as division of *Rhynchium* Spinola). Type species *Rhynchium ornatum* Smith, 1852. Monotypic.

Prorhynchium Saussure, 1855, Ét. Fam. Vesp. **3**: 174 (as division of *Rhynchium* Spinola). Type species *Rhynchium smithii* Saussure, 1855. Monotypic.

Prorrhynchium (!) Saussure, 1856, Ét. Fam. Vesp. **3**: 348, Table des Matières: 8.

Pararhynchium (!) Saussure, 1862, Stett. Entomol. Ztg. 23: 182.

Parrhynchium (!) Dalla Torre, 1894, Cat. Hym. **9**: 42.

Paravespa Radoszkowski, 1886, Hor. Soc. Entomol. Ross. **20**: 46. Type species *Hoplomerus komarowi* Radoszkowski, 1886 (= *Odynerus quadricolor* Morawitz, 1885). Monotypic.

Theletor Kokujev, 1912, Izv. Kavkaz. Muz. **7**: 4 (under description of *Rhynchium caucasicum*). Type species *Rhynchium caucasicum* Kokujev, 1912. Designated by Vecht, 1972, *in* Vecht and Fischer, Hym. Cat. **8**: 4.

subg. **Gestrodynerus** Soika, 1961 (1960), Atti Soc. Ital. Sci. Nat. **99**: 361, 369. Type species *Rygchium gestroi* Magretti, 1884. Original designation.

Parazumia Saussure, 1855, Ét. Fam. Vesp. **3**: 166 (as division of *Montezumia* Saussure). Type species *Odynerus carinulatus* Spinola, 1851. Designated by Bequaert, 1921, Rev. Zool. Afric. **9**: 241.

Pareumenes Saussure, 1855, Ét. Fam. Vesp. **3**: 133 (as division of *Eumenes* Latreille). Type species *Eumenes quadrispinosus* Saussure, 1855. Designated by Bequaert, 1918, Bull. Am. Mus. Nat. Hist. **39:** 271.

subg. **Nortonia** Saussure, 1869, Stett. Entomol. Z. **30**: 53 (as genus). Type species *Odynerus intermedius* Saussure, 1853. Original designation.

Notonia (!) Sonan, 1938, Arb. Morph. Tax. Ent. **5**: 70.

Parifodynerus Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 64, 167. Type species *Parifodynerus parificus* Soika, 1962. Original designation.

Parodontodynerus Bluethgen, 1938 (1937), Konowia **16**: 280 (as subgenus of *"Euodynerus"* Bluethgen). Type species *Eumenes ephippium* Klug, 1817. Original designation.

Paradontodynerus (!) Guichard, 1978, Entomol. Gazette **31**: 45.

Parodynerus Saussure, 1855, Ét. Fam. Vesp. **3**: 245 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Vespa bicincta* Fabricius, 1781. Designated by Soika, 1958 (1957), Boll. Mus. Civ. Ven. **10**: 214.

Pirhosigma Soika, 1978, Boll. Mus. Civ. Ven. **29:** 11, 229. Type species *Eumenes simulans* Saussure, 1875. Original designation.

Plagiolabra Schulthess, 1903 (March), Verh. Zool. Bot. Ges. Wien **53**: 361, 365. Type species *Plagiolabra nigra* Schulthess, 1903. Monotypic.

Leontiniella Brèthes, 1903 (Sept.), An. Mus. Nac. Buenos Aires (3)**2**: 265. Type species *Leontiniella argentina* Brèthes, 1903. Monotypic.

Postepipona Soika, 1974 (1972), Boll. Mus. Civ. Ven. **25**: 77. Type species *Postepipona socotrae* Soika, 1974. Original designation.

Proepipona Soika, 1977, Steenstrupia **4**: 125, 126. Type species *Vespa lateralis* Fabricius, 1781. Original designation.

Protodiscoelius Dalla Torre, 1904, Gen. Ins. **19**: 18 (as division of *Discoelius* Latreille). Type species *"Epipona chilensis* Spinola, 1851 = *Discoelius merula* Haliday, 1836". Designated by Bequaert and Ruiz, 1942 (1940), Rev. Chil. Hist. Nat. **64**: 217.

Neodiscoelius Stange, 1979, Acta Zool. Lilloana **35**: 729; NEW SYNONYMY. Type species *Discoelius merula* Haliday, 1836. Original designation.

Pseudabispa Vecht, 1960, Nova Guinea Zool. **10**(6): 91, 102. Type species *Odynerus abispoides* Perkins, 1912. Original designation.

Pseudacaromenes Soika, 1978, Boll. Mus. Civ. Ven. **29**: 15 (in key). Type species *Eumenes alfkeni* Ducke, 1904. Original designation.

Pseudoacaromenes (!) 1981, Zool. Record 115 (1978) Ins.: 262, List of new generic and subgeneric names: 15, 39.

Pseudalastor Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 65, 131. Type species *Odynerus concolor* Saussure, 1853. Original designation.

Pseudepipona Saussure, 1856, Ét. Fam. Vesp. **3**: 309 (as division of subgenus *"Epipona"* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus herrichii* Saussure, 1856. Monotypic.

Metepipona Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 193 (as subgenus of *Pseudepipona*). Type species *Odynerus peculiaris* Morawitz, 1895. Original designation.

Trichepipona Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 171, 193 (as subgenus of *Pseudepipona*). Type species *Odynerus lativentris* Saussure, 1855. Original designation.

Leptepipona Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 171, 194 (as subgenus of *Pseudepipona*). Type species *Vespa tripunctata* Fabricius, 1787. Original designation.

Pseudopipona (!) Opinion 893, ICZN, 1970, Bull. Zool. Nomencl. **26**: 187.

Pseudepipone (!) Bytinski-Salz and Gusenleitner, 1971, Isr. J. Ent. **6**: 298.

subg. **Deuterepipona** Bluethgen, 1951, Mitt. Muench. Entomol. Ges. **41**: 171, 194 (as genus). Type species *Odynerus ionius* Saussure, 1855. Original designation.

Pseudochilus Saussure, 1856, Ét. Fam. Vesp. **3**: 321 (as division of *"Pterochilus"* Klug). Type species *Pterochilus glabripalpis* Saussure, 1852. Monotypic.

Pseudodontodynerus Bluethgen, 1939, Veroeff, Dts. Kolon. Uebersee-Mus. Bremen **2**: 249. Type species *Odynerus pretiosus* Dusmet, 1928. Monotypic.

Pseudodynerus Saussure, 1855, Ét. Fam. Vesp. **3**: 220 (as division of subgenus *Ancistrocerus* Wesmael of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus luctuosus* Saussure, 1855. Monotypic.

Pseudoleptochilus Bluethgen, 1938 (1937), Konowia **16**: 294. Type species *Odynerus frenchi* Dusmet, 1917. Original designation (as *"Lionotus frenchi* Dusmet").

Pseudonortonia Soika, 1936, Ann. Mus. Civ. Genova **59**: 268. Type species *Odynerus difformis* Saussure, 1853. Original designation.

Subancistroceroides Bluethgen, 1938, Dts. Entomol. Z.: 441, 460 (as subgenus of *"Subancistrocerus* Sauss." *sensu* Bluethgen, 1938). Type species *Odynerus aegyptiacus* Saussure, 1863. Original designation.

Pseudopterocheilus Perkins, 1901, Entomol. Mon. Mag. **37**: 266. Type species *Odynerus pterocheiloides* Perkins, 1899. Original designation.

Pseudopterochilus (!) Dalla Torre, 1904, Gen. Ins. **19:** 39.

Pseudosymmorphus Bluethgen, 1938 (1937), Konowia **16**: 293. Type species *Odynerus hindenburgi* Dusmet, 1917. Original designation.

Pseudozumia Saussure, 1875, Smiths. Misc. Coll. **254**: 128 (as division of *Montezumia* Saussure). Type species *Montezumia indica* Saussure, 1855. Monotypic.

Pseudzumia (!) Dalla Torre, 1894, Cat. Hym. **9**: 38.

Pseumenes Soika, 1935, Ann. Mus. Civ. Genova **57**: 145 (as subgenus of *Pareumenes* Saussure). Type species *Eumenes eximius* Smith, 1861. Original designation.

Psiliglossa Saunders, 1872, Trans. R. Entomol. Soc. Lond.: **42**. New name for *Stenoglossa* Saussure.

Stenoglossa Saussure, 1852, Ét.Fam. Vesp. **1**: 4, *non Stenoglossa* Chaudoir, 1848. Type species *Raphiglossa odyneroides* Saunders, 1850. Monotypic.

Psiloglossa Dalla Torre, 1894, Cat. Hym. **9**: 8. Emendation.

Pterocheilus Klug, 1805, Beitr. Natuurk. **1**: 143. Type species *Vespa phalerata* Panzer, 1797. Designated by Blanchard, 1840, *in* Laporte, Hist. Nat. Ins. **3**: 389.

Pterochilus (!) Illiger, 1807, Mag. Insektenk. **6**: 196.

Pterochile (!) Blanchard, 1840, *in* Laporte, Hist. Nat. Ins. **3**: 389.

Pterochylus (!) Saussure, 1853, Ét.Fam. Vesp. **1**: 239.

Odontopterochilus Kostylev, 1940, Bull. Soc. Nat. Moscou, Biol. (N. S.) **49**: 148 (as subgenus of *Pterocheilus*). Invalid; no type designated. Made available by Vecht, 1971, Entomol. Ber. (Amst.) **31**: 127; with type species *Pterocheilus heptneri* Kostylev, 1940.

Nannopterochilus Bluethgen, 1961, Ab. Dts. Akad. Wiss. Berl. 1961: 62, 86, 231. Type species *Vespa phalerata* Panzer, 1797. Original designation.

subg. **Megapterocheilus** Bohart, 1940, Ann. Entomol. Soc. Am. **33**: 169, 173. Type species *Pterochilus mirandus* Cresson, 1879. Original designation.

subg. **Onchopterocheilus** Bohart, 1940, Ann. Entomol. Soc. Am. **33**: 169, 191. Type species *Pterochilus comptus* Cresson, 1879. Original designation.

subg. **Micropterocheilus** Bohart, 1940, Ann. Entomol. Soc. Am. **33**: 168, 201. Type species *Pterocheilus desertorum* Bohart, 1940. Original designation.

Pteromenes Soika, 1961 (1960), Atti Soc. Ital. Sci. Nat. **99**: 389, 407. Type species *Pterochilus paradisiacus* Soika, 1941. Original designation.

Raphiglossa Saunders, 1850, Trans. R. Entomol. Soc. Lond. (2)**1**: 71. Type species *Raphiglossa eumenoides* Saunders, 1850. Designated by Ashmead, 1902, Can. Ent. **34**: 206.

Raphidoglossa Dalla Torre, 1894, Cat. Hym. **9**: 7. Emendation.

Raphiglossoides Soika, 1936, Boll. Soc. Entomol. Ital. **68**: 77. Type species *Raphiglossoides aethiopicus* Soika, 1936. Original designation.

Rhynchalastor Meade-Waldo, 1910, Ann. Mag. Nat. Hist. (8)**6**(31): 110. Type species *Rhynchalastor fuscipennis* Meade-Waldo, 1910. Monotypic.

Rhynchium Spinola, 1806, emendation of *Rygchium* Spinola, 1806; validated by ICZN, Opinion 747, 1965: 186. Type species *Ryg-*

chium (!) *europaeum* Spinola, 1806 (= *Vespa oculata* Fabricius, 1781). Monotypic.

Rygchium Spinola, 1806, Ins. Ligur. **1**: 84 incorrect original spelling for *Rhynchium*.

Rhynchium Billberg, 1820, Enum. Ins.: 109. Emendation of *Rychium* (!) Spinola.

Rynchium Sturm, 1829, Verz. Ins. Nurnberg: 12. Emendation.

Rhygchium Saussure, 1853, Ét. Fam. Vesp. **1**: xxxi, 276. Emendation.

Rhynchuium (!) Saussure, 1863, Mém. Soc. Phy. Hist. Nat. Genève **17**: 242.

Eurrhynchium Dalla Torre, 1904, Gen. Ins. **19**: 33. New name.

Rygohium (!) Willink, 1982, Bol. Ac. Nac. Sci. **55**: 195.

Smeringodynerus Snelling, 1975, Proc. Entomol. Soc. Wash. **77**: 56. Type species *Odynerus morelios* Saussure, 1857. Original designation.

Sphaeromenes Soika, 1978, Boll. Mus. Civ. Ven. **29**: 12, 225. Type species *Sphaeromenes discrepatus* Soika, 1978. Original designation.

Spinilabochilus Kurzenko, 1981, Hym. Far East: 81, 97. Type species *Spinilabochilus turcmenicus* Kurzenko, 1981. Original designation.

Stellepipona Soika, 1974 (1973), Boll. Mis. Civ. Ven. **24**: 106. Type species *Odynerus stellenboschensis* Cameron, 1905. Original designation.

Stenancistrocerus Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève **17**: 216 (as division of subgenus *Ancistrocerus* Wesmael of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus atropos* Lepeletier, 1841. Designated by Bequaert, 1925, Trans. Am. Entomol. Soc. **51**: 63.

Stenancystrocerus (!) Dalla Torre, 1894, Cat. Hym. **9**: 55–95.

Atropancistrocerus Bluethgen, 1938, Dts. Entomol. Z.: 442, 444, 461. Type species *Odynerus hispanicus* Dusmet, 1903. Original designation.

subg. **Paratropancistrocerus** Bluethgen, 1938, Dts. Entomol. Z.: 442. 461 (as subgenus of *Atropancistrocerus*). Type species *Odynerus transcaspicus* Kostylev, 1935. Original designation.

Stenodyneriellus Soika, 1962 (1961), Boll. Mus. Civ. Ven. **14**: 65, 71. Type species *Stenodyneriellus turneriellus* Soika, 1962. Original designation.

Stenodyneroides Soika, 1940, Ann. Mus. Civ. Genova **60**: 471 (as subgenus of *Odynerus* Latreille). Type species *Odynerus corvus* Meade-Waldo, 1915. Original designation.

Stenodynerus Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève **17**: 228 (as division of subgenus *Odynerus* of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus chinensis* Saussure, 1863. Designated by Bohart, 1939, Pan-Pac. Ent. 15: 100.

Stemodynerus (!) Rohwer, 1913, Proc. U.S. Nat. Mus. **44**: 445.

Nannodynerus Bluethgen, 1938 (1937), Konowia **16**: 281 (as subgenus of "*Euodynerus* Bluethgen"). Type species *Lionotus teutonicus* Bluethgen, 1937. Original designation.

Parhypodynerus Soika, 1974 (1973), Boll. Mus. Civ. Ven. **24**: 110. Type species *Odynerus pavidus* Kohl, 1905. Original designation.

Stenonartonia Soika, 1974 (1973), Boll. Mus. Civ. Ven. **24**: 25. New name for *Paranortonia* Soika.

Paranortonia Soika, 1941, Boll. Soc. Ven. Stor. Nat. **2**: 25 *non Paranortonia* Bequaert, 1940. Type species *Nortonia polybioides* Schulthess, 1904. Original designation.

Stenosigma Soika, 1978, Boll. Mus. Civ. Ven. **29**: 14, 407. Type species *Eumenes allegrus* Zavattari, 1912. Original designation.

Stroudia Gribodo, 1892 (1891), Boll. Soc. Entomol. Ital. **23**: 262. Type species *Stroudia armata* Gribodo, 1892. Monotypic.

Subancistrocerus Saussure, 1855, Ét. Fam. Vesp. **3**: 206 (as division of subgenus *Ancistrocerus* Wesmael of genus *Odynerus* Latreille; validated by ICZN, Opinion 893, 1970: 187). Type species *Odynerus sichelii* Saussure, 1854. Designated by Bequaert, 1925, Trans. Am. Entomol. Soc. **51:** 61.

Epancistrocerus Saussure, 1856, Ét. Fam. Vesp. **3**: 352. New name for *Subancistrocerus* Saussure. Type species *Odynerus sichelii* Saussure, 1854. Designated by Bequaert, 1925, Trans. Am. Entomol. Soc. **51**: 61.

Symmorphoides Soika, 1977 (1976), Boll. Mus. Civ. Ven. **28**: 171, 172. Type species *Symmorphoides maroccanus* Soika, 1976. Original designation.

Symmorphus Wesmael, 1836, Bull. Acad. Sci. Bruxelles **3**: 45 (as subgenus of *Odynerus* Latreille). Type species *Odynerus elegans* Wesmael, 1833. Designated by Richards, 1935, Trans. R. Entomol. Soc. Lond. **83**: 162.

Protodynerus Saussure, 1855, Ét. Fam. Vesp. **3**: 184, 186. New name for *Symmorphus*.

Synomorphus (!) Rohwer, 1917, Proc. U.S. Nat. Mus. **53**: 234.

"Odynerus Latreille" *sensu* Bluethgen, 1938 (1937), Konowia **16**: 274, 291. Type species *Vespa muraria* L., 1758. Designated by Bluethgen, 1938 (1937), Konowia **16**: 274, 291.

Koptodynerus Bluethgen, 1943, Stett. Entomol. Z. **104**: 152 (as subgenus of *"Odynerus* Latreille" *sensu* Bluethgen). Type species *Symmorphus declivus* Harttig, 1932. Monotypic.

subg. **Parasymmorphus** Cumming and Vecht, 1986, Entomol. Ber. (Amst.) **46**: 23. Type species *Odynerus momunganensis* Schulthess, 1934. Original designation.

Synagris Latreille, 1802, Hist. Nat. Crust. Ins. **3**: 360. Type species *Vespa cornuta* L., 1758 (as *Vespa cornuta* F.). Monotypic.

Eusynagris Dalla Torre, 1904, Gen. Ins. 19: 30. New name for *Synagris*.

Catilostenus Meunier, 1888, Nat. Sicil. **7**: 150. Type species *Catilostenus nigroviolaceus* Meunier, 1888. Monotypic. Identity doubtful.

subg. **Paragris** Saussure, 1855, Ét. Fam. Vesp. **3**: 156 (as division of *Synagris*). Type species *Synagris humberti* Saussure, 1855. Designated by Ashmead, 1902, Can. Ent. **34**: 210 (as *P. hubertii* !).

Hypagris Saussure, 1855, Ét. Fam. Vesp. **3**: 157 (as division of *Synagris*). Type species *Synagris abdominalis* Saussure, 1855 (= *Synagris analis* Saussure, 1852). Designated by Ashmead, 1902, Can. Ent. **34**: 210.

Antagris Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève **17**: 181 (as division of *Synagris*). Type species *Synagris aequatorialis* Saussure, 1852 (= *Synagris spiniventris* Illiger, 1802). Designated by Ashmead, 1902, Can. Ent. **34**: 210.

subg. **Pseudagris** Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève **17**: 203 (as division of *Synagris*). Type species *Synagris carinata* Saussure, 1863. Monotypic.

subg. **Rhynchagris** Maidl, 1914, Anz. Ak. Wiss. Wien **51**: 91. Type species *Synagris vicaria* Stadelmann, 1898. Monotypic.

Syneuodynerus Bluethgen, 1951, Boll. Soc. Entomol. Ital. **81**: 67, 75 (as subgenus of "*Euodynerus* Bluethgen"). Type species *Odynerus egregius* Herrich-Schaeffer, 1839. Original designation. *Syneodynerus* (!) Kurzenko, 1981, Hym. Far East: 101.

Tachyancistrocerus Soika, 1952, Boll. Soc. Venez. Stor. Nat. **6**: 37. New name for *Subancistrocerus* Bluethgen.

"*Subancistrocerus* (Saussure) nov. gen." Bluethgen 1938, Dts. Entomol. Z: 441, 460 *non Subancistrocerus* Saussure, 1855. Type species *Odynerus rhodensis* Saussure, 1855. Original designation.

Tachymenes Soika, 1983 (1982), Boll. Mus. Civ. Ven. **33**: 118. Type species *Odynerus vulneratus* Saussure, 1855. Original designation.

Tricarinodynerus Soika, 1952 (1951), Riv. Biol. Colon. **11**: 73, 79. Type species *Odynerus guerinii* Saussure, 1852. Original designation.

Carinodynerus Soika, 1957 Brit. Mus. (Nat. Hist.) Exped. S. W. Arabia **1**(31): 478 (as subgenus of *Pseudepipona* Saussure). Type species *Odynerus guerinii* Saussure, 1852. Original designation.

Tricomenes Soika, 1978, Boll. Mus. Civ. Ven. **29**: 10, 254. Type species *Eumenes pilosa* Fox, 1899. Original designation.

Tropidodynerus Bluethgen, 1939, Veroeff, Dts. Kolon. Ueberssee-Mus. Bremen **2**(3): 259, 260. Type species *Polistes interrupta* Brullé, 1832. Original designation.

Xanthodynerus Bluethgen, 1954, Dts. Entomol. Z. (N. F.) **1**: 255 (as subgenus of "*Euodynerus* Bluethgen"). Type species *Odynerus octavus* Soika, 1943. Original designation.

Xenorhynchium Vecht, 1963, Zool. Verh. (Leiden) **60**: 111. Type species *Vespa nitidula* Fabricius, 1798. Original designation.

Zeta Saussure, 1855, Ét. Fam. Vesp. **3**: 132, 146 (as division of *Eumenes* Latreille). Type species *Sphex abdominalis* Drury, 1770. Designated by Bequaert, 1926, Ann. S. Afr. Mus. **23**: 487.

Zeteumenes Bertoni, 1921, Rev. Soc. Cient. Paraguay **1**: 117. Type species *Vespa canaliculata* Olivier, 1791 (= *Sphex argillacea* L., 1758). Designated by Vecht, 1977, Proc. K. Ned. Akad. Weten. (C)80: 242.

Zetamenes (!) Bertoni, 1926, Rev. Soc. Cient. Paraguay **2**: 75.

Beteumenes Bertoni, 1934, Rev. Soc. Cient. Paraguay **3**: 109 (as subgenus of *Zeteumenes*). Invalid; no type designated.

Zetheumenidion Bequaert, 1926, Ann. S. Afr. Mus. **23**: 487 (as subgenus of *Eumenes* Latreille). Type species *Eumenes femoratus* Schulthess, 1910. Original designation.

Zethus Fabricius, 1804, Syst. Piez.: xii, 282. Type species *Vespa coeruleopennis* Fabricius, 1798. Designated by Latreille, 1810, Con. Gén. Crust. Arach. Ins.: 328, 438.

Didymogastra Perty, 1833, Delect. Anim. Artic. Brasil: 144. Type species *Didymogastra fusca* Perty, 1833. Monotypic.

Lethus (!) Say, 1837, Boston J. Nat. Hist. **1**: 387.

Heros Saussure, 1855, Ét. Fam. Vesp. **3**: 115 (as division of *Zethus*), *non Heros* Haeckel, 1840. Type species *Zethus gigas* Spinola, 1841 (= *Vespa coeruleopennis* Fabricius, 1798). Monotypic.

Wettsteinia Dalla Torre, 1904, Gen. Ins. **19**: 13. Type species *Labus sichelianus* Saussure, 1875. Designated by Bohart and Stange, 1965, Univ. Calif. Publ. Ent. **40**: 25.

Euzethus Dalla Torre, 1904, Gen. Ins. **19**: 14. New name.

Laboides Zavattari, 1912, Arch. Naturgesch. **78A**(4): 65. Type species *Labus sichelianus* Saussure, 1875. Designated by Bohart and Stange, 1965, Univ. Calif. Publ. Ent. **40**: 25.

subg. **Zethusculus** Saussure, 1855, Ét. Fam. Vesp. **3**: 118. Type species *Zethus jurinei* Saussure, 1852. Designated by Ashmead, 1902, Can. Ent. **34**: 205.

subg. **Zethoides** Fox, 1899, Proc. Acad. Nat. Sci. Philad.: 436. Type species *Zethoides smithii* Fox, 1899, (*non Zethus smithii* Saussure, 1855; = *Zethus chapadensis* Bohart and Stange, 1965). Monotypic.

Baeoprymna Cameron, 1912, Timehri **2**: 225. Type species *Baeoprymna rufoornata* Cameron, 1912 (= *Zethus miniatus* Saussure, 1858). Monotypic.

Protozethus Bertoni, 1926, Rev. Soc. Cient. Paraguay **2**: 75. Type species *Zethus olmecus* Saussure, 1875. Original designation.

subg. **Madecazethus** Soika, 1979, Boll. Mus. Civ. Ven. **30**: 20, 53. Type species *Labus madecassus* Schulthess, 1907. Original designation.

Nomina dubia in Eumeninae

Eumenestiferus Meunier, 1888, Nat. Sicil. **7**: 300. Type species *Eumenestiferus brasiliensis* Meunier, 1888. Monotypic. Unidentified.

Micragris Saussure, 1855, Ét. Fam. Vesp. **3**: 158 (as division of *Synagris* Latreille). Type species *Synagris spinolae* Saussure, 1855. Monotypic. Unidentified.

Nomina nuda in Eumeninae

Allepipona Bluethgen, 1951, Mitt. Munch. Entomol. Ges. **41**: 194.

Antalastoroides Saussure, 1856, Ét. Fam. Vesp. **3**: 328 (hypothetical group).

Austrodynerus Soika, 1958 (1957), Boll. Mus. Civ. Ven. **10**: 119.

Lissodynerus Soika, 1974 (1973), Boll. Mus. Civ. Ven. **24**: 119.

Acknowledgements

I thank J. van der Vecht for critically reviewing the manuscript. An earlier version was submitted to Cornell University as part of a doctoral dissertation (Carpenter, 1983). G. C. Eickwort, D. M. Bates, J. L. Cisne and Q. D. Wheeler, members of the author's special committee, read and commented upon this version. Arnold S. Menke, U.S. National Museum, provided valuable comments on a later version.

Summary

A synonymic checklist of the genus-group names in the Eumeninae is provided. Presently, 177 genera with 34 additional subgenera are considered valid. *Neodiscoelius* Stange, 1979, is newly synonymized with *Protodiscoelius,* Dalla Torre, 1904; *Hypalastoroides depressus* Soika, 1969, is synonymized with *Odynerus relativus* Fox, 1902; the subgenus *Cephalastor* Soika, 1982, is raised to genus; and type-species are designated for *Nesodynerus* Perkins, 1901, and *Stenolabus* Schulthess, 1910.

Literature Cited

Bluethgen, P.

1938 (1937). Systematisches Verzeichnis der Faltenwespen Mitteleuropas, Skandinaviens und Englands. Konowia **16**: 270–295.

Carpenter, J. M.

1981 (1982). The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Syst. Ent. 7: 11–38.

1983. Phylogenetic studies in Vespoidea (Hymenoptera). PhD Thesis, Cornell University.

Carpenter, J. M. and J. M. Cumming.

1985. A character analysis of the North American potter wasps (Hymenoptera: Vespidae; Eumeninae). J. Nat. Hist. **19**: 877–916.

Dalla Torre, K. W.

1904. Vespidae, Gen. Ins. **19**: 1–108.

International Commission on Zoological Nomenclature.

1965. Opinion 747. *Rygchium* Spinola, 1806 (Insecta, Hymenoptera): Validation of emendation of *Rhynchium*. Bull. Zool. Nomencl. **22**: 186–187.

1970. Opinion 893. Eumenidae names of Saussure (Hymenoptera): Grant of availability to certain names proposed for secondary divisions of genera. Bull. Zool. Nomencl. **26**: 187–191.

1985. Opinion 1363. *Ancistroceroides* Saussure, 1855 (Insecta, Hymenoptera): Type species designated. Bull. Zool. Nomencl. **42**: 353–354.

Krombein, K. V., P. D. Hurd, D. R. Smith and B. D. Burks.

1979. Catalog of Hymenoptera in America North of Mexico. Smiths. Inst. Press, Washington, D.C.

REVIEW OF THE FOSSIL TIPHIIDAE, WITH DESCRIPTION OF A NEW SPECIES (HYMENOPTERA)*

By A. P. Rasnitsyn

Paleontological Institute,
Academy of Sciences of the USSR,
Profusoyuznaja, 113, 117868,
Moscow USSR

Through the courtesy of Professor Frank M. Carpenter (Harvard University, Cambridge, Mass.) and Dr. Paul E. S. Whalley (British Museum, Natural History, London, U.K.) I have been able to study the type specimens (good photographs of the specimen in one case) of all described extinct species ever attributed to the Tiphiidae. Five of them have been described as members of the subfamily Anthoboscinae by Cockerell: in 1906 (*Lithotiphia scudderi, Geotiphia foxiana*), 1910 (*G. sternbergi, G. halictina*) and 1927 (*G. pachysoma*); while *Hoplisidea kohliana* was described originally as a member of the Sphecidae (Cockerell, 1906) and later transferred to the Anthoboscinae by Evans (1966).

From my study of these specimens I have found that the latter species most probably belongs to the Sceliphronini (Sphecidae) and I will treat it elsewhere. The five other species are discussed below and one new species is described. All the species described by Cockerell are from the Lower Oligocene of Florissant, Colorado; the new one is from the ?Upper Oligocene of the Sikhote-Alin Mts., Maritime Province of the USSR. Only the holotypes are known for all these species and each specimen is a female, suggesting a female biased tiphiid population during the Oligocene.

Only two other fossil specimens of Tiphiidae have been mentioned in the literature; both were found in Baltic amber collected by A. Menge and both were identified by Brische (1886) as "Tiphia (?)". Unfortunately, Menge's collection is apparently lost (Heie, 1967, p. 119).

Manuscript received by the editor August 3, 1985

The species treated here (figures 1–7) can be assigned to the Tiphiidae on the basis of the strongly fossorial nature of the legs (mid and hind tibiae thick and spiny), combined with the pleisiomorphic wing venation; the latter differs distinctly from that of the Scoliidae, which do have similar fossorial adaptations. In one case (Fig. 2) this indirect evidence is confirmed by the structure of the mesosternum, which shows the pair of lamellae that characteristically partly cover the midcoxae.

The fossil species show a habitus and female wing venation typical for the Anthoboscinae. Nevertheless, they do not belong to that subfamily, mainly because their antennal sockets are overlain with tubercles, clearly seen in one case (Fig. 6) and less clear in another (Fig. 7). There are additional features distinguishing the fossils from Anthoboscinae, *viz.,* flagellum straight or variously bent (Figs. 1, 2, 4, 6) instead of tightly curled (as in all female Anthoboscinae studied), femora lacking genual plates (Figs. 1–3, 7) or propodeum with longitudinal lines (Figs. 4, 5).

All Tiphiidae with the antennal sockets partly covered by frontal tubercles or ridges belong to the Myzininae and Methochinae. The latter subfamily is not involved here, since its members have thin tibiae bearing only weak spines. [I follow V. Gorbatovsky (personal communication) in treating *Pterombrus* Smith as a member of the subfamily Methochinae]. Therefore, the Myzininae is the only subfamily with the characters of the fossils and in particular with those of *Geotiphia.* [*Lithotiphia* is poorly known but I consider it similar enough to the former genus to classify them together and not to reject *Lithotiphia* as a tiphiid *incertae sedis*]. Within the Myzininae the fossils take an isolated position because of the very primitive, male-like wing venation of the females.

Both of these extinct genera can be identified by the following diagnoses. *Lithotiphia* (Fig. 1): forewing with cu-a cross-vein antefurcal; head capsule with a short oral cavity, distant from occipital carina; hind tibiae very strongly swollen. *Geotiphia* (Figs. 2–7): fore wing with cu-a interstitial or postfurcal; oral cavity longer, with hypostomae reaching occipital carina; hind tibiae less swollen. The latter genus possibly deserves to be divided into two genera, since *sternbergi* and *pachysoma,* in contrast to other species, show mid and/or hind femora with the genual plates, and the propodeum with longitudinal lines. The propodeal structure is unknown in any other

Figure 1. *Lithotiphia scudderi* Cockerell, holotype, no. 2022, Museum of Comparative Zoology, Harvard University. Wing cells are lettered. Scale line in all figures, 3 mm.

species and I hesitate to create another new genus on a sole character. The following is a descriptive account of the species in these two genera. The details shown in the figures are generally not described below.

Lithotiphia scudderi Cockerell
Figure 1

Lithotiphia scudderi Cockerell, 1906, p. 51

Body length, 12.3 mm; fore wing length, about 5 mm (Length is measured here from base to apex of cell 3r). Gastral terga with light spots. Integumental sculpture not discernible because of covering by Canada balsam. Holotype: M.C.Z. no. 2022.

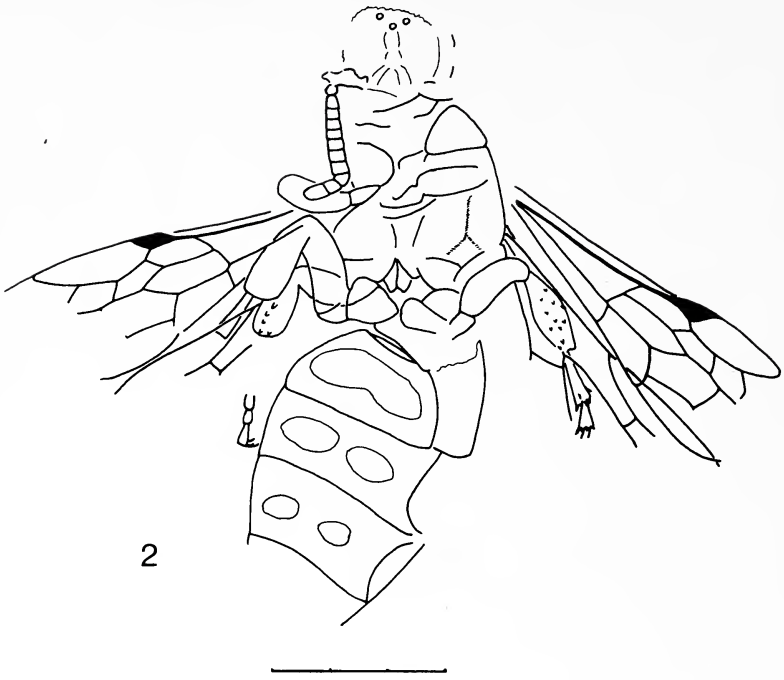


Figure 2. *Geotiphia foxiana* Cockerell, holotype, no. 2021, Museum of Comparative Zoology, Harvard University.

Geotiphia foxiana Cockerell
Figure 2

Geotiphia foxiana Cockerell, 1906, p. 52

Body length, as preserved, 11 mm (probably originally 12 mm.); fore wing length, 6.2 mm. Integumental sculpture not discernible. Ground color moderately dark, the flagellum, tibiae, tarsi, veins, and pterostigma less dark; metasomal sterna with light spots sublaterally, 2nd sternum having the spots large and contiguous. Color pattern of terga unknown. Wing membrane not infumate. Holotype: M.C.Z. no. 2021.

Geotiphia halictina Cockerell
Figure 3

Geotiphia halictina Cockerell, 1910, p. 279

Body length, 18 mm; fore wing length, 3.5 mm. Venation similar to that of *foxiana,* but differing in smaller size and the position of cell

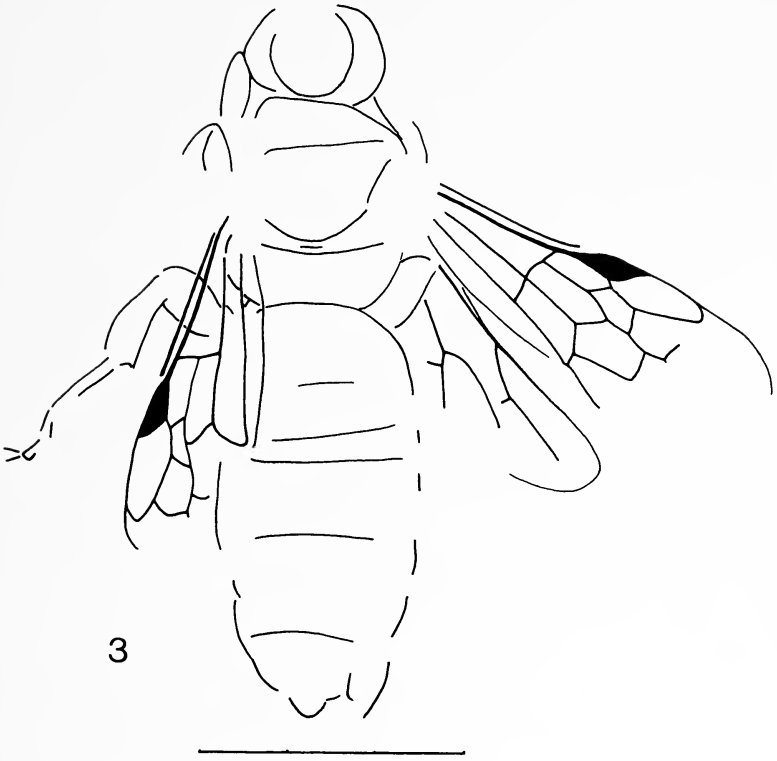


Figure 3. *Geotiphia halictina* Cockerell, drawing based on photograph of holotype, no. 18619, Museum of the University of Colorado.

3r remote from wing margin apically. Integumental sculpture and color pattern unknown. (Description based on photograph of holotype).

Geotiphia sternbergi Cockerell
Figure 4

Geotiphia sternbergi Cockerell, 1910, p. 277

Body length, 8 mm; fore wing length, 12 mm. Head with posterior surface punctate dorsally and laterally, finely punctatorugose medially. Thorax with distinct, moderately large punctures dorsally; lateral adscutellar depression, metanotum and propodeum finely reticulate. Gastral terga with sculpture fine and sparse, not clear in detail. Ground color dark (not known for fore and mid

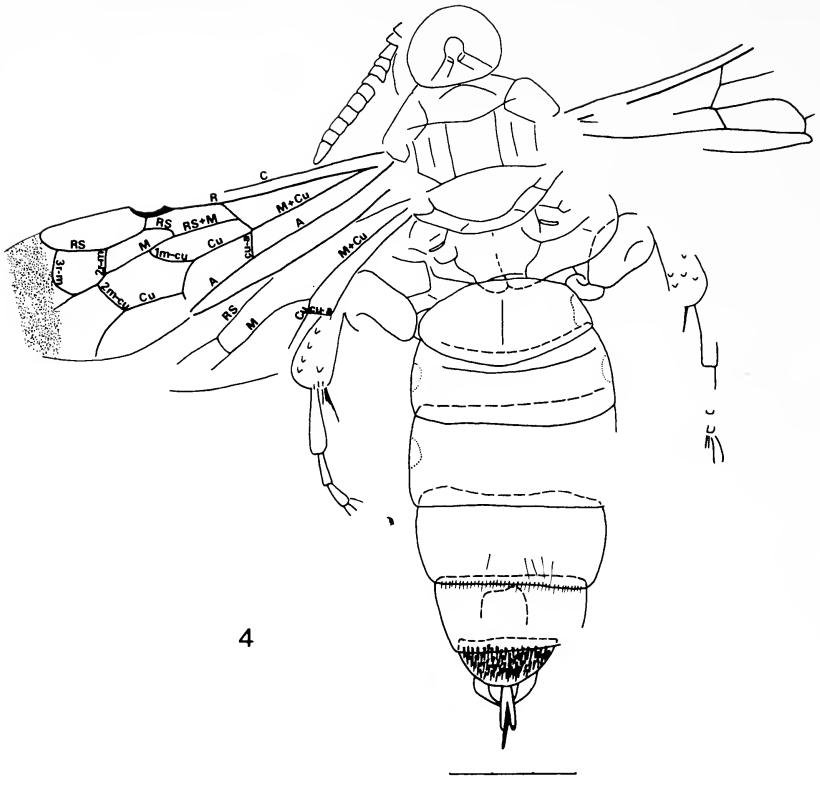


Figure 4. *Geotiphia sternbergi* Cockerell, holotype, no. 18868, American Museum of Natural History, New York. Wing veins are lettered.

legs), anterior metasomal segments with small light spots laterally. Fore wing apex infumate. Differs from the above species by its large size, modified antennal segments, and in having the hind femur with genual plate; fore wing with cell 2rm very long, and possibly in having the propodeum with longitudinal lines. Holotype: A.M.N.H., no. 18868.

Geotiphia pachysoma Cockerell
Figures 5 and 6

Geotiphia pachysoma Cockerell, 1927, p. 432.

Body length, 9.2 mm; fore wing length, 6.0 mm. Head punctato-rugose dorsomedially in part, thorax smooth, with distinct but weak

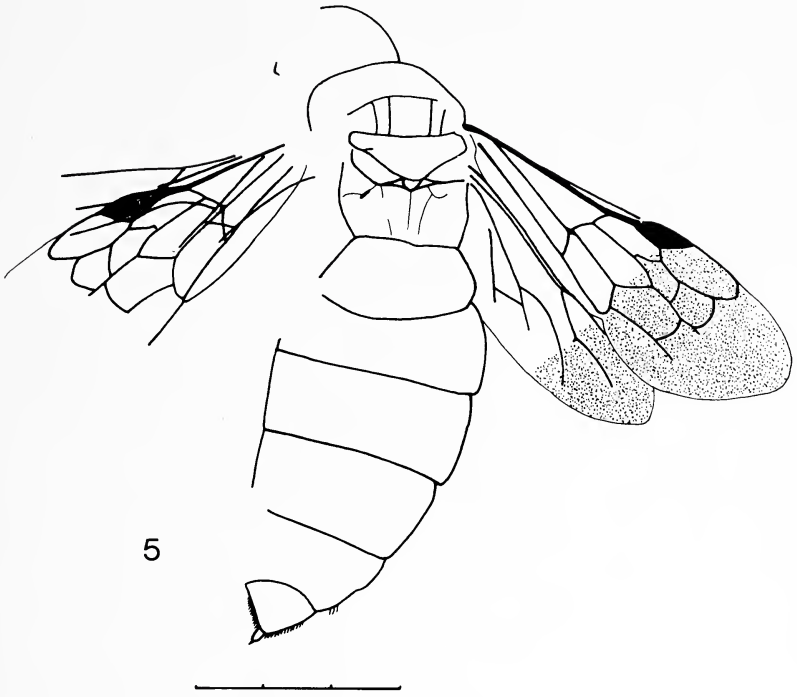


Figure 5. *Geotiphia pachysoma* Cockerell, holotype, no. In. 26929, British Museum (N.H.), London. Dorsal view.

punctures dorsally; lateral parts of metanotum striate longitudinally. Body with ground color dark, without obvious light spots; wing membrane infumate in apical two-fifths. Similar to *sternbergi* in having genual plates and dissected propodeum, differing in small size and in having cell 2 rm shorter; genual plates longer. Holotype: B.M. (N.H.), no. In 26929.

Geotiphia orientalis, new species
Figure 7

Fore wing length about 6 mm. Pterostigma rather long, with 2r-rs arising halfway before apex; cell 3r rounded at costal margin; RS between RS+M and 2r-rs almost straight; cells 1r, 2rm and 3rm all relatively short; 2rm and 3rm of subequal length; 1m-cu just before the middle of 2rm; 2m-cu at the middle of 3rm, which has the

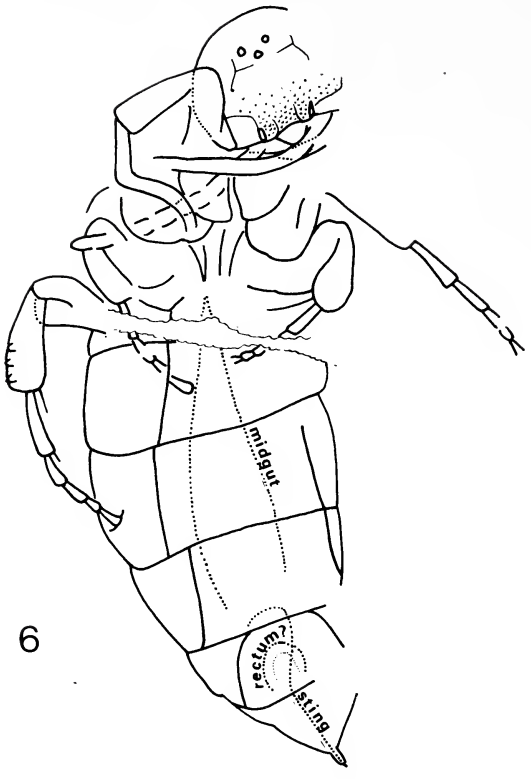


Figure 6. Same as Fig. 5, ventral view.

posterior side very short and the distal side (3r-m) strongly arched; crossvein cu-a at the fork of M+Cu; posterior genual plates absent on mid and hind femora. Surface sculpturing indistinct. Body structure as preserved lacks taxonomically important features, the details in part difficult to interpret. Ground color moderately dark; tibiae, tarsi, venation, pterostigma, and metasomal segments 2 and 3 less dark and without light spots (subsequent segments not preserved). Wing membrane not infumate.

Holotype (only specimen known): no. 3429/100, Paleontological Institute, Moscow, USSR; collected at Bolshya Svetlovodnaya River, Pozharsky District, Maritime Province, USSR: ?Upper Oligocene.

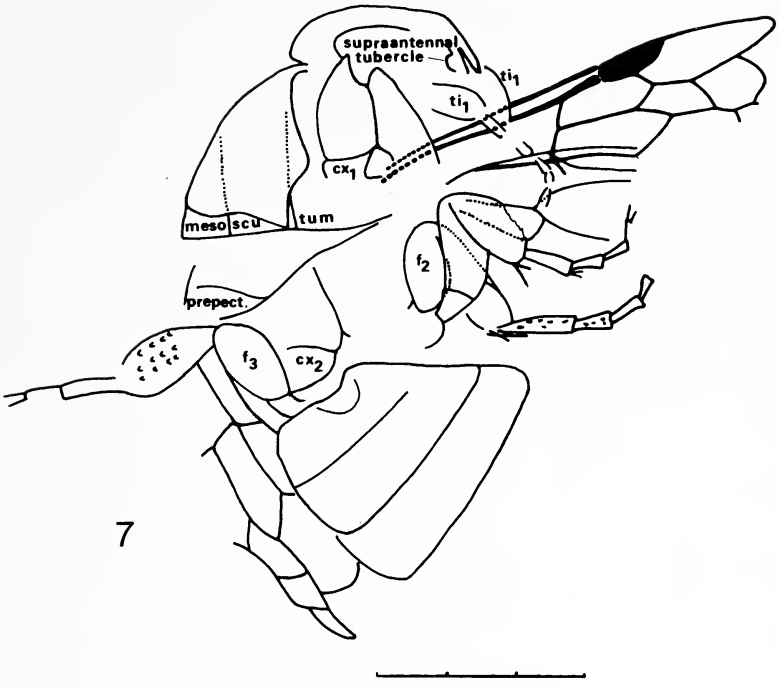


Figure 7. *Geotiphia orientalis,* holotype, no. 3429/100. Paleontol. Inst. Acad. Sciences, USSR, Moscow.

Comparison. As preserved this species is very similar to *foxiana,* differing in having a longer pterostigma, the posterior side of cell 3rm shorter, and the metasomal segments without light spots [The latter difference may be meaningless because the color pattern is known only for the metasonal sterna in *foxiana* and possibly only for terga in *orientalis*].

The above data show considerable taxonomic and anagenetic evolution of the subfamily Myzininae since the early Oligocene, an interval of about 35 million years. Both fossil genera have been replaced with a wide array of living genera, and even the most primitive modern genus, *Myzinum* Latreille, is probably further away from its Oligocene predecessors than these predecessors are from their anthoboscine ancestor. A paleontological history is not

known for any living myzinine genera, probably because of their preference for environments unfavorable to fossilization (xeric biotopes or, in the case of *Hylomesa,* tropical forests), but all of them can be easily derived from *Geotiphia* morphologically (but not from *Lithotiphia,* because of the apomorphic position of the cu-a crossvein). *Geotiphia* can be characterized in short as an anthoboscine with supraantennal tubercles, a position not consistent with the current phylogenetic scheme showing synapomorphies for all Tiphiidae other than Anthoboscinae and additional synapomorphies for all Tiphiidae except Anthoboscinae and Thynninae (Brothers, 1975). An alternative scheme with Myzininae independent of other subfamilies (excluding Anthoboscinae and probably Metochinae) seems to me more realistic.

The paleontological records indicate the minimal age of the Myzininae as Early Oligocene. The records seem too scanty, however, to help in identifying the geographic area where the subfamily arose.

Summary

Types of the previously described fossil Tiphiidae are studied. Two genera and six species are recognized, each species known only from the holotype: *Lithotiphia* Cockerell, with only one species, *scudderi* Cockerell; and *Geotiphia* Cockerell, with *foxiana* Cockerell (type-species), *halictina* Cockerell, *orientalis,* n.sp., *sternbergi* Cockerell, and *pachysoma* Cockerell. The fossils are found to represent the most primitive members of the subfamily Myzininae, indicating that the subfamily originated from the Anthoboscinae independently of the Thynninae, Tiphiinae, and Brachycistidinae. *Hoplisidea kohliana* Cockerell is now determined as belonging to the Sceliphronini of the family Sphecidae and will be treated elsewhere. All species mentioned are from the Lower Oligocene of Florissant, Colorado, except the new one, *G. orientalis,* which is from the ?Upper Oligocene of Sikhote-Alin Mts., Maritime Province of USSR.

Literature Cited

Brischke, D.
1886. Die Hymenopteren des Bernsteins. Schrift. naturf. Gesellsch. Danzig, n.f., **6**: 278–279.

Brothers, D. J.
1975. Phylogeny and classification of the Aculeate Hymenoptera, with special reference to Mutillidae. Univ. Kansas Sci. Bull., **50**(11): 483–648.

Cockerell, T. D. A.
1906. Fossil Hymenoptera from Florissant, Colorado. Bull. Mus. Comp. Zoology, Harvard Univ., **50**: 33–58.
1910. Fossil insects and a crustacean from Florissant, Colorado. Bull. Amer. Mus. Nat. Hist., **28**: 275–288.
1927. Hymenoptera and a caddis larva from the Miocene of Colorado. Ann. Mag. Nat. Hist., (9)**20**: 429–435.

Evans, H. E.
1966. The comparative ethology and evolution of the sand wasps. Harvard Univ. Press, Cambridge, Mass., p. 1–526.

Heie, O.
1967. Studies on fossil aphids (Homoptera, Aphidodea). Spol. Zool. Mus. Hauniensis, **26**: 1–274.

AN EARLY RECORD OF TANDEM RUNNING IN LEPTOTHORACINE ANTS: GOTTFRID ADLERZ, 1896

By
Robin J. Stuart[1]
Department of Zoology, Erindale College, University of Toronto,
Mississauga, Ontario, Canada L5L 1C6

Tandem running in ants is a recruitment technique in which one ant leads a single follower to a particular target or target area. It has been observed in various subfamilies, including the Myrmicinae, Ponerinae and Formicinae, and appears to function in recruiting nestmates to food discoveries, new nest sites, and into battle. Detailed experimental analyses have revealed that tandem running in some species is mediated by chemical and tactile cues, and various authors have suggested that this recruitment strategy may have been the evolutionary precursor of more sophisticated forms of group and mass recruitment (see Wilson 1971, Hölldobler 1978, Stuart and Alloway 1983).

The term "tandem running" was first used by Wilson (1959) to describe the behaviour of *Cardiocondyla venustula* and *C. emeryi* workers as they recruited nestmates to new food sources. However, Wilson (1959, 1971) attributed the first observation of tandem running to Hingston (1929), and his description of foraging in *Camponotus sericeus*. Nonetheless, Gottfrid Adlerz appears to have observed this behaviour even earlier. Adlerz (1896), writing in Swedish, described part of a nest emigration which he observed in nature and which involved a mixed colony of the obligatory slave maker *Harpagoxenus* (=*Tomognathus*) *sublaevis* and its *Leptothorax* slaves. In translation, Adlerz described the event as follows (see p. 9 of the original text):

> "On one occasion, I observed a *Tomognathus-Leptothorax* community being moved. The move had already started when I arrived. The distance moved was only from one side of the stump

[1]Present Address: Museum of Comparative Zoology Laboratories, Harvard University, Cambridge MA 02138 U.S.A.
Manuscript received by the editor October 10, 1985.

to the other and the move was obviously caused by a nearby community of stack ants (*Formica rufa*) which disturbed the ants at their previous location. During a period of 20 minutes, 8 *Tomognathus* workers were seen being carried in the usual manner by the *Leptothorax* workers. In addition, one *Tomognathus* worker was seen walking at the heels of a *Leptothorax* worker toward the new nest. The former held its head and antennae on the abdomen of the *Leptothorax* worker and seemed to get very agitated if it lost its guide during an unexpected turn and did not find it immediately. As is usual during this kind of guidance, the following ant carefully duplicated every little turn made by the guide."

The last few lines of this passage are a fairly accurate description of a tandem run; and the last line indicates that Adlerz was quite familiar with this recruitment technique.

Recent studies of the nest emigration behaviour of various *Harpagoxenus* species by Stuart and Alloway (1985) tend to confirm Adlerz's observations. Slaves in these mixed colonies are generally responsible for the bulk of the moving effort during nest emigrations: they transport brood and their adult nestmates, and lead tandem runs between the two nests. Slave-maker workers sometimes follow in slave-led tandem runs, and *H. americanus* and *H. canadensis* followers are relatively common. However, Stuart and Alloway did not observe any *H. sublaevis* followers in their study. Nonetheless, *H. sublaevis* followers have been observed in slave-led tandem runs to food (Buschinger and Winter 1977), and they probably occur occasionally during nest emigrations as well.

Various species of nonparasitic leptothoracine ants use tandem runs for recruiting nestmates to food (Möglich et al. 1974), during nest emigrations (Möglich 1978), and for recruitment into battle (Stuart and Alloway 1983); and certain leptothoracine slave makers, including *H. sublaevis* and *H. canadensis,* lead tandem runs during their slave raids (Buschinger et al. 1980, Stuart and Alloway 1983). Other slave makers in this group, including *H. americanus,* lead processions during their raids (Wesson 1939, Alloway 1979, Buschinger et al. 1980) and these processions constitute one of the more advanced recruitment techniques thought to be evolutionarily derived from tandem running (Wilson 1971, Stuart and Alloway

1983). *H. canadensis* appears to be an unusual obligatory slave maker, in that it will also lead tandem runs to food and during nest emigrations; behaviours which may be indicative of the relatively primitive nature of this species (Stuart and Alloway 1985).

Thus, Adlerz may have been the first to report tandem running in ants; and the tandem run he described apparently involved a *Leptothorax* slave leading a *Harpagoxenus sublaevis* slave maker during a nest emigration.

Acknowledgments

The author thanks Vivian Sterne for translating the Adlerz article. Financial support was provided by an Ontario Graduate Scholarship to the author and a Natural Sciences and Engineering Research Council of Canada grant to T. M. Alloway.

References

Alloway, T. M. 1979. Raiding behaviour of two species of slave-making ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* Wesson (Hymenoptera: Formicidae). Anim. Behav. **27**: 202–210.

Adlerz, G. 1896. Myrmecologiska studier III. *Tomognathus sublaevis* Mayr. Bihang Till K. Svenska Vet.-Akad. Handlingar **21** (IV-4): 1–76. (Translation)

Buschinger, A., and U. Winter. 1977. Rekrutierung von Nestgenossen mittles Tandemlaufen bei Sklavenraubzugen der dulotischen Ameise *Harpagoxenus sublaevis* (Nyl.). Ins. Soc. **24**: 183–190.

Buschinger, A., W. Ehrhardt and U. Winter. 1980. The organization of slave raids in dulotic ants—a comparative study (Hymenoptera; Formicidae). Z. Tierpsychol. **53**: 245–264.

Hingston, R. W. G. 1929. Instinct and intelligence. Macmillan Company, New York. xv + 296 pp.

Hölldobler, B. 1978. Ethological aspects of chemical communication in ants. Adv. Study Behav. **8**: 75–115.

Möglich, M. 1978. Social organization of nest emigration in *Leptothorax* (Hymenoptera; Formicidae). Ins. Soc. **25**: 205–225.

Möglich, M., U. Maschwitz, and B. Hölldobler. 1974. Tandem calling: A new kind of signal in ant communication. Science **186**: 1046–1047.

Stuart, R. J., and T. M. Alloway. 1983. The slave-making ant, *Harpagoxenus canadensis* M. R. Smith, and its host-species, *Leptothorax muscorum* (Nylander): Slave raiding and territoriality. Behaviour **85**: 58–90.

Stuart, R. J., and T. M. Alloway. 1985. Behavioural evolution and domestic degeneration in obligatory slave-making ants (Hymenoptera: Formicidae: Leptothoracini). Anim. Behav. **33**: 1080–1088.

WESSON, L. G. 1939. Contributions to the natural history of *Harpagoxenus americanus* Emery (Hymenoptera: Formicidae). Trans. Amer. Entomol. Soc. **65**: 97–122.

WILSON, E. O. 1959. Communication by tandem running in the ant genus *Cardiocondyla*. Psyche **66**: 29–34.

WILSON, E. O. 1971. The insect societies. Harvard Univ. Press, Cambridge, Mass. x + 548 pp.

NOTES ON THE BEHAVIOR OF THE DIMORPHIC ANT *OLIGOMYRMEX OVERBECKI** (HYMENOPTERA: FORMICIDAE)

By Mark W. Moffett

Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138

Species of the myrmicine genus *Oligomyrmex* are common in tropical Asia, although the ants are easily overlooked because of their small size and inconspicuous activities. The genus is of special interest because of the well developed worker dimorphism shown by all species. Some natural history information is available on *Erebomyrma* (Eidmann, 1936; Wilson, 1962, 1986), the American sister group to *Oligomyrmex* which has only recently been resurrected from synonomy with that genus (Wilson, 1986). However, the natural history of Old World *Oligomyrmex* ants has never been investigated.

I have made preliminary behavioral observations on a colony of *Oligomyrmex overbecki* Viehmeyer collected in Singapore (fig. 1). This species is clearly one of the world's smallest ants, with minor workers having head widths of 0.29–0.32 mm, while the "miniature" majors have head widths of 0.42–0.45 mm.

Materials and Methods

The study colony was collected on the grounds of the Botanic Gardens of Singapore, under bark still firmly attached to the trunk of a large *Eugenia grandis* tree (Myrtaceae), within 50 cm of ground level. The colony was placed in a plastic box 20 × 10 × 7 cm deep, with a moistened paper-mache bottom gouged towards one end with several small, shallow chambers, which were then covered with a sheet of glass. The ants moved into the artificial nest chambers, where they could readily be observed through the glass.

**Manuscript received by the editor January 26, 1986*

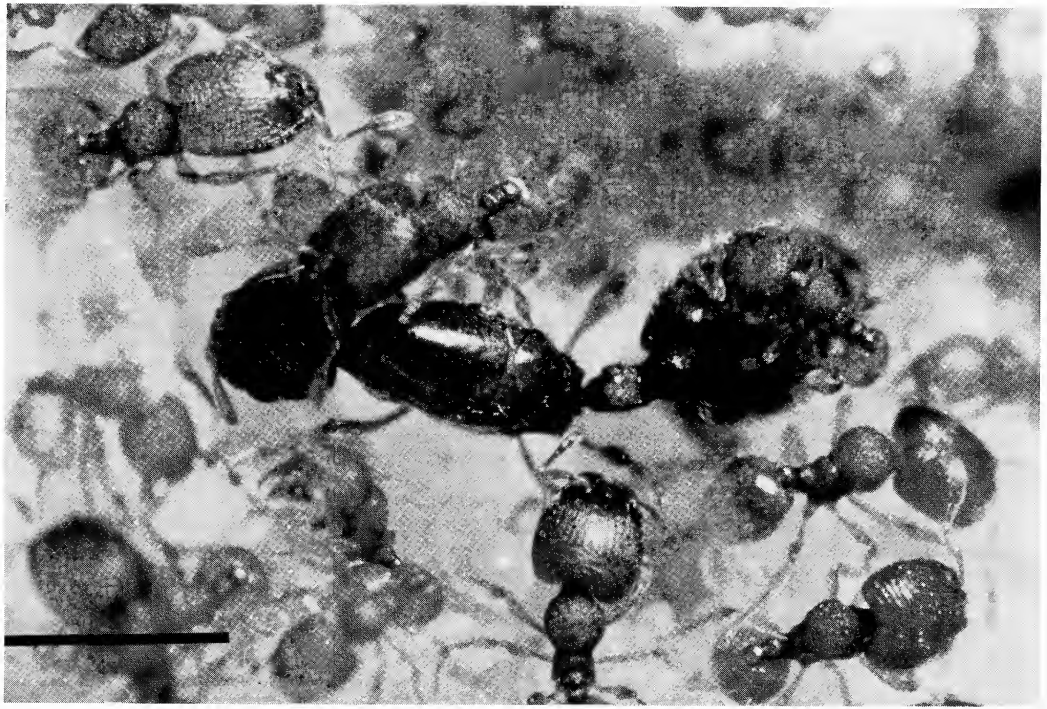


Fig. 1. Portion of *Oligomyrmex overbecki* study colony, showing the queen (center), minor and major workers, and brood. Scale bar = 1.0 mm.

A behavioral repertoire of the workers was compiled during 14 hours within a four day period beginning five weeks after the colony was collected. Estimates of total repertory size were made by fitting the observed behavioral frequencies to a lognormal Poisson distribution as described by Fagen and Goldman (1977), using a computer program supplied by R. M. Fagen. Additional behavioral data was gathered during roughly 25 hours of observations before the repertoire study.

While collecting the repertoire data, light-colored (callow) minors, which were uniformly golden-yellow to light brownish yellow, were distinguished from more darkly pigmented minors (varying from yellowish brown to brown, with antennae, legs and gaster lighter). In addition, the non-callows were subdivided into "repletes," which had their gasters moderately expanded with yellowish fluid, and non-repletes, which had small, contracted gasters. (By this criterion, all major workers and all callow minor workers were judged to be "replete.")

Voucher specimens from the study colony have been deposited in the Museum of Comparative Zoology (Harvard University).

Results

Nesting habits: The workers, queen and brood were tightly massed together between two small adjacent pieces of superficial bark. No food was seen within the nest. The nest area was originally estimated to contain about 400 workers, but upon return to the United States for study, 31 majors and about 180 minors remained. The original proportion of major workers probably approached ten percent.

Repertoire: The complete behavioral repertoire of the worker castes and subcastes is presented in Table 1. During the period in which the worker data was collected, 27 behavioral acts were observed for the queen, including 19 instances of nipping at immatures (described below), five self-grooming events and three instances of licking large larvae. The total repertoire size is estimated to be between 32–36 for the minor caste (data from all subcastes combined), and between 6–11 for the majors (95% confidence intervals).

Table 1. Repertoiries of *Oligomyrmex overbecki* worker castes, including subdivisions of the minor caste (see text). Numbers represent the proportion that each behavior represented of the total number of acts observed for each type of worker.

	Replete Minor	Non-replete Minor	Callow Minor	Major
Self-grooming	0.2443	0.2632	0.2237	0.6074
Allogroom minor	0.1401	0.1219	0.0461	0
Allogroom major	0.0104	0.0042	0.0066	0
Allogroom queen	0.0048	0.0014	0	0
Lick eggs	0.0248	0.0028	0.0921	0
Lick small larva	0.0200	0.0125	0.0066	0.0123
Lick large larva	0.2284	0.1759	0.1645	0.1411
Lick pupa	0.0587	0.0111	0.1974	0.0061
Carry eggs	0.0483	0.0069	0.1908	0
Carry small larva	0.0041	0.0028	0.0197	0
Carry large larva	0.0352	0.0457	0	0
Carry pupa	0.0028	0.0014	0	0
Carry minor worker	0.0035	0	0	0
Pull on queen	0.0014	0	0	0
Nip at immature	0.0076	0.0263	0.0066	0.2209
Assist in:				
larval ecdysis	0.0021	0.0014	0	0
ecdysis to pupa	0.0104	0.0042	0	0
adult eclosion	0.0035	0.0042	0	0
meconium removal	0.0035	0	0	0
Manipulate meconium	0.0193	0.0208	0.0197	0
Remove liquid waste	0.0062	0.0042	0	0
Handle nest material	0.0200	0.0706	0.0066	0
Forage	0.0179	0.1371	0	0
Retrieve solid food	0.0007	0.0014	0	0
Eat solid food	0.0248	0.0180	0	0
Feed on immatures	0.0304	0.0291	0	0
Feed larva solid food	0.0041	0	0	0
Regurgitate to:				
larva	0.0048	0.0028	0.0197	0
minor worker	0.0110	0.0248	0	0.0123
major worker	0.0048	0.0042	0	0
queen	0.0014	0	0	0
Carry or eat				
dead nestmate	0.0007	0.0014	0	0
No. acts observed	1449	722	152	163

The most conspicuous difference between the minor worker subcastes was that darkly pigmented non-repletes formed the bulk of the foragers. The repertoire data indicate several other differences in the frequency of behaviors (differences judged significant when $p < 0.05$ with chi-square test). Callow workers carried and licked eggs with greater frequency than did darker colored minors, but carried large immatures less frequently than did the latter. In comparison to darkly pigmented minors, callows rarely fed on solid foods and rarely allogroomed other workers. They also regurgitated to larvae more often than did the darker subcastes, yet apparently seldom regurgitated to other adult ants (difference in frequencies was not significant in the latter case).

Darkly-pigmented replete minors were intermediate between callow and non-replete minors in the frequencies of performance of many of those behaviors that varied most markedly between the minor subcastes. This suggests the possibility that these minors could be intermediate in age between callow minors (which were consistently replete) and non-replete minors.

Majors rarely foraged. During my observations only four majors were seen outside the nest of the captive colony, and one major was observed on a foraging route near the nest entrance in the field. Major workers apparently only fed by regurgitation.

The *O. overbecki* queen did not attract a large retinue of workers, but commonly one or two minors climbed onto her alitrunk or gaster. In addition, twice I observed replete minors briefly pulling on an antenna or mandible of the queen. Only rarely would a major climb onto the queen, and the density of majors was not noticeably greater near the queen than elsewhere.

Occasionally a major, minor, or the queen briefly appeared to try to grip or bite immatures, most commonly large larvae ("nip at brood" in Table 1). The function of this behavior is unclear, for although consumption of brood by minor workers was common, this biting behavior was most frequently performed by majors and apparently never damaged the immatures.

Larvae fed directly on fragments of insect corpses and from food regurgitated to them by minors.

Foraging Pattern and Diet: During my field observations columns of minor workers extended at least 30 cm from the nest on

the bark of the tree. In captivity, foragers often followed trunk routes at least 3–5 cm long before departing from them to forage singly.

Foraging minor workers fed at crushed fruit flies, fragments of freshly killed cockroaches, honey water baits, and Bhatkar diet (Bhatkar and Whitcomb, 1970). The ants avoided wounded fruit flies, and did not recruite minor and major workers to wounded prey as has been observed for *Erebomyrma nevermanni* (Wilson, 1986).

Soon after most large baits were presented, ants began arriving at the bait using a well-defined route, suggesting an odor trail had been laid down. However, recruitment behavior was difficult to document because of the tiny size of the ants and their weak response to food, even following periods of food deprivation.

Typically food was torn into small pieces and carried into the nest by solitary individuals. Whole dead fruit flies near the nest entrances were sometimes dragged into the nest by groups of 2–5 workers. However, this group transport behavior was poorly coordinated, as workers often pulled in conflicting directions.

Repletes: The *O. overbecki* majors were mildly replete ("semi-replete"), with their gasters never expanding to a size much greater than that of their heads. Moreover, the majors were no more replete than replete minor workers (judging by the volume of the gaster relative to that of the trunk).

Emigrations: Two shifts in nest location were documented in the laboratory. These followed periods of mild stress in which a 60 watt bulb was positioned 25 cm above the glass-covered nest chamber, while an unoccupied shaded chamber was provided 4–5 cm away. Within ten minutes the ants became more active, with darkly pigmented minors and a few majors leaving the nest chambers to explore the nest environs. Gradually more and more workers moved back and forth between the nest chambers and the shaded chamber, until it was clear that a set route had been established. Traffic along the emigration route was relatively steady throughout the period of brood transfer, with the number of ants passing an arbitrary point on the route exceeding 20 per minute.

The first immature was carried out of the nest 50 minutes into the second emigration; the sequence of brood transfer is documented in Figure 2. There was no group transport of immatures and no adult

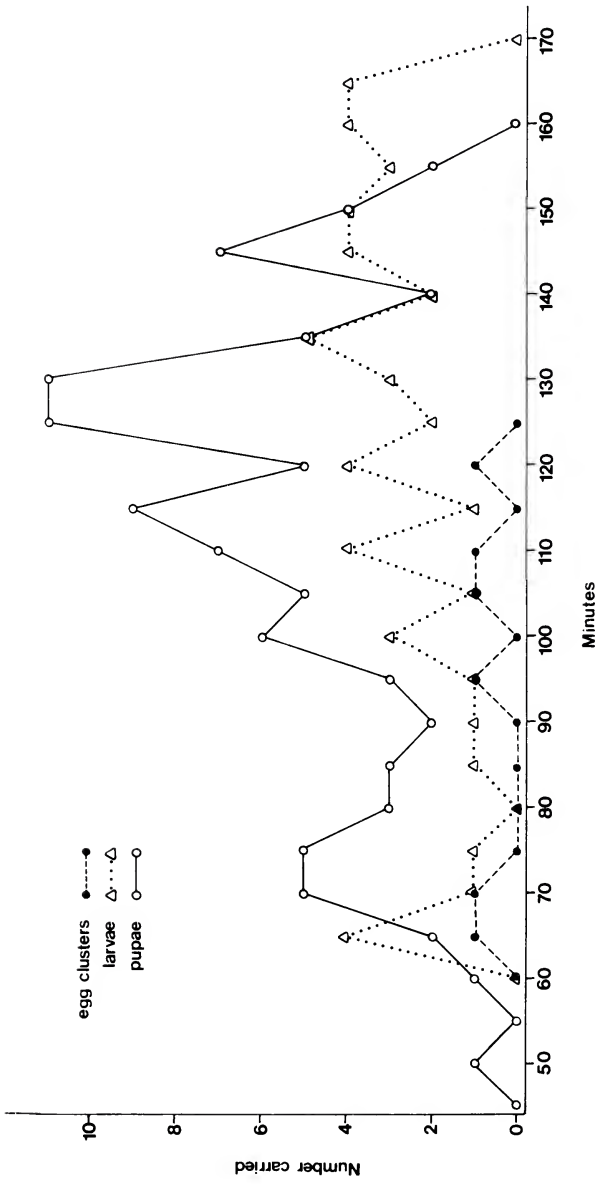


Fig. 2. Transfer of brood during an *Oligomyrmex overbecki* emigration. Times are given as the number of minutes since a strong light was first shined on the ants.

transport (although adult transport of minor workers was observed at other times; see Table 1). Eggs were completely transferred early in both emigrations. The last immatures to be transferred were larvae, not because workers selected pupae over larvae, but because the clumped larvae were difficult to pull apart for transport.

Only minor workers carried brood. Callow minors aided in pulling larvae and pupae free of piles of brood, but were clumsy at carrying larger immatures, which were quickly turned over to darker workers. Callows did, however, occasionally carry small larvae and eggs, taking egg clusters at a higher frequency than did other minors ($p < 0.01$, Fisher's exact probability test). Both replete and non-replete darkly pigmented minors transferred brood, and there were no significant differences between the frequency with which these subcastes carried different brood stages (for each brood stage $p > 0.05$).

The queen emigrated soon after brood transfer began in the first emigration, and ten minutes before the start of brood transfer during the second emigration. She moved rapidly within a small entourage of minors, but no workers rode on her during her journey.

Alarm and Defense: In three trials in which a small *Solenopsis geminata* worker with excised gaster was dropped into the brood area, most workers and the queen fled to adjacent nest chambers, with some minor workers carrying brood. Usually several major workers and a few minors stayed close to the intruder, mandibles open and facing the *Solenopsis*. Sometimes the ants attempted to bite the intruder. As described for *Erebomyrma nevermanni* (Wilson, 1986), the proportion of major workers near the intruder was clearly higher than in the colony as a whole. The ants responded similarly to freshly crushed minor heads presented on applicator sticks, suggesting the head as a source of alarm pheromones. Majors were particularly attracted to crushed minor heads, approaching them with their antennae directed ahead and mandibles open. There was virtually no response to crushed thoraxes and gasters.

Discussion

The major workers of *Oligomyrmex overbecki* apparently function primarily in colony defense and as repletes. The replete condition is very poorly developed (the ants are "semi-replete" in the sense of Wilson, 1986). Major workers also participated to a limited

extent in brood care. It is possible that the repertoire of majors is normally more restricted, but that high minor worker mortality in the captive colony and the resulting altered caste ratios led to an expansion of the major worker repertoire. The relationship between worker caste ratios and major repertoires for dimorphic ants is only beginning to be explored (see Wilson 1984, 1986).

Observations on a *Oligomyrmex* cf. *solidaris* colony collected in a rotten log from Bako National Park in Sarawak indicates that the majors of this species also are semi-replete and are crucial to colony defense. *O.* cf. *sodalis* majors were quick to attack *Pheidologeton silenus* and *Pheidole megacephala* workers dropped into the nest areas, and were much more efficient than minor workers in inflicting damage on the enemy. The importance of rapid and effective response to workers of these ant species was dramatized when the artificial nest container housing the *O.* cf. *sodalis* colony was raided by *Pheidole megacephala* ants. Within a four hour period the *Pheidole* had completely destroyed the *Oligomyrmex* colony of several hundred individuals and emigrated into their nest container.

Minor workers of *O. overbecki* show a pattern of temporal polyethism common for ants (Wilson, 1971), caring for immatures (particularly smaller immatures) as callows and shifting towards foraging activities as they age. Probably only younger workers are semi-repletes, with the ants losing their replete condition at about the time they begin to forage.

Oligomyrmex overbecki (as well as *O.* cf. *sodalis,* pers. obser.) forms trunk trail foraging routes, as do a variety of other pheidologetine ants: *Erebomyrma nevermanni* (Wilson, 1986); *Pheidologeton diversus* (Moffett, 1984) and all other *Pheidologeton* species (pers. obser.); and *Lophomyrmex bedoti* (Moffett, 1986).

Acknowledgements

I thank E. O. Wilson and D. H. Murphy for encouragement and advice. The research was supported by grants from the National Geographic Society and Harvard University.

Literature Cited

Bhatkar, A. and W. H. Whitcomb.
1970. Artificial diet for rearing various species of ants. Fla. Entomol. **53**: 229–232.

EIDMANN, H.
1936. Okologisch-faunistische Studien an sudbrasilianischen Ameisen. Arbeit. phys. angew. Ent. Berlin-Dehlem **3**: 26–48, 81–113.

FAGEN, R. M. AND R. GOLDMAN.
1977. Behavioral catalogue analysis methods. Anim. Behav. **25**: 261–274.

MOFFETT, M. W.
1984. Swarm raiding in a myrmicine ant. Naturwissenschaften **71**: 588–589.
1986. Observations on *Lophomyrmex* ants from Kalimantan, Java, and Malaysia. Malayan Nat. Journ., in press.

WILSON, E. O.
1962. The Trinidad cave ant *Erebomyrma* (= *Spelaeomyrmex*) *urichi* (Wheeler), with a comment on cavernicolous ants in general. Psyche **69**: 63–72.
1971. *The Insect Societies.* Belknap Press of Harvard University Press, Cambridge, 548 pp.
1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. **16**: 89–98.
1986. Caste and division of labor in *Erebomyrma,* a genus of dimorphic ants (Hymenoptera: Formicidae: Myrmicinae). Insectes Sociaux, in press.

PUPATION IN MYCETOPHILID FLIES: A CORRECTION

By William G. Eberhard

Smithsonian Tropical Research Institute and
Escuela de Biología, Universidad de Costa Rica
Ciudad Universitaria, Costa Rica

In a previous paper (Eberhard 1970) I made several claims regarding two species of the mycetophilid fly genus *Leptomorphus:* 1) the larval cuticle is not shed prior to pupation; 2) the last two and one half segments of the larva are discarded at pupation; and 3) the larval head capsule is engulfed by the pupa during pupation (Eberhard 1970). Recent, more detailed observations of *Leptomorphus* sp. have shown that points 1 and 3 are probably wrong, and this note is an attempt to present a more accurate account of pupation.

Observations were made during Sept. 1984 near San Jose, Costa Rica on larvae living on the undersurface of a fungus-covered board, where they inhabited silken sheets with slime trails similar to those of *L. bifasciatus* and *L. subcaeruleus* (Eberhard 1970). One observation of the process of pupation was made under a dissecting microscope. This larva hung on an approximately horizontal pupal line fastened at either end to a glass slide, and was observed from above (i.e. from the larva's ventral surface); occasionally I tilted the slide so as to check the larva in lateral view. Species identification in the genus *Leptomorphus* is not presently possible (R. Gagné, pers. comm.); voucher specimens of adults reared from the larvae observed are deposited in the U.S. National Museum.

Results

The overall sequence of events was the same as that described for *L. bifasciatus* and *L. subcaeruleus* (Eberhard 1970) except that larvae were on lines for somewhat less than 24 hours before pupating. Although the head capsule was nearly engulfed by the swollen anterior portion of the larva's body when pupation began, it did not disappear. Instead, as the anterior end of the animal's body assumed

Manuscript received by the editor October 2, 1985.

the new (pupal) shape, the head capsule moved smoothly posteriorly along the center line of the animal's ventral surface. The capsule paused briefly when it reached the "collar" or the anterior end of the band of silk that fastened the larva to the pupal line, then moved on smoothly, passing beneath the mat of silk threads holding the larva to the pupal line. As the head capsule neared the posterior end of the body, the cuticle there began to wrinkle during each contraction of the animal's body, also as noted previously (Eberhard 1970). When the posterior end of the pupa broke free from the remains of the larva, the head capsule was left as part of the mass of larval material that remained attached to the line. Careful dissections of some of these masses in water revealed the presence of not only the head capsule but also a long tubular sheath of very thin, transparent cuticle that bore the rows of dark denticles found near segmental boundaries on the ventral surfaces of larvae (Eberhard 1970). Thus the entire larval cuticle was shed during pupation, and the head capsule was not engulfed.

With respect to point 2 (posterior segments of larval body discarded during pupation), the new evidence does not clearly contradict previous descriptions. Several minutes prior to the migration of the head capsule to the posterior end of the larva, the last two and one half segments of the larva's body had darkened to a caramel brown color, and the material inside was amorphous and inert when viewed through the larval cuticle. In contrast, there were clear internal movements of well defined structures just anterior to this area, and it appeared that the posterior tip of the pupa had already formed and was being repeatedly pushed posteriorly against the inert brown material. When the larval cuticle was finally discarded (above), these posterior two and one half segments did not wrinkle or contract as did the rest of the larval cuticle, but retained their form, and the rows of denticles marking the segmental boundaries on their ventral surface remained clearly visible and as far apart as they had been in the intact larva.

Discussion

Probably the pupation process in the *Leptomorphus* species of previous reports was the same as that described here. The larval head capsule is small and partially transparent, and difficult to see without magnification. The observations of larval head capsules on

the ventral surfaces of pupal abdominal segments (Eberhard 1970) probably represent cases in which the larval skin was only partially shed, and broke near the tip of the pupal abdomen.

It has been argued that silk attachments to larval cuticle should be shed along with the larval cuticle (Eberhard 1970, Malloch 1917). Although this seems reasonable, it is clearly not the case in *Leptomorphus* sp. How the larval skin is shed so smoothly without disturbing, as far as can be seen, the silk lines that form the only attachment of the animal hanging on its pupation line remains a mystery.

Acknowledgements

I am grateful to R. Gagné for kindly identifying specimens, and the Vicerrectoría de Investigación of the Universidad de Costa Rica for financial support.

References

Eberhard, W. G.

1970. The natural history of the fungus gnats *Leptomorphus bifasciatus* (Say) and *L. subcaeruleus* (Coquillett) (Diptera: Mycetophilidae). Psyche **77**: 361–383.

Malloch, J. R.

1917. A preliminary classification of Diptera, exclusive of Pupiparia, based upon larval and pupal characters, with keys to imagines in certain families, Part I. Bull. Ill. State Lab. Nat. Hist. **12**(3): 161–407, pls. 28–57.

NEW PSELAPHIDAE FROM NEW HAMPSHIRE (COLEOPTERA)[1]

By Donald S. Chandler

Department of Entomology,
University of New Hampshire,
Durham, NH 03824

Two species of undescribed Pselaphidae were discovered during a comparison of the fauna of an uncut and a 40 year-old forest. The species are described here to provide names for a forthcoming paper comparing the pselaphid fauna of these two sites. Holotypes were cleared, disarticulated, and mounted on slides in Canada Balsam. Both are placed in the Field Museum of Natural History, Chicago. All measurements of specimens are in millimeters.

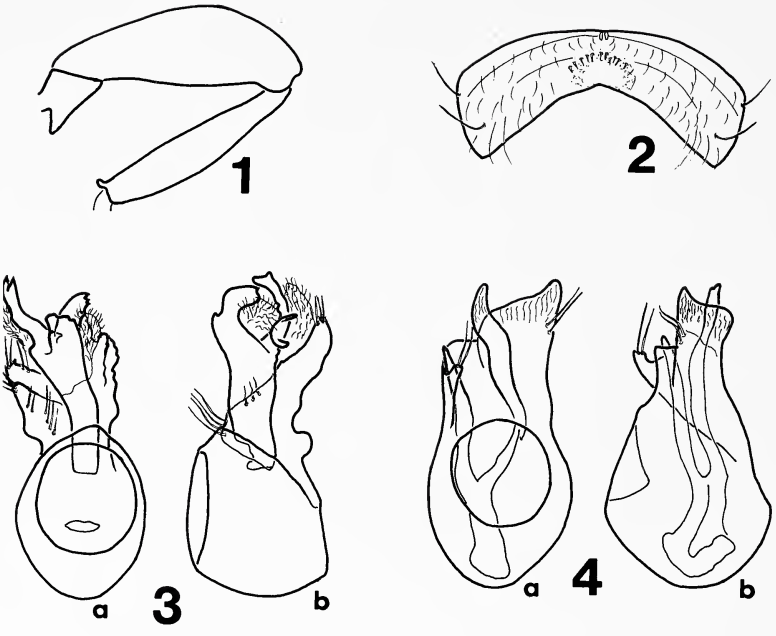
I would like to thank certain individuals for the loan of specimens, greatly extending the known ranges of these two new species. The abbreviations used to indicate specimen deposition follows the individual's affiliation: Rickard Baranowski, Lund University, Sweden (RBC); J. Milton Campbell, Biosystematics Research Institute, Ottawa, Canada (CNCI); Michael A. Ivie, Montana State University, Bozeman (DZEC); and Alfred F. Newton, Jr., Field Museum of Natural History, Chicago (FMNH). Specimens otherwise lacking an indication of deposition are in the collections of the author and the University of New Hampshire. I would like to thank J. F. Burger and R. Marcel Reeves, University of New Hampshire, for reviewing the manuscript.

Euplectus silvicolus n. sp.
(Figs. 1–3)

Length 1.36–1.44. Head glabrous, punctures indistinct, vertex with arms of distinct U-shaped impression originating from nude vertexal foveae; mandibles with five teeth on inner margin, third

[1]Scientific Contribution Number 1413 from the New Hampshire Agricultural Experiment Station.

Manuscript received by the editor March 11, 1986.



Figs. 1–3. *Euplectus silvicolus* n. sp., male. 1. ventral view last leg. 2. ventral view sternite VI. 3a. dorsal view aedeagus; 3b. left lateral view aedeagus.

Fig. 4. *Actizona borealis* n. sp., male aedeagus. a. dorsal view; b. left lateral view.

tooth largest. Elytra with four basal foveae. Tergites I-III with basal carinae, depressions between basal carinae only conspicuously setate on tergites I-II, I-III equal in length, IV half again as long as III.

Males with small spur at apices of all tibiae, metatrochanters at base with large medially directed spur; sternites IV-V simple, convex medially, VI obscurely depressed at middle, short aciculate setae in depression forming arc, division of sternite VII arcuate to left.

Females lacking spurs of tibiae and metatrochanters; sternites evenly convex.

Specimens examined, 27. *HOLOTYPE* male, *New Hampshire,* Carroll Co., The Bowl, 2.5 mi NW Wonalancet, VIII-6-1985, D. S.

Chandler, sift conifer logs. *PARATYPES:* 1 male, 1 female, same data except IX-1-1984; 1 male, same data except VIII-21-1985; 6 males, 10 females, same data except VI-8/14-1984 (2), VI-15/20-1984 (1), VI-28/VII-4-1984 (1), VIII-2/10-1984 (2), VIII-11/16-1984 (1), V-23/VI-4-1985 (1), VII-2/10-1985 (6), VII-24/30-1985 (1), VIII-22/28-1985 (1), flight intercept trap; 1 male, 1 mi N Wonalancet, East Fork Spring Brook, 1900′, VII-23-1985, D. S. Chandler, sift hemlock logs; 1 male, 1 female, same data except VII-2/10-1985, VII-31/VIII-6-1985, flight intercept trap. Coos Co.: Norton Pool, 2 mi E East Inlet Dam, IX-7-1984, D. S. Chandler, sift rotten spruce/fir logs. CANADA: *Nova Scotia:* 1 male, Cape Breton Highlands National Park, MacKenzie Mountain, PG648868, VII-4-1983, R. Vockeroth, pan traps (CNCI); 1 female, same data except Lone Shieling, PG729861, VI-25-1983, Y. Bousquet, pans (CNCI).

Biology: This uncommon species was only found in rotten conifer logs in an extensive litter survey at The Bowl. Most specimens were collected by flight intercept traps.

Discussion: This species is quite distinct among the Nearctic species of *Euplectus* by the presence of basal carinae on tergite III, spur of the male metatrochanters, simple sternites IV-VI, and smooth vertexal area. Since two species of *Euplectus* have been introduced to North America from Europe, the major faunal works of Jeannel (1950) for France and Besuchet (1974) for Central Europe were checked to be certain this species had not been previously described. In Wagner's (1975) recent revision of the Nearctic species of *Euplectus,* this species would be placed in the *californicus*-group. *Silvicolus* may be separated at couplet 5 of Wagner's key by the lack of any papilliform setae in the depression of sternite VI. This species differs from the generic diagnosis of Grigarick and Schuster (1980) in possessing basal carinae on tergite III, which are lacking in all other Nearctic species and also in the twenty Palearctic species in my collection.

Actizona borealis n. sp.
(Fig. 4)

Length 1.20–1.32. Head with pubescent vertexal foveae, penultimate antennomeres symmetrical, antennal club with parallel margins, twice as long as wide. Elytra with three basal foveae.

Promesocoxal foveae present, metasternal foveae separated by over two foveal diameters. Tergite lengths subequal, I-II with faint short basal carinae.

Males with protrochanters angulate on posterior margin, protibiae with small preapical spur; mesotrochanters posteriorly angulate, apical spur on inner margin of mesotibiae; sternites II-III with small setate tubercle near postero-lateral margins, VI simple, VII oval and setae over surface.

Females lacking spurs of tibiae and trochanters, lacking tubercles of sternites II-III.

Specimens examined, 8. *HOLOTYPE* male, *New Hampshire,* Coos Co., Jefferson Notch, 910 m, VII-14/31-1982, A. Newton & M. Thayer, window trap. *PARATYPES: New Hampshire:* Carroll Co.: 2 males, 2 mi NW Wonalancet, VI-8/14-1984, VI-15/20-1984, D. S. Chandler, window trap; 1 male, The Bowl, 2.5 mi NW Wonalancet, VIII-16-1984, sift rotten wood; 1 female, same data except XI-23-1984, R. M. Reeves, sift birch stump; 1 male, same data except, VII-23-1985, D. S. Chandler, sift rotten beech logs. CANADA: *British Columbia:* 1 male, Princeton, South Wash Creek, VII-22-1983, Lindgren funnel trap (DZEC); 1 male, Monashee Mountain near Cherryville, 1400–1600 m, VIII-12-1982, R. Baranowski (RBC), sifting litter and moss in spruce forest.

Biology: Collected in rotten beech and birch logs in uncut forests in New Hampshire.

Discussion: This species is very similar to *Actizona chuskae* Chandler from Arizona (Chandler 1985) in appearance and male characters. The genitalic form of *borealis* is identical in the British Columbia and New Hampshire specimens, and differs from that of *chuskae* in the form of the apex and internal spines of the aedeagus. These genitalic differences and the pubescent vertexal foveae of *borealis* readily separate the two species.

SUMMARY

Two undescribed species of Pselaphidae, *Euplectus silvicolus* n. sp. and *Actizona borealis* n. sp., were discovered during a faunal comparison of the forest floor Coleoptera of cut and uncut forests in New Hampshire.

Literature Cited

Besuchet, C.

1974. 24. Familie: Pselaphidae, pp. 305–362. *In:* Die Kaefer Mitteleuropas. Band 5, Staphylinidae II (Hypocyphtinae and Aleocharinae), Pselaphidae, 381 pp. Eds. H. Freude, K. W. Harde, and G. A. Lohse. Goecke & Evers, Krefeld.

Chandler, D. S.

1985. The Euplectini of Arizona (Coleoptera: Pselaphidae). Entomography **3**: 107–126.

Grigarick, A. A. and R. O. Schuster.

1980. Discrimination of genera of Euplectini of North and Central America (Coleoptera: Pselaphidae). Univ. Calif. Publs Ent. **87**: vi + 56 pp., 79 plates.

Jeannel, R.

1950. Coleopteres Pselaphides. Faune Fr. **53**: iii + 421 pp.

Wagner, J. A.

1975. Review of the genera *Euplectus, Pycnoplectus, Leptoplectus,* and *Acolonia* (Coleoptera: Pselaphidae) including Nearctic species north of Mexico. Entomologica am. **49**: 125–207.

A PRESUMPTIVE PHEROMONE-EMITTING STRUCTURE IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)*

By Torbjörn Kronestedt

Department of Entomology,
Swedish Museum of Natural History,
S-104 05 Stockholm, Sweden

The occurrence of pheromones in lycosid spiders has long been indicated on behavioural grounds. (For a review on chemical communication in spiders, see Tietjen and Rovner 1982.) There are bioassay evidences for *(1)* contact sex pheromones deposited on the substrate by females (Bristowe and Locket, 1926; Rovner, 1968; Hegdekar and Dondale, 1969; Richter et al., 1971; Dijkstra, 1976; Robert and Krafft, 1981), *(2)* contact sex pheromones associated with draglines laid by females (Kaston, 1936; Engelhardt, 1964; Richter et al., 1971; Dondale and Hegdekar, 1973; Tietjen, 1977, 1979b; Tietjen and Rovner, 1980; Robert and Krafft, 1981), *(3)* contact sex pheromones associated with female integument (Kaston, 1936), and *(4)* airborne sex pheromones given off by females (Tietjen, 1979a). Candidates for contact pheromone perception are chemosensitive hairs occurring on legs and palps. The number of these hairs is considerably increased in adult males in comparison to immatures and adult females (Tietjen and Rovner, 1980, 1982), and in certain lycosid genera this increase is rather drastic (Kronestedt, 1979a). No site of production and release of pheromones in wolf spiders has so far been found (Tietjen and Rovner, 1982). The present note focuses on a type of structure which is presumably involved in the release of pheromones in this spider family.

Studies on courtship behaviour in various lycosid species have been undertaken for supplementing morphological data in taxonomic contexts as well as for finding connections between adult male secondary sex characters and species-specific behavioural elements. Among the species studied, the adult male of *Alopecosa cuneata* (Clerck) has a unique character in its first tibiae being tumid

Manuscript received by the editor January 8, 1986.

(Fig. 1), the significance of which was unknown until the complete courtship sequence was observed (Kronestedt, 1979b, and ms. in prep.). Unlike what is common in lycosids, the female in this species plays a ritualistic active part in the premating display. The male is unable to mount the female before the following sequence has been passed through. The female will grasp one of the male's first tibiae with her chelicerae and pull him towards her, all the time holding her grip around his first tibia. This phase will last for approx. 10 s. After being released, the male will immediately mount the female.

On each side of the swollen first tibiae there is an oblique depression which may aid the female in maintaining her grip. Moreover, these tibiae are black and strongly sclerotized (except for the depressions). Their unique shape is evidently essential in the premating display of *A. cuneata,* and thus also a strong isolating mechanism when connected to behaviour. What releases the grasping behaviour of the female? No definite answer can be given until further extensive experiments have been made. However, in trying to find whether there is any chemical cue involved, the male tibia was examined using SEM.

The cuticle of the first tibia in male *A. cuneata* is equipped with numerous pores (Fig. 2a), a condition hitherto unknown among lycosids. These pores could well be the emitting site for some type of aphrodisiac. In the closely related species *A. pulverulenta* (Clerck), with normal first tibiae in the adult male, less abundant and more scattered leg pores were observed (Fig. 2b). The latter condition was also found in adult females of the mentioned *Alopecosa* species and in both sexes of other lycosid species as well (Fig. 2c, d). Therefore, it is assumed that the situation in male *A. cuneata* is a special adaptation of a commonly occurring contact pheromone releasing system in lycosid spiders. If these presumptive pheromones are, at least in part, volatile, they are also candidates in olfactory communication, for which other receptors may operate (e. g. the tarsal organ: Dumpert, 1978).

Most investigators have focused on the means by which males find and recognize females. However, it is of utmost importance for the female to identify the proper male, as males are often less discriminant. Chemical recognition of males by females in lycosids is little studied but probably of significance (Tietjen and Rovner,

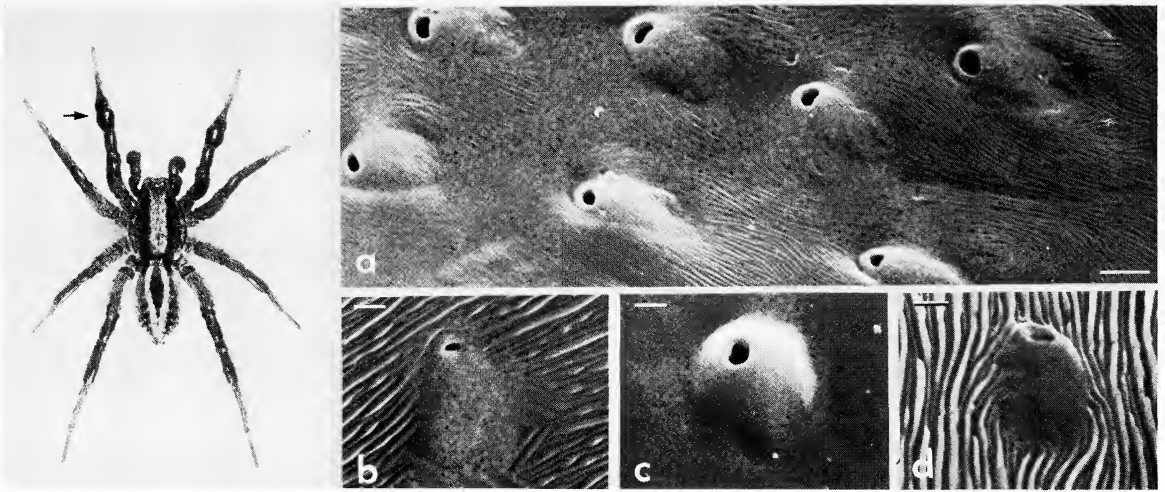


Fig. 1. (Left). *Alopecosa cuneata,* adult male. Note tumid first tibiae (arrow), one of which is gripped by the female during premating display.

Fig. 2. (Right). Presumably pheromone-releasing pores dorsally on adult male first tibia. a) *Alopecosa cuneata,* b) *A. pulverulenta,* c) *Pardosa fulvipes,* d) *Trochosa spinipalpis.* Scale: 2 μm (a), 1 μm (b–d).

1982), as already assumed for nocturnal species of the genus *Trochosa* (Engelhardt, 1964).

Semiochemicals play an indispensible rôle in spider communication. Locating sites of pheromone production and perception is essential for understanding behaviours and morphological adaptations of sexual significance.

Specimens of *Alopecosa cuneata* (Clerck), *A. pulverulenta* (Clerck), *Pardosa fulvipes* (Collett), and *Trochosa spinipalpis* F.O.P.-Cambridge were all collected in pitfall traps with formalin in the vicinity of Stockholm, Sweden. The material was stored in ethanol, and parts used for SEM were dehydrated in an ethanol series, kept in xylene for one or two days, cleaned in ultrasonic cleaner, air-dried, mounted on SEM stubs, and sputter-coated with Pd-Au. Examination was carried out with a JEOL JSM-35 at 15kV.

Summary

The cuticle of lycosid spider legs is shown to be equipped with pores presumably involved in the release of sex pheromones. The pores occur in both sexes. The male of *Alopecosa cuneata* has an increased number of pores on its first tibiae, and the premating behaviour in this species speaks in favour of the male producing some aphrodisiac from the leg pores.

Literature Cited

Bristowe, W. S. and Locket, G. H. 1926. The courtship of British lycosid spiders, and its probable significance. Proc. zool. Soc. Lond. **1926**: 317–347.

Dijkstra, H. 1976. Searching behaviour and tactochemical orientation in males of the wolfspider *Pardosa amentata* (Cl.) (Araneae, Lycosidae). Proc. K. ned. Akad. Wet. (C) **79**: 235–244.

Dondale, C. D. and Hegdekar, B. M. 1973. The contact sex pheromone of *Pardosa lapidicina* Emerton (Araneida: Lycosidae). Can. J. Zool. **51**: 400–401.

Dumpert, K. 1978. Spider odor receptor: Electrophysiological proof. Experientia **34**: 754–755.

Engelhardt, W. 1964. Die mitteleuropäischen Arten der Gattung *Trochosa* C. L. Koch, 1848 (Araneae, Lycosidae). Morphologie, Chemotaxonomie, Biologie, Autökologie. Z. Morph. Ökol. Tiere **54**: 219–392.

Hegdekar, B. M. and Dondale, C. D. 1969. A contact sex pheromone and some response parameters in lycosid spiders. Can. J. Zool. **47**: 1–4.

Kaston, B. J. 1936. The senses involved in the courtship of some vagabond spiders. Entomologica am. (N. S.) **16**: 97–167.

KRONESTEDT, T. 1979a. Study on chemosensitive hairs in wolf spiders (Araneae, Lycosidae) by scanning electron microscopy. Zool. Scr. **8**: 279–285.

KRONESTEDT, T. 1979b. Etologiska karaktärer vid taxonomiska studier av vargspindlar. Ent. Tidskr. **100**: 194–199.

RICHTER, C. J. J., STOLTING, H. C. J. AND VLIJM, L. 1971. Silk production in adult females of the wolf spider *Pardosa amentata* (Lycosidae, Araneae). J. Zool., Lond. **165**: 285–290.

ROBERT, T. AND KRAFFT, B. 1981. Contribution à l'étude des méchanismes de la communication tacto-chimique intervenant dans le rapprochement des sexes chez *Pardosa hortensis* Thorell (Araneae, Lycosidae). Atti Soc. tosc. Sci. nat. Memorie (B) **88** (Suppl.): 143–153.

ROVNER, J. S. 1968. An analysis of display in the lycosid spider *Lycosa rabida* Walckenaer. Anim. Behav. **16**: 358–369.

TIETJEN, W. J. 1977. Dragline-following by male lycosid spiders. Psyche **84**: 165–178.

TIETJEN, W. J. 1979a. Tests for olfactory communication in four species of wolf spiders (Araneae, Lycosidae). J. Arachnol. **6**: 197–206.

TIETJEN, W. J. 1979b. Is the sex pheromone of *Lycosa rabida* (Araneae: Lycosidae) deposited on a substratum? J. Arachnol. **6**: 207–212.

TIETJEN, W. J. AND ROVNER, J. S. 1980. Trail-following behaviour in two species of wolf spiders: Sensory and etho-ecological concomitants. Anim. Behav. **28**: 735–741.

TIETJEN, W. J. AND ROVNER, J. S. 1982. Chemical communication in lycosids and other spiders. *In* Spider communication. Mechanisms and ecological significance (P. N. Witt and J. S. Rovner, eds.): 249–279. Princeton Univ. Press, Princeton, N.J.

A NEW ARBORICOLOUS *THYREODON* FROM COSTA RICA (HYMENOPTERA ICHNEUMONIDAE: OPHIONINAE).

By Charles C. Porter[1]
Department of Biological Sciences, Fordham University
Bronx, NY 10458

Through courtesy of Daniel H. Janzen of the Department of Biology at the University of Pennsylvania, I have received for study a new *Thyreodon* of the *Atricolor* group (Porter 1984), reared by him in Costa Rican Tropical Deciduous Forest at Santa Rosa National Park. I herewith describe this ecologically aberrant *Thyreodon.*

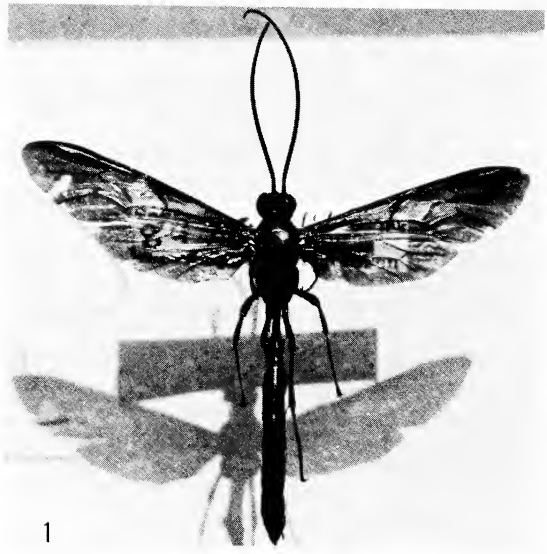
1. **Thyreodon santarosae** Porter, new species
(Figs. 1, 2)

Female. *Color:* antenna varying from almost all black to extensively dusky, brown, or dull yellowish brown; head and body shining black to brownish black (more lustrous on gaster) and with variably developed, diffuse, dull to (occasionally) light brown staining that usually is best developed on mandible and on gastric tergites 2 and 3 in part; legs sometimes entirely black or often with variable brownish suffusion on coxae and trochanters, trochantelli and femora shining medium brown with some dusky staining, and tibiae and tarsi dull pale brown with dusky only on last tarsomere; wings varying from almost entirely blackish to subdued golden yellow with blackish on apical 0.3 of fore wing, sometimes also near base of fore wing, as well as on apical 0.3 of hind wing and conspicuously (but often not extensively) in anellan cell of hind wing.

Length of fore wing: 15.6–19.0 mm. *Flagellum:* with 57–60 segments; 1st segment 2.0–2.3 as long as deep at apex. *Mandible:* with numerous, medium sized to large, basally denser, but mostly well discrete punctures. *Malar space:* 0.54–0.63 as long as basal width of mandible. *Temple:* 0.70–0.88 as long as eye in dorsal view; rounded

[1]Research Associate, Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, P.O. Box 1269, Gainesville FL 32602.

Manuscript received by the editor September 20, 1985



Figs. 1 and 2. *Thyreodon santarosae,* ♀. Paratypes. Dorsal views of entire insects. Fig. 1. Morph with dark wings and dark legs. Fig. 2. Morph with largely yellowish wings and partly pale legs. Note that males resemble females in dorsal view.

off and not receding or slightly expanded behind eyes. *Occipital carina:* bent mesad well above base of mandible, not approaching hypostomal carina. *Clypeus:* with abundant, commingled small to large punctures, most of which are separated by conspicuous smooth interspaces. *Lateral ocellus:* 0.77–0.90 as long as OOL. *Mesoscutum:* notauli not crested near base, broad and shallow, often (not always) becoming much weaker apicad, traceable 0.8 length of mesoscutum, scarcely convergent rearward; surface shining with numerous, small to medium sized, sharp punctures that are mostly separated by at least their diameters and sometimes in general by more than their diameters. *Scutellum:* high, convex, and shining with mostly subadjacent to adjacent small to medium sized, sharp punctures and with lateral carinae developed only at its base. *Mesopleuron:* sternaulus faint but usually percurrent; surface shining and with abundant, medium sized to small, sharp punctures that are mostly subadjacent to a little reticulately adjacent on lower 0.5 but which average slightly sparser on upper 0.5; speculum smooth and polished. *Lower metapleuron:* dully shining with small to medium sized, sharp, subadjacent punctures and some coarse peripheral wrinkling. *Propodeum:* swollen, contours rounded, the dorsal, lateral, and apical faces not sharply discrete; basal face shining with long and dense appressed grayish setae, its median field gently swollen and with the punctures very dense and tiny, its lateral field more shining with larger and more widely spaced punctures that expose much polished integument basad; lateral face with long and dense appressed setae and sometimes with variably developed moderately strong and mostly longitudinal wrinkles, as well as always with abundant medium sized, mostly subadjacent to adjacent (or sometimes extensively adjacent) punctures; apical face in comparison to rest of propodeum at least in large part contrastingly smooth and brilliantly polished with tiny punctures that emit long but little overlapping setae and often with many long and oblique, well separated and rather fine wrinkles.

MALE. *Color:* shows same range of variation as noted for female and, in addition, is marked with dull to bright yellow as follows: usually on basal 20–25 flagellomeres below (becoming duller distad); with a small to large ventral blotch on scape; on as little as 0.5 to as much as almost all of face (and sometimes also on

much of interantennal crest), except for brown on antennal sockets, brown also on a large to very large, quadrangular to (more often) dorsally narrowed median facial blotch (which is occasionally reduced to a small pale brown tinge and which sometimes, when conspicuous, surrounds a yellow area along clypeo-frontal suture), and also brown on a large to small or even obsolete area in and (frequently) above and below anterior tentorial pit, which may be confluent dorsally with the median brown facial area; sometimes also with yellow in malar space and broadly bordering hind orbit to as much as upper 0.2 of eye; and yellow also on most of clypeus except for its pale brown apical margin (clypeus rarely in large part brown with yellow only laterad); on most of basal 0.7 of mandible; on maxillary palpomeres 1–3; sometimes on an anterio-ventral fore coxal blotch; occasionally on a small dorso-lateral mid coxal blotch; on a broad anterio-dorsal stripe on fore and sometimes mid trochanters (yellow on mid trochanter often dull and weakly developed); sometimes also anterio-dorsally on fore and mid trochantelli; on a broad anterio-dorsal front femoral stripe; and rarely also on part of mid femur anterio-dorsally.

Length of fore wing: 14.6–18.5 mm. *Malar space:* 0.63–0.71 as long as basal width of mandible. *Hind tarsus:* segments 1–4 beneath with setae longer and denser than in female, pale gray, obliquely outstanding, closely packed, 0.4 as long as depth of tarsomeres. *Clasper:* in lateral view with dorsal margin on apical 0.46 broadly concave; dorso-apical angle semi-acute (not spiniform) and slightly upcurved; apical margin reclivously oblique; apico-ventral angle blunt. Other characters as described for female.

Type Material. Holotype ♂: COSTA RICA, Guanacaste Province, Santa Rosa National Park, D. H. Janzen, 1984 (Washington). Paratypes: 13♀ and 9♂: same data as Holotype: 2♀ (Washington), 1♀ and 1♂ (Cambridge), 1♀ (College Station), 1♀ and 1♂ (Gainesville), 1♀ and 1♂ (Lawrence), 1♀ and 1♂ (London), 1♀ and 1♂ (Los Angeles), 1♀ and 1♂ (New York), 1♀ and 1♂ (Ottawa); 1♀ and 1♂ (Philadelphia); 1♀ and 1♂ (Townes); 1♀ (Porter).

Variation. *Thyreodon santarosae* shows unusually marked intrapopulation variability in wing and leg color. This variation correlates appreciably but imperfectly with sex. Of the 13♀ examined, 10 have the wings predominantly yellow and in 9 of these

specimens all the tibiae and tarsi are pale brown (legs wholly black in the 10th yellow-winged ♀), whereas both wings and legs are black in the 3 remaining ♀. Among the 10 ♂, 1 has yellow wings but dark legs, 1 black wings but pale legs, and 8 both black legs and wings.

RELATIONSHIPS. *Thyreodon santarosae* belongs to the *Atricolor* group of *Thyreodon* (Porter 1984). This assemblage includes robust species with inflated temples, often weakly impressed notauli, and without a transverse or longitudinal crest at the anterior end of the notauli. It has several undescribed Sonoran, Middle American, Caribbean and South American species plus the Nearctic *T. atricolor* (Olivier), the Sonoran *T. fernaldi* Hooker, and *T. ornatipennis* Cresson from the Mexican wet tropics.

Thyreodon santarosae differs most trenchantly from its relatives in the extensively smooth and polished apical propodeal face (hind face of propodeum coarsely reticulo-rugose in *T. atricolor* and *T. fernaldi,* finely and densely puncto-reticulate in *T. ornatipennis).* Other diagnostic features are its laterally almost ecarinate scutellum; smooth speculum; and relatively sparse (mostly subadjacent or more distant) mandibular, clypeal, mesoscutal, and mesopleural punctures.

FIELD OBSERVATIONS AND HOSTS. Santa Rosa National Park, the type locality, is in Tropical Deciduous Forest at 250–350 m on the Pacific Coast of Guanacaste Province, Costa Rica. Daniel H. Janzen reared the entire type series from "larvae of Saturniidae in the Subfamily Ceratocampinae...collected at 3–20 m above the ground" (personal communication). The parasites emerged during April to December 1984. No individuals of *T. santarosae* were obtained by hand nets or Malaise Traps.

This species appears to be unique among *Thyreodon* for its apparent restriction to intermediate and higher strata of a Tropical Forest community and because it attacks ceratocampine caterpillars. Most other *Thyreodon* fly close to the ground or around understory shrubs at no more than 2 m altitude, and the only previous rearing data for this genus involve sphingid Lepidoptera that pupate in the ground (Porter 1984).

SPECIFIC NAME. For Costa Rica's Santa Rosa National Park, where Dan Janzen has found enthusiastic support for his ecological studies.

Collections

Listed below are the collections in which type material of *T. santarosae* is to be deposited. Institutional collections are coded by the names of the cities where they are housed, individual collections according to the surnames of their owners.

CAMBRIDGE. Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

COLLEGE STATION. Department of Entomology, Texas A&M University, College Station, TX 77843.

GAINESVILLE. Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville FL 32602.

LAWRENCE. Department of Entomology, Snow Entomological Museum, The University of Kansas, Lawrence, KS 66045.

LONDON. Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, England.

LOS ANGELES. Natural History Museum, Los Angeles County Museum of Natural History, Exposition Park, 900 Exposition Boulevard, Los Angeles, CA 90007.

NEW YORK. Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024.

OTTAWA. Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, Ottawa, K1A 06C, Canada.

PHILADELPHIA. Department of Biology, University of Pennsylvania, Philadelphia, PA 19104.

TOWNES. American Entomological Institute, c/o Dr. Virendra Gupta, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville FL 32602.

PORTER. Collection of Charles C. Porter, 301 North 39th Street, McAllen, TX 78501.

WASHINGTON. Department of Entomology, U. S. National Museum, NHB 168, Washington, DC 20560.

Acknowledgments

This paper was supported by Servicio de Parques Nacionales de Costa Rica and by Daniel H. Janzen's National Science Foundation Grant BSR 8403531.

Summary

Thyreodon santarosae n. sp. differs from its relatives in the *Atricolor* species group by having the hind propodeal face broadly polished. It was obtained only by rearing from ceratocampine saturniids (Lepidoptera) in Tropical Deciduous Forest at Santa Rosa National Park in northeast lowland Costa Rica. Host larvae were collected at 3–20 m in the forest overstory. Other known *Thyreodon* are active near ground level and those few that have been reared parasitize sphingid Lepidoptera.

Literature Cited

Porter, C. 1984. *Laticinctus* group *Thyreodon* in the northern Neotropics. *Wasmann Journal of Biology* **42**: 40–71..

DISTINGUISHING THE JUMPING SPIDERS *ERIS MILITARIS* AND *ERIS FLAVA* IN NORTH AMERICA (ARANEAE: SALTICIDAE)*

By Wayne Maddison

Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138

The jumping spiders now identified as *Eris marginata* are among the most frequently encountered in North America, for they are common on trees, shrubs and herbs throughout much of the continent. However, two species have been confused under this name. One is an abundant transamerican species whose proper name is *Eris militaris;* the other is *Eris flava,* widely distributed in eastern North America though common only in the southeast. In this paper I describe how they may be distinguished. The abbreviation MCZ refers to the Museum of Comparative Zoology; ZMB to the Zoologisches Museum, Humboldt-Universität zu Berlin.

Eris militaris (Hentz), NEW COMBINATION
Figures 2–7, 14

Attus militaris Hentz 1845: 201, pl. xvii, fig. 10♀, 11♂. Type material lost or destroyed (see Remarks, below), from North Carolina and Alabama. Neotype here designated, 1♂ in MCZ from North Carolina with label "NC: JACKSON CO., Coyle Farm, 1.5 mi SW of Webster, 7 Sept. 1975; F. Coyle."

Plexippus albovittatus C. L. Koch 1846: 118, fig. 1178♀. Syntypes in ZMB 1♀ with labels "P. albovittatus 1739" and "1739", and 1♀ with label "P. albovittatus ZMB 1739", examined. Type locality Pennsylvania (Koch, 1846). NEW SYNONYMY.

Eris aurigera C. L. Koch 1846: 189, fig. 1237♂. Syntypes in ZMB 1♂ with carapace and abdomen in alcohol with labels "Eris aurigera C. L. Koch*, 1774" and "Typus" and remaining body parts mounted on cover slip in small box with label "(Eris aurigera Koch*) Dendryphantes marginatus Walck., ZMB 1774a, D. militaris Hentz, XI, Syntypus" and 1♂ mounted on cover slip with label "Eris aurigera*, C. L. Koch, ♂ Rf.?, 1774b, Syntyp., Paraphidippus", both examined.

Euophrys humilis C. L. Koch 1846: 217, fig. 1262♀. Holotype 1♀ in ZMB with labels "Holotypus", "1804", "ZU 1804", "Euophrys humilis", "Pennsylvanien, Zimmermann leg.", "Zool. Mus. Berlin", examined.

Manuscript received by the editor January 15, 1986.

Icius albovittatus Keyserling 1884: 502, fig. 10♀. Syntypes 1♀ 1 immature in MCZ with labels "15 Icius albovittatus Keys., ♀ Massachusetts", "15", examined. (Junior homonym of *Icius albovittatus* Keyserling, 1883.)

Icius moestus Banks 1892: 77, pl. V, fig. 33♂. Holotype in MCZ 1♂ with labels "Icius moestus Bks", "Dendryphantes moestus Bks type", "Ithaca, N.Y.", "Nathan Banks Coll.", examined.

Dendryphantes marginatus:—Simon 1901: 624 (not *Attus marginatus* Walckenaer; see Remarks below).

Dendryphantes louisianus Chamberlin 1924: 34, fig. 51♀. Holotype in MCZ 1♀with label "*Dendryphantes louisianus* Ch. ♀ Type, La.: Kenner, R. V. Chamberlin Coll.", examined.

Phidippus molinor Chamberlin 1925: 133, fig. 49♀. Holotype in MCZ 1♀ with label "*Dendryphantes molinor* Chamb., ♀ holotype, Utah: Mill Creek Canyon, R. V. Chamberlin Coll. 1071", examined.

Paraphidippus marginatus:—Chickering 1944: 180 (in part), figs. 78–82.

Paraphidippus marginatus:—Kaston, 1948: 479.

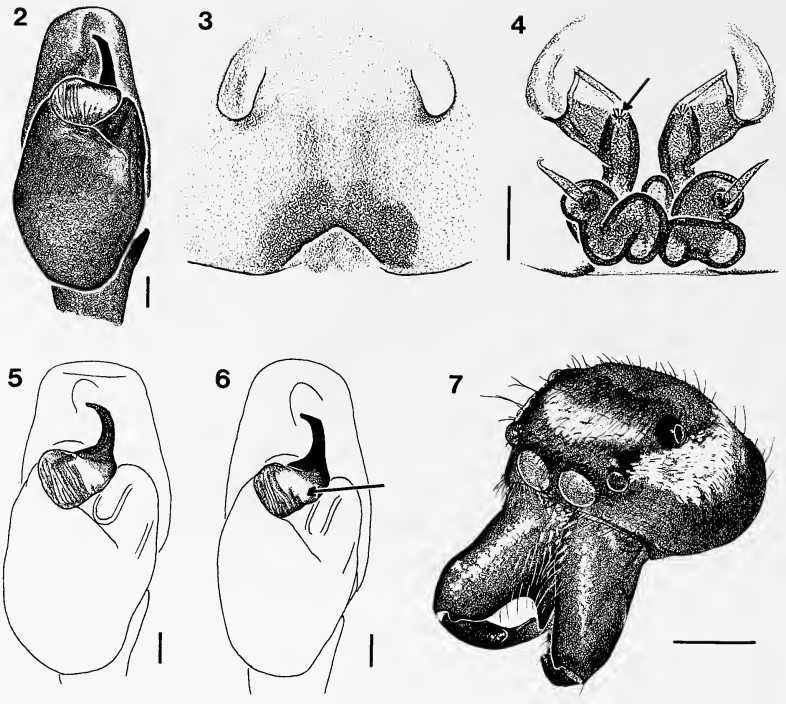
Eris marginata:—Kaston 1973: 118 (in part), figs. 51–54.

Remarks on synonymy: It is unfortunate that most workers since about 1930 have accepted without question Simon's (1901: 624) synonymy of *Attus militaris* Hentz 1845 with *Attus marginatus* Walckenaer 1837, for the synonymy is incorrect: Walckenaer's original description (p. 466) and Abbot's figure (number 444) clearly refer to *Hentzia palmarum* (Hentz). Walckenaer refers to an elongate abdomen, a fawn-brown first pair of legs, yellow posterior legs, and chelicerae elongate and held in front, whereas *Eris militaris* has an abdomen of typical width, posterior legs strongly marked with dark brown, and chelicerae robust and divergent. Abbot's drawing (see Figure 1), on which Walckenaer based his description of *A. marginatus,* unambiguously portrays a male *Hentzia palmarum,* given that his specimen was from Georgia. Because the name *marginatus* is inappropriate for the transamerican *Eris* species, another name must be used. The type material for the next oldest name, *Attus militaris,* is apparently lost or destroyed. Burgess (1875, vii) said that only 60 specimens glued on cards remained of Hentz's collections, the remainder having been destroyed. The surviving specimens were in the collection of the Boston Society of Natural History, which has subsequently become the Boston Museum of Science. The Museum of Science no longer has these specimens nor any record of them (D. Salvatore, pers. comm.), nor does the MCZ, which received many of the Society's collections. I presume Hentz's types to have been lost or destroyed. Without the type material the interpretation of *Attus militaris* is not entirely clear, for Hentz's

Fig. 1. Abbot's figure 444 on which Walckenaer (1837) based his description of *Attus marginatus.* Abbot's legend reads "444. Aranea. Taken 4th April, two upon a Myrtle on the side of a Pond in the Oak Woods of Burke County. Rare." From a color slide taken by Allen Brady of Abbot's (1792) original in the British Museum (Natural History).

1845 description might refer to either the transamerican or the eastern species. Still, his failure to describe a white marginal band in the male, and his illustration showing a dark femur on the male palp (better seen in his original color drawing) both suggest that he had the transamerican species. Therefore, I have designated a male of this species as neotype for *Attus militaris.* This is advantageous for nomenclatural stability, for Hentz's name was the only name commonly used before 1930 for the abundant transamerican species. In contrast, I have been unable to find any use of Koch's names *albovittatus, aurigera,* and *humilis* since 1864, except in synonymies and catalogues.

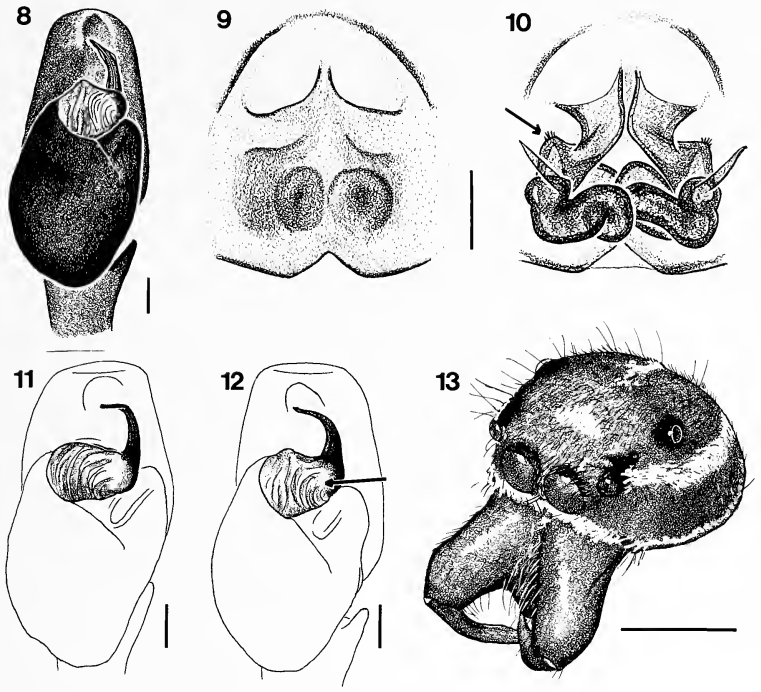
Male carapace margin and clypeus brown (Fig. 7), without white scales, or if the clypeus has white scales, then they only rarely extend along margin past palps. Longitudinal white bands extending back



Figs. 2–7. *Eris militaris* 2. Left palp, ventral view (Port Elgin, Ontario). 3. Epigynum,ventral view (Dwight, Ontario). 4. Cleared epigynum, dorsal view (Dwight, Ontario); arrow shows flowerlike gland opening. 5. Left palp, oblique view from the ventral-retrolateral-distal (Pine Lake, Michigan), and 6. Same (Forsyth, Georgia); arrow shows lack of wrinkles on retrolateral half of embolar base. 7. Male carapace and chelicerae (Walloon Lake, Michigan), oblique view. Scale bars 0.1 mm for 2–6; 1 mm for 7.

from anterior lateral eyes usually broad. *Palp* femur and patella as dark as the more distal segments. *Embolus* shorter and stouter, and more broadly joined to the embolar base (Figs. 5, 6) than in *flava.* Wrinkles on the ventral surface of the embolar base usually straight, and absent from the retrolateral half (Figs. 2, 5, 6; see arrow in Fig. 6).

Female carapace generally with a continuous covering of white scales above margin beneath anterior lateral eyes. *Epigynal openings* usually smaller and more laterally facing (Fig. 3) than in *flava.*



Figs. 8–13. *Eris flava* 8. Left palp, ventral view (Florida City, Florida). 9. Epigynum, ventral view (Point Pelee, Ontario). 10. Cleared epigynum, dorsal view (Point Pelee, Ontario); arrow shows flowerlike gland opening. 11. Left palp, oblique view from the ventral-retrolateral-distal (Pine Lake, Michigan), and 12. Same (Florida City, Florida); arrow shows curled wrinkles on retrolateral half of embolar base. 13. Male carapace and chelicerae (S. of St. Joseph, Michigan), oblique view. Scale bars 0.1 mm for 8–12; 1 mm for 13.

Each duct proceeds medially to a flower-like structure (apparently gland openings; see arrow in Fig. 4), then posteriorly.

Habitat varied; common on trees and shrubs. Distribution shown in Fig. 14.

Eris flava (Peckham and Peckham)
Figures 8–13, 15

Dendryphantes flavus Peckham & Peckham 1888: 39, pl. I, fig. 27♀, pl. III, figs. 27, 27a♀. Syntypes in MCZ 3♀, 1 immature ♀ with label "Dendryphantes flavus

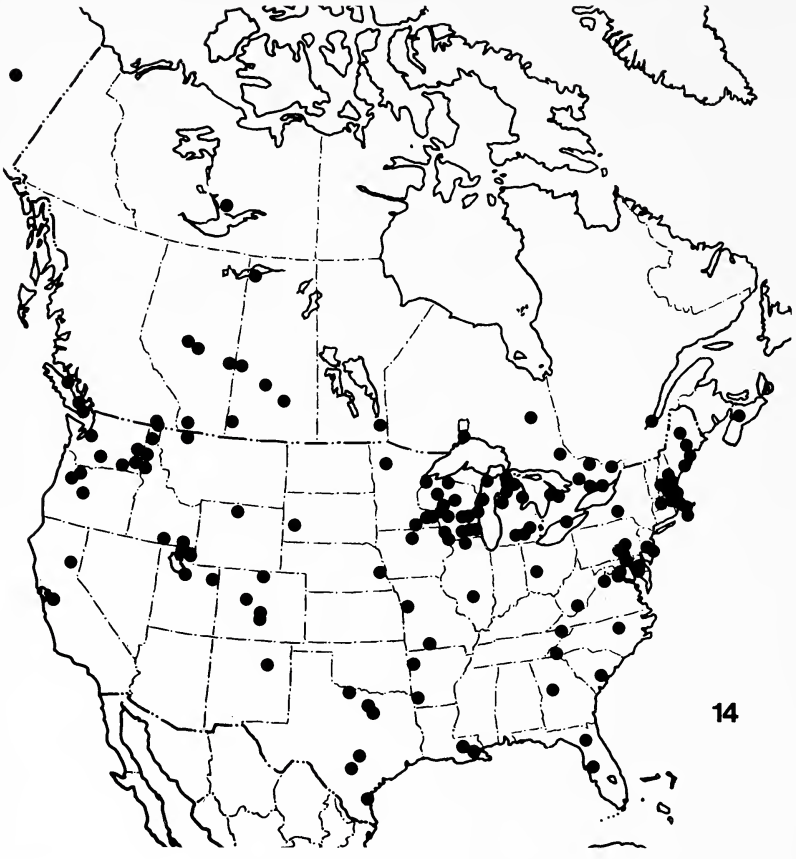


Fig. 14. Distribution of *Eris militaris.*

Pkm., 1888. New York. Type. ♀", examined. Type vial also contains one immature *Phidippus.*

Dendryphantes armatus Banks 1909: 167, fig. 5♂. Syntypes in MCZ 7♂ with labels "S. de las Vegas, Cuba 10–17. 07", Dendryphantes armatus Bks.", "type", "D. militaris H, armatus B, Cuba", "Nathan Banks Coll.", examined. NEW SYNONYMY.

Paraphidippus militaris:—Bryant 1940: 502.

Paraphidippus marginatus:—Chickering 1944: 180 (in part).

Eris marginata:—Kaston 1973: 118 (in part).

Eris flava:—Kaston 1973: 120, figs. 66–67.

Remarks on synonymy: *Eris flava* was thought to be an uncommonly collected species known only from females (Kaston, 1973).

While less common than *militaris,* many males are available in collections (including the Peckham and Banks collections), identified as *militaris* or *marginata.* Chickering's Michigan collections are mixed *E. militaris* and *E. flava.* Though most of Kaston's identifications were correct, at least some Floridian males he identified as *E. marginata* prior to his 1973 paper are *E. flava.*

Male carapace with marginal band of white scales extending across clypeus (Fig. 13) and usually back well past the palps. Longitudinal white bands extending back from ALE usually narrower than in *militaris. Palp* femur and often patella distinctly paler than more distal segments. *Embolus* longer and thinner than in *militaris,* arising more abruptly and more directly behind the embolar base (Figs. 11, 12). Wrinkles on embolar base, especially the more retrolateral ones, are distally curled retrolaterally (Figs. 8, 11, 12; see arrow in Fig. 12).

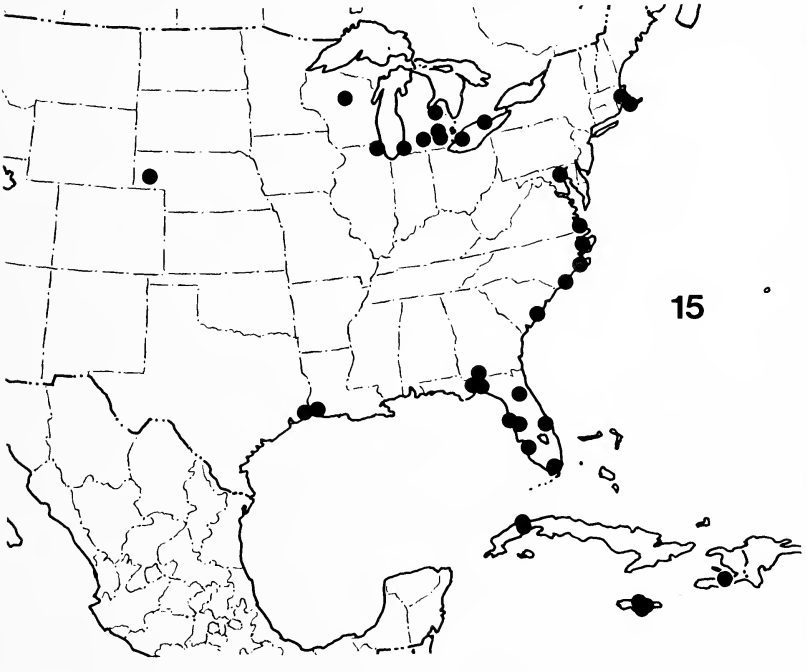


Fig. 15. Distribution of *Eris flava.* The specimen from the North Platte River at Bridgeport, Nebraska was collected by me, and the identification checked carefully.

Female carapace with patch barren of scales just above the marginal white band at a point below anterior lateral eyes. *Epigynal openings* wider and face more anteriorly (Fig. 9) than in *militaris*. Each duct first proceeds posteriorly and then laterally to the flower-like structure (Fig. 10, arrow), then posteriorly. The epigynal ducts are the best distinguishing feature.

Habitat information is sparse, but the species appears to prefer marshes and fields. Found in cedar swamp (Mass.), sweeping grass and herbs near river (Nebr.), on vegetation in marshy area (Ont.), meadow (Ill.), on *Nelumbo lutea* and in fields (Fla.). Distribution shown in Fig. 15.

Acknowledgements

All but a few of the specimens examined are in the MCZ. The types of Koch names were kindly loaned by M. Moritz and S. Fischer of the ZMB. For the loan of the remaining specimens, I thank E. Schlinger and D. Wagner (Essig Museum, University of California, Berkeley) and W. J. Gertsch (American Museum of Natural History). H. W. Levi and D. R. Maddison gave useful comments on the manuscript.

References

Abbot, J.
1792. Drawings of the Insects of Georgia, in America, vol. 14, Spiders. Unpublished manuscript in the British Museum (Natural History) (Copy seen).

Banks, N.
1892. The spider fauna of the Upper Cayuga Lake Basin. Proc. Acad. Nat. Sci. Philadelphia, 1892: 11–81, 5 pl.
1909. Arachnida of Cuba. Estación central agronómica de Cuba, Second Report, Part II, pp. 150–174.

Bryant, E. B.
1942. Cuban spiders in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., **86**: 259–532+22 pl.

Burgess, E.
1875. Preface, pages v–xiii, *in* A collection of the arachnological writings of Nicholas Marcellus Hentz, M. D., Boston Soc. Nat. Hist.

Chamberlin, R. V.
1924. Descriptions of new American and Chinese spiders, with notes on other Chinese species. Proc. U.S. Nat. Mus., **63**(13): 1–38.
1925. New North American spiders. Proc. California Acad. Sci., (4) **14**(7): 105–142.

CHICKERING, A. M.
1944. The Salticidae (jumping spiders) of Michigan. Papers Michigan Acad. Sci., Arts & Letters, **29**: 139–222.
HENTZ, N. M.
1832. On North American spiders. American J. Sci., **21**: 99–122.
1845. Descriptions and figures of the Araneides of the United States. Boston J. Nat. Hist., **5**: 189–202.
KASTON, B. J.
1948. Spiders of Connecticut. Connecticut State Geol. and Nat. Hist. Survey, **70**: 1–874.
1973. Four new species of *Metaphidippus,* with notes on related jumping spiders (Araneae: Salticidae) from the eastern and central United States. Trans. Amer. Micros. Soc., **92**: 106–122.
KOCH, C. L.
1846. Die Arachniden. Dreizehnter Band. Nürnberg, pp. 1–234.
PECKHAM, G. W. AND E. G. PECKHAM
1888. Attidae of North America. Trans. Wisconsin Acad. Sci., Arts & Letters, **7**: 3–104.
1909. Revision of the Attidae of North America. Trans. Wisconsin Acad. Sci., Arts & Letters **16**: 355–646.
SIMON, E.
1901. Histoire Naturelle des Araignées. Deuxième édition. Tome 2, fasc. 3, pp. 381–668. Paris.
WALCKENAER, C. A.
1837. Histoire naturelle des Insectes. Aptères. Tome 1. Paris, pp. 1–682.

EVIDENCE OF WORKERS SERVING AS QUEENS IN THE GENUS *DIACAMMA* (Hymenoptera: Formicidae)

By Mark W. Moffett
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

There is no morphologically distinguishable queen caste known in the ponerine genus *Diacamma.* Wheeler and Chapman (1922) observed a typical *Diacamma* worker copulating with a normal male, and it has been assumed that some workers are functioning as reproductives. I report an experiment that supports this view.

Ants in the *D. rugosum* complex at Sullia in Karnataka State, southern India, live in polydomous colonies; foragers move freely between nests within a colony, which are separated by one to several meters. Each nest is a blind-ended tunnel 10–25 cm deep containing brood and between about 50–120 workers. When individual nests within a colony were collected and kept in captivity, some workers foraged frequently, while the remainder never left the artificial nest tubes.

In a preliminary experiment conducted during February and March, 1982, the ants taken from one nest were sorted into foraging and non-foraging behavioral types and then further divided into groups of 5–6, with eight groups of foragers (total 45 ants) and four groups of non-foragers (total 21 ants); every group was provided a separate test tube "nest" with stoppered water source and no brood. The foraging ants continued to come and go from their nest tubes, and in none of these groups were any eggs produced over a period of a month. Non-foraging ants continued to stay within their nest tubes and eventually had to be provided food within the tubes. In all four non-foraging groups the test tubes soon held brood, and the five immatures that survived to the pupal stage (three from one tube and two from another) were workers.

This indicates that part of the worker population is fertilized and is serving as queens, as is the case with the African ponerine *Ophthalmopone berthoudi* (Peeters and Crewe, 1984, 1985), which also lacks winged gynes.

I am grateful to R. Gadagkar and M. Gadgil for aid during my stay in India.

LITERATURE CITED

PEETERS, C. AND R. CREWE. 1984. Insemination controls the reproductive division of labor in a ponerine ant. *Naturwissenschaften* **71:** 50–51.

_____ 1985. Worker reproduction in the ponerine ant *Ophthalmopone berthoudi*: an alternative form of eusocial reproduction. *Behav. Ecol. Sociobiol.* **18:** 29–37.

WHEELER, W.M. AND J.W. CHAPMAN. 1922. The mating of *Diacamma*. *Psyche* **29:** 203–211.

NEW SPECIES AND GENERA OF AMISEGINAE FROM ASIA (CHRYSIDIDAE, HYMENOPTERA)*

By Lynn Siri Kimsey

Department of Entomology,
University of California, Davis 95616

In a large shipment of miscellaneous, non-American chrysidids sent to me by Henry Townes of the American Entomological Institute, Gainesville, Florida, all of the Amiseginae turned out to be new species. The majority of these were collected by E. and M. Becker in the Pasoh Forest Reserve in Malaysia. The new species of *Cladobethylus* and *Isegama* represent range extensions for both genera. *Cladobethylus* was previously known from Sri Lanka and Mindanao, Philippines. *Isegama* has been previously described only from Sri Lanka.

Holotypes have been deposited in the American Entomological Institute, Gainesville, Florida.

A variety of structures, dimensions and abbreviations, used below, need explanation. The malar space is the distance between the base of the mandible and the ocular margin. On the mesopleuron there are 2 possible carinae and/or sulci. The scrobal sulcus extends transversely across the mesopleuron from the scrobal pit. The oblique mesopleural carina originates below the pronotal lobe, and extends ventrally. Subantennal distance is the length between a line drawn across the lower edge of the antennal sockets and the clypeal apex. Abbreviations used below are: F = flagellum, MOD = midocellus diameter, PD = puncture diameter and T = gastral tergum.

Atoposega simulans Kimsey, new species
(Figs. 1, 6)

Holotype female. Body length 5 mm. Face (fig. 1); scapal basin with numerous coarse cross-ridges, bordered along ocular margin by large punctures less than 0.6 PD apart; malar space 3 MOD;

Manuscript received by the editor April 4, 1986.

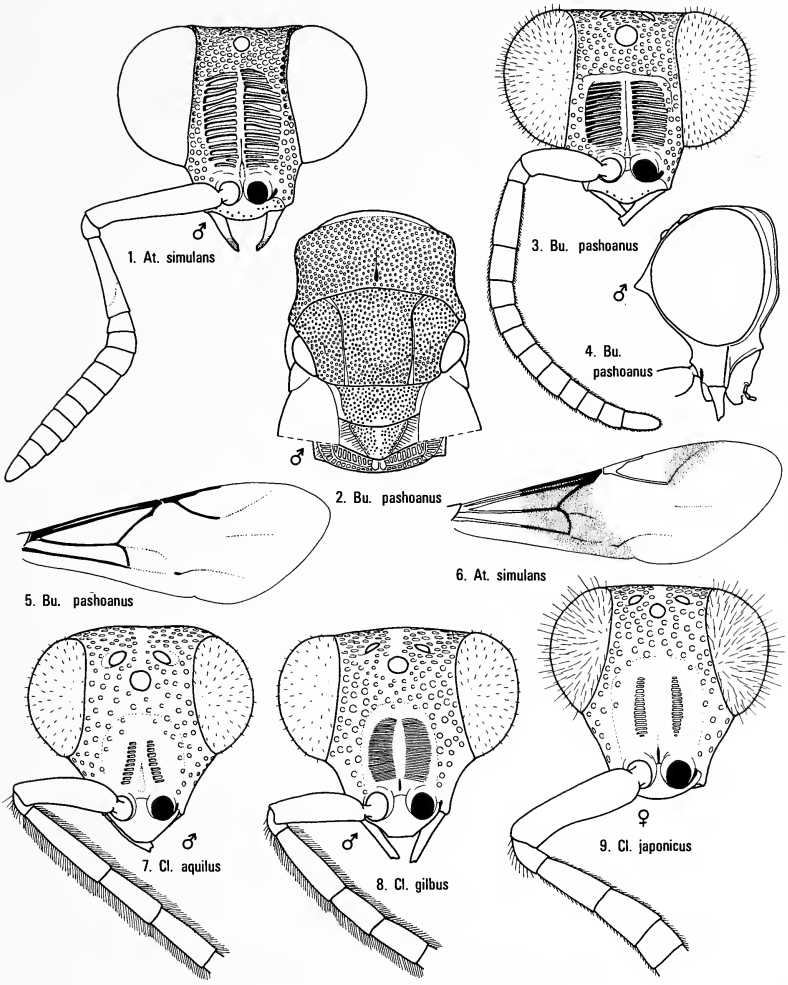
head width 1.3 times length; midocellus 2.5 MOD from ocular margin; subantennal distance 1 MOD; ocelli arranged in broad triangle; hindocellus 1.2 diameters from ocular margin; F-I length 3× breadth; F-II length 0.6× breadth; pronotum 0.5× as long as combined median lengths of scutum, scutellum and metanotum; mesopleuron with large dense punctures, without scrobal sulcus; scutal punctures coarse and contiguous, somewhat arranged in rows; metanotum 0.8× scutellar length; forewing (fig. 6) densely setose with dark bands across wing at medial vein and at apex of RS (fig. 6), entire wing brown-stained; hindfemur ventral surface coarsely punctate; T-I and II polished and impunctate medially with lateral zone of fine scratches and punctures; T-III-IV with apical band of tiny punctures. Head black; scape light brown; pedicel and F-I whitish, except apex of F-I blackish; F-II-XI blackish; thorax red, except dorsal and posterior face of propodeum black; legs and coxae red, except foretarsomeres, hindtibial apex and venter of hindfemur dark brown; abdomen shiny black, with faint green tints on T-I-II laterally.

Holotype female: MALAYSIA: Pasoh Forest Res., Negri S., 17 April 1980, P. and M. Becker (GAINESVILLE). Paratypes: 10 females, same data as type, except various dates from 8 July 1978 to 3 November 1979.

Discussion. This species appears to be structurally intermediate between the other species of *Atoposega: lineata* Krombein and *rieki* (Krombein). *A. simulans* has the long pronotum, patterned wings and larger size of *lineata,* and T-I-II laterally "scratched" with metallic tints and the forefemur rough and coarsely punctate, as in *rieki.*

Bupon Kimsey, new genus

Diagnosis. Malar space with vertical sulcus; vertex with coarse close punctation; brow with strongly projecting transverse ridge (figs. 3, 4); eyes encircled by irregular carina; occipital carina well-developed; scapal basin coarsely cross-ridged; male flagellum short and cylindrical; pronotum about half as long as combined lengths of scutum, scutellum and metanotum, with oblong pit posteromedially and on lateral lobe; mesopleuron without scrobal sulcus or oblique



Figs. 1, 3, 7–9. Front view of face. Fig. 2. Dorsal view of thorax. Fig. 4. Lateral view of head. Figs. 5, 6. Forewing.

mesopleural carina; forewing (fig. 5) with long slender stigma + R1, RS extended by evenly curved streak, medial vein arises before cu-a; metanotum 0.9× as long as scutellum, medial enclosure punctate, differently sculptured from lateral area; propodeum with short dorsal surface, abruptly declivous posteriorly, lateral angles short and blunt; hindcoxa with dorsobasal carina; terga sharp-edged laterally, covered with dense small punctures; tarsal claw with large perpendicular submedial tooth.

Type: *Bupon pasohanus* Kimsey.

Etymology. *Bu* - great, *pons* - bridge (Latin, masculine).

Discussion. The most unusual diagnostic feature of *Bupon* is the strongly projecting transverse frontal carina. The only other amisegine genus with any indication of such a carina is *Perissosega* where it is faint by comparison. In other respects *Bupon* more closely resembles *Cladobethylus,* based on the lack of most of the derived characteristics found in the Amiseginae. Two derived characteristics that are found in *Bupon* and will immediately distinguish this group are the transverse facial carina and the short, relatively broad male flagellum.

Bupon pasohanus Kimsey new species
(Figs. 2–5)

Holotype male. Body length 4.5 mm. Face (figs. 3, 4); scapal basin with coarse cross-ridges, deeply sunken below transverse shelf-like ridge, punctures 0.2–0.5 PD apart; eye encircled by carina; clypeal apex broadly rounded; subantennal distance 1 MOD; malar space 2.1 MOD, with vertical sulcus; ocelli arranged in broad triangle; hindocelli 0.8 diameter from ocular margin; midocellus 1.8 MOD from ocular margin; occipital carina complete; pronotum 0.5× combined lengths of scutum, scutellum and metanotum; with oblong pit posteromedially and on lateral lobe; thorax (fig. 2), with dorsal punctures coarse and contiguous; mesopleuron sculptured like pronotum, without scrobal sulcus; propodeal posterior face finely and densely rugose, lateral angle short and blunt; terga sharp-edged laterally, with coarse small punctures 0.5 PD apart. Body black; legs including coxae yellow, except hindtarsomeres and apices of hindfemur and tibia blackish; antenna dark brown, except scape paler beneath.

Holotype male: MALAYSIA: Pasoh Forest Res., Negri S., E. and M. Becker, 27 July 1979, secondary forest (GAINESVILLE). Paratypes: 30 males, collected from June 1978 to April 1980.

Cladobethylus aquilus Kimsey, new species
(Fig. 7)

Holotype male. Body length 3 mm. Face (fig. 7); scapal basin primarily smooth with short strip of cross-ridges on either side of broad medial stripe; clypeus long and rounded apically, subantennal distance 1.1 MOD; malar space 3.5 MOD long; head about as long as wide; midocellus 2 MOD from ocular margin; ocelli arranged in nearly equilateral triangle; hindocelli separated from ocular margin by 0.8 diameters; pronotum about 1.2× as long as scutum; mesopleuron with long parallel-sided scrobal sulcus, punctures slightly larger than on pronotum; metapleuron smooth below hindwing base; propodeum with posteromedial stripe smooth but somewhat irregular, bordered by carina laterally; terga with basal zone of tiny punctures 0.5–2 PD apart. Body black, except pronotum and scutum with faint blue tint; legs including coxae yellow; antennae dark brown; mandibles yellowish brown.

Female unknown.

Holotype male: PAPUA NEW GUINEA: Bulolo, 900 m, 13 February–13 March 1979, J. Sedlacek (GAINESVILLE). Paratypes: 4 males, same data as type, 1 male Baiyer River, 6–25 February 1979, 1100 m.

Discussion. The face of *aquilus* resembles that of *C. ceylonicus* Krombein based on the strongly converging lower sides of the face and the greatly reduced cross-ridging in the scapal basin. However, *aquilus* can be distinguished from this and other *Cladobethylus* species by the long clypeus, smooth metapleuron, dorsum with faint blue tints, dark brown antenna, and pronotum longer than the scutum.

Cladobethylus gilbus Kimsey, new species
(Fig. 8)

Holotype male. Body length 4 mm. Face (fig. 8); scapal basin with numerous fine cross-ridges, bordered by large punctures less than 0.6 PD apart; head venter with 2 ovoid foveae along midline of genal

bridge; malar space 3.2 MOD long; head 1.2× as wide as long; midocellus 2.5 MOD from ocular margin; ocelli arranged in a nearly equilateral triangle; hindocelli separated from ocular margin by 1 diameter; subantennal distance 0.9 MOD; clypeal apex truncate; pronotum with fine short posteromedial line; mesopleuron without scrobal sulcus, punctation same as pronotum; metapleuron with zone of cross-ridging below hindwing base; propodeum with broad, polished, impunctate, vaguely margined, posteromedial stripe; terga polished and impunctate. Body black, except pronotum and scutum with faint blue tints; antennae, legs including coxae yellow, and mandibles yellow with red tips.

Female unknown.

Holotype male: MALAYSIA: Pasoh Forest Res., Negri S., 5 November 1978. P. and M. Becker (GAINESVILLE). Paratypes: 106 males and 50 females, same data as type, except dates from May 1978 to May 1980.

Discussion. *C. gilbus* males have two ovoid foveae underneath the head, one on either side of the genal bridge. I have seen no other *Cladobethylus* males with this modification. Otherwise, *gilbus* can be distinguished by the densely cross-ridged scapal basin, yellow antennae, truncate, clypeal apex, subequal pronotum and scutum (in length), blue-tinted pronotum and scutum and metapleuron with short zone of cross-ridging.

Cladobethylus japonicus Kimsey, new species
(Fig. 9)

Holotype female. Body length 2.5 mm; face (fig. 9); scapal basin smooth with short strip of cross-ridges on either side of broad medial stripe; clypeus short, broadly rounded; subantennal distance 0.6 MOD; malar space 5 MOD long; face broad across genal region, about as broad as long; midocellus 2.6 MOD from ocular margin; ocelli arranged in nearly equilateral triangle; hindocelli separated from ocular margin by 0.3 diameters; mesopleuron with long parallel-sided scrobal sulcus, punctures larger than on pronotum; metapleuron cross-ridged from hindwing base nearly to midcoxa; propodeum posteromedial stripe rough and enclosed by strong carina; T-I smooth and impunctate; T-II-IV smooth with tiny scattered punctures 4–6 PD apart. Body black with bluish tints on vertex and

pronotum; legs including coxae yellow; scape dark brown becoming paler distally; pedicel and F-I-III yellow, remaining flagellomeres brown; mandibles brown.

Male unknown.

Holotype female: JAPAN: Kyoto, 8 August 1980, H. and M. Townes (GAINESVILLE).

Discussion. This species has several unusual features. The eyes have very long dense setulae, the hindocelli are very close to the ocular margins and the malar space is also very long. In addition, the lower face is quite broad, the scapal basin has only narrow stripes of cross-ridging, the pronotum is longer than the scutum, the metapleuron is cross-ridged from wing base to caxa, and only the pedicel and F-I-III are yellow, the rest of the antenna is brown.

Isegama malaysiana Kimsey, new species
(Fig. 17)

Holotype female. Body length 3 mm. Face (fig. 17) polished with sparse small punctures, 3–5 PD apart; eyes without distinct setulae; scapal basin shallow with faint cross-ridges; lower face strongly converging; eyes bulging farthest below middle; gena bulging along lower third of eye; malar space 3.2 MOD long; clypeus short, subantennal distance 0.4 MOD; midocellus 2 MOD from ocular margin; ocelli arranged in broad triangle; hindocellus nearly touching ocular margin; vertex strongly convex; pronotum flattened, with medial groove and pit before lateral lobe, subequal to scutal length; mesopleuron with moderate punctures about 1 PD apart on anterior half, posterior half impunctate and polished, scrobal sulcus straight, narrow and parallel-sided, oblique mesopleural carina well-developed; metanotum 0.8× scutellar length, medial enclosure smooth with tiny punctures, about 1 PD apart; propodeum with dorsal enclosures polished and impunctate, posterior face rugose; T-I-III covered with close small punctures, nearly contiguous anteriorly but becoming more dispersed posteriorly, with impunctate medial stripe; T-IV covered with small punctures. Head, thorax and abdomen black, with blue tints on head, pronotum, scutum, scutellum and medial enclosure of metanotum; scape, pedicel and F-I-III yellow, F-IV to apex brown; legs including coxae yellow, wings faintly brown tinted.

Male. Same as female except face more coarsely punctate, punctures 0.5–1.0 PD apart, eyes normal; F-I 3× as long as broad; terga more closely and coarsely punctate, without clearly indicated impunctate medial stripe; head and thorax without metallic tints; entire antennae reddish brown; femora dark brown becoming paler distally; coxae black.

Holotype female. MALAYSIA: Pasoh Forest Res., Negri S., 11 August 1979, forest gap, P. and M. Becker (GAINESVILLE). Paratype male, same data as type, except 29 February 1979.

Discussion. The face of *malaysiana* most closely resembles that of *meaculpa* Krombein due to the bulging eyes and strongly converging lower face. However, it differs significantly from *meaculpa* and *aridula* Krombein based on characteristics of the female, including the head only slightly wider than long, the scape, pedicel, F-I-II, and the legs entirely yellow, and in both sexes the thoracic dorsum with punctures relatively shallow and well-separated, the pronotum and scutum subequal in length, and the metanotum and propodeum without rugulae between the major ribbing.

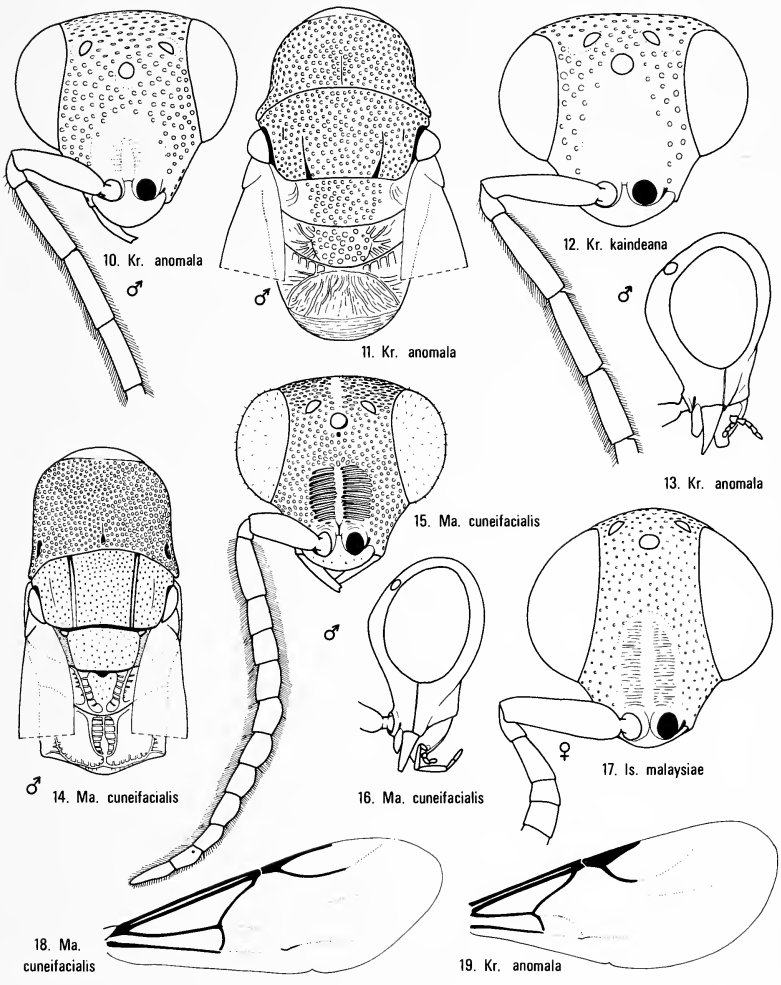
Kryptosega Kimsey, new genus

Diagnosis. Malar space with vertical sulcus; occipital carina well-developed, at least dorsally; scapal basin shallow, with some cross-ridging; male flagellum elongate and cylindrical; pronotum with shallow, occasionally faint, posteromedial groove and pit before lateral lobe, 0.8–0.9× scutal length (fig. 11); mesopleuron with scrobal sulcus indicated by broad dorsally carinate groove or nearly absent, without oblique mesopleural carina; scutum with notauli deep posteriorly and obsolescent anteriorly, parapsides present; metanotum with poorly defined, punctate medial area, 0.8× as long as scutellum; propodeum rounded laterally and posteriorly, with relatively long dorsal surface; hindcoxa without dorsobasal carina; tarsal claw with large medial tooth; male fully winged, forewing (fig. 19), stigma broad and elongate, without indication of R1, RS extended by evenly curved dark streak, medial vein arising before cu-a; terga sharp-edged laterally and finely punctate.

Female unknown.

Type: *Kryptosega anomala* Kimsey.

Etymology: *Krypto*—hidden, *sega*—taken from *Amisega* Cameron.



Figs. 10, 12, 15, 17. Front view of face. Figs. 13, 16. Lateral view of head. Figs. 11, 14. Dorsal view of thorax. Figs. 18, 19. Forewing.

Discussion. This genus does not appear to be closely related to any of the other Amiseginae. *Kryptosega* lacks most of the derived characteristics found in other genera, except that it has no hindcoxal carina and no indication of a lateral propodeal angle. Further study is necessary to determine the relationships of *Kryptosega.*

Kryptosega anomala Kimsey, new species
(Figs. 10, 11, 13, 19)

Holotype male. Body length 3 mm. Face (figs. 10, 13); scapal basin flattened and impunctate; frons with punctures 0.5–1.0 PD apart; malar space 4.4 MOD; head about as long as wide; midocellus 3.6 MOD from ocular margin; ocelli arranged in broad triangle; hindocellus separated from ocular margin by 0.3 diameter; clypeus long and rounded apically; subantennal distance 1.8 MOD; F-I length 4.3× breadth; F-II 3.6× as long as broad; pronotal, scutal and scutellar punctures 0.2–0.5 PD apart; pronotum and scutum subequal in length; scutum with notauli absent anteriorly; mesopleuron with broad irregularly margined depression extending from near pronotal lobe to scrobe, punctures 0.2–1.0 PD apart; metanotum 0.8× as long as scutellum, medial enclosure with large nearly contiguous punctures; propodeal dorsal surface with irregular longitudinal carinae, posterior surface with extensive transverse carinae; terga with sparse small punctures 2–3 PD apart. Head and thorax black without metallic tints; abdomen black, except reddish brown basally; scape and pedicel brown; flagellum black; coxae whitish, legs otherwise pale brown becoming darker on tarsi; mandibles yellowish becoming red apically.

Holotype male - NEW GUINEA: Mt. Kainde, 13 February–12 March 1979, 2300 m, J. Sedlacek (GAINESVILLE). Paratypes: 5 males, same data as type except also collected 18 January–14 February 1979 and 19 December 1978–8 January 1979.

Discussion. *K. anomala* can be distinguished from *kaindeana* by the coarser punctation, longer malar space and subantennal distance, and nonmetallic color.

Kryptosega kaindeana Kimsey, new species
(Fig. 12)

Holotype male. Body length 2.5 mm. Face (fig. 12); scapal basin impunctate and highly polished; frons with punctures shallow,

0.5–1.0 PD apart; malar space 2.3 MOD; midocellus 2.6 MOD from ocular margin; ocelli arranged in nearly equilateral triangle; hindocellus 1 diameter from ocular margin; head 1.2× as wide as long; clypeus short, broadly rounded; subantennal distance 0.9 MOD; F-I length 4.3× breadth; F-II 3.5× as long as broad; pronotal, scutal and scutellar punctures shallow and 0.5–1.0 PD apart; pronotum 0.8× scutal length; scutum with notauli complete; mesopleuron with short depression near pronotal lobe, broadly separated from scrobe, punctures large, 0.5–1 PD apart; metanotum 0.9× as long as scutellum, medial enclosure punctures shallow and nearly contiguous; propodeum strongly bulging posteromedially, dorsal surface irregularly rugose, posterior surface smooth; terga with sparse tiny punctures 2–4 PD apart. Head and thorax black with bronze tints dorsally; abdomen black, except reddish brown basally and faint bluish tints dorsally; antenna dark brown; mandibles whitish basally, red apically; coxae whitish, legs otherwise pale brown except hindtibial apex and tarsomeres dark brown.

Holotype male - NEW GUINEA: Mt. Kainde, 19 December 1978–18 January 1979, 2300 m, J. Sedlacek (GAINESVILLE). One paratype male same data as type, except 18 January–14 February 1979.

Discussion. Unlike *anomala, kaindeana* is bronze colored dorsally. In addition, the integument appears glossy and is less coarsely punctate and the face, particularly the malar space and subantennal distance, are shorter.

Magdalium Kimsey, new genus

Diagnosis. Malar space with vertical sulcus; vertex with impunctate medial stripe extending from midocellus to occiput; occipital carina absent; scapal basin shallow, coarsely cross-ridged; male flagellum broad, F-V-XI bulging medially (fig. 15); female flagellum short and broad, flattened on one side; pronotum long and flat, with oblong pits posteromedially and on lateral lobe, 0.6× combined lengths of scutum, scutellum and metanotum (fig. 14); mesopleuron with short oblique mesopleural carina, and scrobal sulcus long and parallel-sided; scutum with notauli deep and straight, parapsides faint; metanotum as long as scutellum, medial enclosure differently sculptured than laterally; propodeum with long dorsal surface and abruptly declivous posterior, lateral angles short and blunt; hindcoxa with dorsobasal carina; tarsal claw with large perpendicular,

medial tooth; male forewing (fig. 18), stigma long and slender, R1 not indicated, RS extended by evenly curved streak, medial vein arising at cu-a; terga sharp-edged laterally, densely punctate except T-I-II with impunctate medial welt.

Type: *Magdalium cuneifacialis* Kimsey.

Etymology: *Magdalium* = cylindrical figure (Latin, neuter)

Discussion. These are relatively large amisegines, which most closely resemble *Isegama,* based on having a scrobal sulcus and oblique mesopleural carina, short broad male flagellomeres and the forewing medial vein arising at cu-a. However, *Magdalium* can be distinguished by the odd lobular male flagellomeres, long flattened pronotum, the absence of a well-defined occipital carina and the long compressed body shape. Also, *Magdalium* has an impunctate stripe on the vertex extending between the midocellus and the occiput much as in *Cladobethylus.*

Magdalium cuneifacialis Kimsey, new species
(Figs. 14–16, 18)

Holotype male. Body length 5 mm. Face (figs. 15, 16); scapal basin with polished medial stripe and coarse cross-ridges laterally, punctures about 1 PD apart; malar space 4 MOD long, with vertical sulcus; head as wide as long; occipital carina present dorsally; midocellus 2.5 MOD from ocular margin; ocelli arranged in broad triangle; vertex with impunctate medial stripe from midocellus to occiput; hindocellus 1 diameter from ocular margin; pronotum long and flat, 0.6× combined lengths of scutum, scutellum and metanotum along midline, with large pit posteromedially and on lateral lobe; mesopleuron with subalar fossa, short oblique mesopleural carina and scrobal sulcus long and parallel-sided; notal punctures 0.2–0.5 PD, larger on head and pronotum than scutum; scutum with notauli deep and straight; metanotum 0.9× as long as scutellum; propodeum with short blunt lateral angles; T-I-II punctures dense and nearly contiguous, except impunctate medial welt; T-III-V with posterior band of punctures. Head, thorax and abdomen black; scape, pedicel and F-I-IV red; F-V-XI dark brown; forefemur dark brown, reddish apically, midleg, foretibia and tarsi red, hindleg all dark brown; entire body with long erect reddish setae.

Female. Same as male, except clypeus shorter; F-I 1.9–2.0× as long as broad; F-II 0.7× as long as broad; scape, pedicel and basal half of F-I red; rest of flagellum dark brown.

Holotype male: MALAYSIA: Pasoh Forest Res., Negri S., 17 April 1980, P. and M. Becker (GAINESVILLE). Paratypes: 9 males, 4 females, same data as type, except differing dates, from 19 August 1978 to 29 May 1980.

Summary

Three new species of *Cladobethylus,* 1 new *Atoposega,* 1 new *Isegama* and 3 new genera, *Magdalium* (*cuneifacialis*), *Kryptosega* (*anomala* and *kaindeana*) and *Bupon* (*pasohanus*), are described. Most of this material was collected in the Pasoh Forest Reserve in Malaysia. The others, including *Cladobethylus aquilus* and both species of *Kryptosega* are from New Guinea, and *C. japonicus* is from Japan.

Acknowledgments

This study was made possible by Henry Townes, and numerous fruitful discussions of Amiseginae with Karl V. Krombein, and was supported by NSF Research Grant No. BSR-8407392.

CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room 154, Biological Laboratories, Divinity Avenue, Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

BACK VOLUMES OF PSYCHE

Requests for information about back volumes of Psyche should be sent directly to the editor.

F.M. Carpenter
Editorial Office, Psyche
16 Divinity Avenue
Cambridge, Mass. 02138

FOR SALE

Reprints of articles by W. M. Wheeler

The Cambridge Entomological Club has for sale numerous reprints of Dr. Wheeler's articles that were filed in his office at Harvard University at the time of his death in 1937. Included are about 12,700 individual reprints of 250 publications. The cost of the reprints has been set at 5¢ a page, including postage; for orders under $5 there will be an additional handling charge of 50¢. A list of the reprints is available for $1.00 from the W. M. Wheeler Reprint Committee, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138. Checks should be made payable to the Cambridge Entomological Club.

ISSN 0033-2615

PSYCHE

A JOURNAL OF ENTOMOLOGY

founded in 1874 by the Cambridge Entomological Club

Vol. 93 1986 Nos. 3–4

CONTENTS

SMITHSONIAN
MAY 1 8 1987
LIBRARIES

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1986–1987

President ..... JAMES M. CARPENTER
Vice-President ..... EDWARD ARMSTRONG
Secretary ..... DAVID MADDISON
Treasurer ..... FRANK M. CARPENTER
Executive Committee ..... HEATHER HERMANN
W. DAVID WINTER

EDITORIAL BOARD OF PSYCHE

F. M. CARPENTER, (Editor), *Fisher Professor of Natural History,* Emeritus, *Harvard University*

W. L. BROWN, JR., *Professor of Entomology, Cornell University and Associate in Entomology, Museum of Comparative Zoology*

B. K. HÖLLDOBLER, *Alexander Agassiz Professor of Zoology, Harvard University*

H. W. LEVI, *Alexander Agassiz Professor of Zoology, Harvard University*

M. D. BOWERS, *Assistant Professor of Biology, Harvard University*

E. O. WILSON, *Baird Professor of Science, Harvard University*

J. M. CARPENTER, *Assistant Professor of Biology, Harvard University*

PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: $17.00, domestic, and $18.00, foreign.

Checks and remittances should be addressed to Treasurer, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138.

Orders for missing numbers, notices of change of address, etc., should be sent to the Editorial Office of Psyche, 16 Divinity Avenue, Cambridge, Mass. 02138. For previous volumes, see notice on inside back cover.

IMPORTANT NOTICE TO CONTRIBUTORS

Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

Authors are required to bear part of the printing costs, at the rate of $29.00 per printed page. The actual cost of preparing cuts for all illustrations must be borne by contributors: the cost for full page plates from line drawings is ordinarily $10.00 each, and for full page half-tones, $12.00 each; smaller sizes in proportion. There is ordinarily no additional charge for setting tables of less than six columns; for tables of six or more columns the cost is $25.00 per page.

Psyche, vol. 93, no. 1–2, for 1986, was mailed October 15, 1986

The Lexington Press, Inc., Lexington, Massachusetts

PSYCHE

Vol. 93 1986 Nos. 3–4

THE CHOICE OF WEB-MONITORING SITES BY A GREEN *MIAGRAMMOPES* SPECIES (ARANEAE: ULOBORIDAE)*

By Brent D. Opell

Department of Biology
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061

Introduction

The varied and effective predatory strategies of spiders have drawn more attention than have their antipredator adaptations to threats from birds, wasps, damselflies, and other spiders (Bristowe 1941, Dorris 1970, Blanke 1972, Jackson & Blest 1982a, b). As the majority of their predators are visual hunters, it is not surprising that many spiders employ either protective resemblance or eucrypsis (as defined by Robinson 1969a) to escape detection. In general, protective resemblance seems to be more common among spiders that use a capture web and eucrypsis among hunting spiders that employ sit-and-wait tactics. Protective resemblance usually involves anatomical modification and is frequently enhanced by postural specializations (Robinson 1969b). Both of these antipredator adaptations are often enhanced by a spider's color.

In order for protective resemblance and eucrypsis to be effective, animals employing these strategies should select a background whose color or texture closely matches their own. Such background selection has been demonstrated for adult moths (Kettlewell 1955, Sargent 1966, 1984; Sargent & Keiper 1969, Malcom & Hanks 1973), butterfly pupae (West & Hazel 1979), and grasshoppers (Giles 1982). Several studies have demonstrated the protective

Manuscript received by the editor May 16, 1986

benefits of correct background selection in both immature and adult insects (Hazel & West 1979, Erichsen et al. 1980, West & Hazel 1982, Sims & Shapiro 1983a, b). This study investigates background selection by spiders of the genus *Miagrammopes*.

Members of the tropical genus *Miagrammopes* spin reduced capture webs consisting of a horizontal thread which may either be sticky or non-sticky and may have one or several vertical or diagonal sticky (cribellar) capture threads extending from it (Lubin et al. 1978, Opell 1984). These spiders monitor their reduced webs from one of the attachment points, where their postures and body form make them cryptic. Brown species that spin their webs among twigs and vines resemble thorns or broken twig bases, whereas green species that spin webs on moss-covered vegetation resemble extending moss phyllidia (Fig. 1). After subduing and wrapping prey, these spiders return to one of their web's attachment points and resume their typical cryptic posture while feeding.

Most individuals of the green *Miagrammopes* species I observed in Costa Rica monitored their webs from moss-covered twigs. This occurred despite the fact that some webs were also anchored to bare twigs. In order to test the hypothesis that members of this species select moss-covered twigs over bare twigs as web-monitoring sites, I conducted a series of choice experiments.

Materials and Methods

The species used in this study is an undescribed member of the *Miagrammopes aspinatus* species group (Opell 1984). Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology. Spiders used in this study were collected from stands of abandoned cacao *(Theobroma cacao)* at the Organization for Tropical Studies' La Selva research station located near the town of Puerto Viejo de Sarapiqui, Heredia Province, Costa Rica. Prior to their release onto experimental frames, these spiders were kept for two to four days in small, cotton stoppered glass vials. During this time, their carapace and leg lengths were measured with a micrometer-equipped dissecting microscope. Because adult males do not spin capture webs, only immatures and adult females were used in this study.

Experimental frames (Fig. 2) were constructed of 2 mm diameter hardwood applicator sticks glued together with epoxy and bound

Figure 1. Adult female *Miagrammopes* sp. feeding on a small beetle held with the pedipalps while monitoring an attachment line of the capture web. Setal tufts at the distal end of the extended first legs make them resemble the moss to which the web is attached. Scale bar represents 2 mm.

by thread. To one set of opposite vertical elements were wired moss-covered cacao twigs and to the other set, bare cacao twigs. All twigs were taken from the same tree and had a diameter of about 7 mm. Two of the four frames employed bare twigs that had no evidence of moss cover and two twigs whose moss covering was removed without damage to the bark. Frames hung 98 cm apart along a taut, north-south suspension line. To account for the possible influence of air currents, frames were oriented so that the moss-covered twigs occupied alternate sectors (East and West sectors, North and South sectors, etc.).

From 26 June until 6 July 1985, these frames hung in the abandoned cacao plantation from which specimens were collected. From 7–15 July 1985, these study frames were transferred to a roofed enclosure (cabina) whose screened north, east, and south walls were covered with light colored curtains to exclude direct sunlight. Here, frame orientation and spacing were identical to that described above. In this enclosure, spiders were exposed only to natural light. Each frame's bare and moss-covered twigs were watered daily at about 8:30 and 13:00. At the end of the study, moss on the twigs showed no signs of thinning or turning brown and bare twigs showed no signs of moss growth.

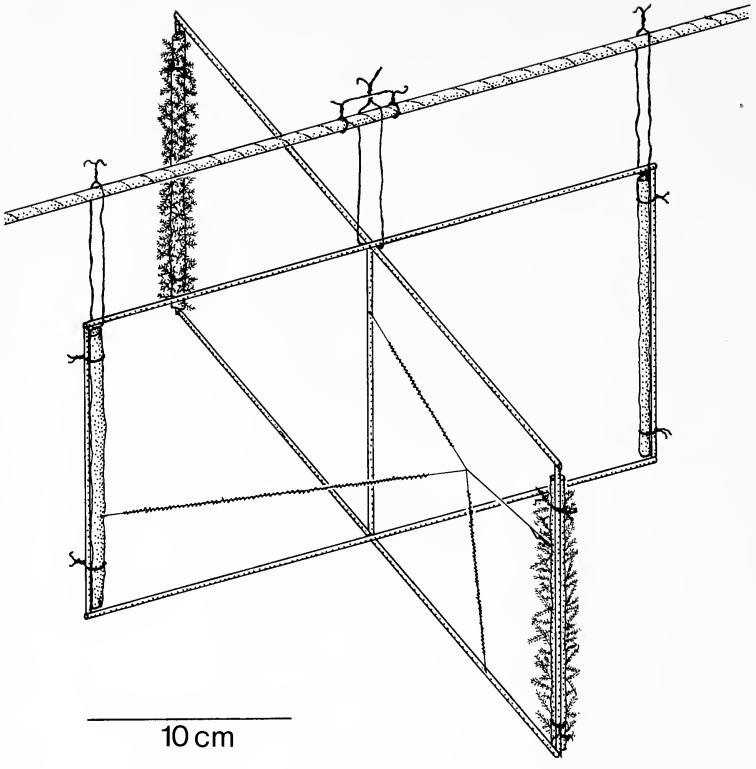


Figure 2. Diagram of the frame used in this study, showing a spider monitoring its web from the front, moss-covered sector.

Frames and suspension lines were cleaned of all visible silk strands before spiders were released at 16:00 onto the top center of each frame. Frames were checked the following morning at 8:00 and the presence of webs and position of spiders recorded. A capture web was defined as a web with sticky (cribellar) prey capture silk. In contrast with the non-sticky, single-line resting web, the capture web usually consisted of multiple, diverging threads. Spiders always hung near one of the web's attachment points (Fig. 1) and it was noted whether this was a moss-covered or bare site. During the first three days and last day of the study only a single specimen was released onto each frame. On other days, one large and one small specimen were released on each frame. This was done to compensate

for what initially promised to be a high percentage of spiders leaving the frames. The size difference made it possible to distinguish individuals on each frame and to record which had made a web. After web production and position were recorded specimens were collected and released in the forest. A plot of first femur length against carapace length for the specimens used in this study plus the values of 61 additional specimens was used to assign the instar values to spiders. Chi-square tests were used to evaluate the results of this study.

Results

Earlier instars were more commonly found than later instars and, therefore, are represented by a larger sample size. Of the 21 capture webs constructed in the forest, nine were spun by third instars, six by fourth instars, four by fifth instars, one by an adult female, and one by a specimen of uncertain age. Of the 28 capture webs spun in the enclosure, four were spun by third instars, 14 by fourth instars, six by fifth instars, and four by adult females. Significantly more ($0.05 > p > 0.025$) spiders produced capture webs in the enclosure than in the forest (Table I). All capture webs made within frames were monitored from a moss-covered twig. In the enclosure, six specimens constructed their capture webs outside the frame and monitored them from wires used to attach frames to the support line. In most of these cases, the spider's web was not anchored to a moss-covered twig and the highest attachment point was the favored monitoring site. When these six capture webs are compared with the other 22 indoor webs monitored from moss, moss is still the favored site ($0.025 > p > 0.01$).

In neither habitat was there a significant difference in the moss-covered frame sectors from which webs were monitored (Table I). However, these results were more clear-cut in the enclosure ($0.975 > p > 0.90$) than in the forest ($0.50 > p > 0.10$). In the latter setting, moss-covered twigs on East and South frame sectors appear to be favored. This may be explained by stronger and/or more unidirectional wind currents in the latter setting. On seven occasions I used a web dusting device to expel a cloud of corn starch into the air of the forest site. On three instances the wind was blowing to the east, on three to the southeast, and one to the southwest. These observations suggest that a spider's dragline had a greater chance of being carried

Table I. Site from which capture webs were monitored.

Habitat	Twig Covering	Frame Sector				Support Wires	Total
		East	South	West	North		
Forest:	Moss	10	6	2	3	—	21
(70*)	Bare	0	0	0	0	0	0
Enclosure:	Moss	7	5	4	6	—	22
(60*)	Bare	0	0	0	0	6	6

*Total number of spiders released in each habitat.

to a frame's East and South sectors and that, when moss-covered, the twig attached to this sector would be favored over the opposite moss-covered twig as a web-monitoring site.

Discussion

This species' preference for moss as a web-monitoring site enhances its protective resemblance. The exposed first legs of these green species have a tuft of green tibial setae that look like the small phyllidia of an extending moss plant (Fig. 1). Although these setal tufts are found in brown *Miagrammopes* species, they are more prominent in green species, where they become disproportionately larger in subadult and adult individuals. During the night *Miagrammopes* often abandon their typical day-time position adjacent to a twig and hang on the monitoring line a centimeter or more from its attachment point to a twig.

Choice of a web-monitoring site by *Miagrammopes* is facilitated by the fact that most of their simple, irregular webs have no single attachment point from which they must be monitored. A few webs have a particular thread that probably serves as an optimal monitoring line by virtue of its single attachment point to several diverging lines. However, most newly constructed *Miagrammopes* webs consist of an approximately horizontal thread with one or several independently diverging vertical or diagonal threads. Either end of this horizontal thread could serve as a monitoring site. I have seen disturbed *Miagrammopes* run to the opposite end of their horizontal threads and begin monitoring their webs from this new position.

The greater number of missing individuals noted in the forest than in the enclosure experiments probably resulted from a higher rate of spiders ballooning from the forest frames. Three factors suggest that this difference is not due to predators removing spiders that chose bare twigs as web-monitoring sites. First, release and observation times were chosen so that most of site selection and web construction took place at night when threats from visually hunting predators were lowest. Second, during this study, no predatory insects were seen on the experimental frames or their supporting lines. Third, none of the spiders in the predator-free enclosure chose bare twigs as web-monitoring sites.

This study does not address the mechanism by which individuals select moss-covered twigs. Experimental studies on cryptic insects

show that two methods may be used in selecting a matching background. Gillis (1982) showed that in one grasshopper species individuals select backgrounds whose color matches that of their circumocular regions. By contrast, Sargent (1968) found that background selection in some moths was hereditary and was unaffected by painting their circumocular scales. Color vision has not been demonstrated in *Miagrammopes*. However, the eyes of the species used in this study are well developed and have low f-numbers, indicating that they are effective in low light intensities (Opell and Cushing, in press). Tactile or moisture properties of the moss may also be important cues for its choice as a web-monitoring site. Unlike striped moths that must assume the proper orientation in order to take full advantage of their cryptic markings (Sargent 1969), the webs of *Miagrammopes* assure that they will assume the proper attitude after they have selected the correct background.

Summary

Members of the spider genus *Miagrammopes* construct simple capture webs consisting of only a few threads and assume a stick-like posture as they actively monitor these webs. A green Costa Rican species showed a statistically significant preference for moss-covered twigs as web-monitoring sites. This choice was observed in both a forest setting and a screened enclosure, and occurred on experimental frames which required spiders to attach their webs to both bare and moss-covered twigs.

Acknowledgements

I am grateful to the Organization for Tropical Studies for permitting me to use its facilities and to David and Deborah Clark, co-directors of the organization's La Selva research station, for their help. This study was supported by National Science Foundation grant BSR-8407979 to the author.

References

Blanke, R.

1972. Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskal (Araneae, Araneidae) in Andalusien. Forma et Functio, 5: 125–206.

Bristowe, W. S.
1941. The Comity of Spiders. Ray Soc., No. **128**. London.
Dorris, P. F.
1970. Spiders collected from mud-dauber nests in in Mississippi. J. Kansas Ent. Soc., **43**: 10–11.
Erichsen, J. T., J. R. Krebs, and A. I. Houston.
1980. Optimal foraging and cryptic prey. J. Anim. Ecol., **49**: 271–276.
Gillis, J. E.
1982. Substrate color-matching cues in the cryptic grasshopper *Circotettix rabula rabula.* Anim. Behav., **30**: 113–116.
Hazel, W. N. and D. A. West.
1979. Environmental control of pupal colour in swallow-tail butterflies (Lepidoptera: Papilioninae): *Battus philenor* (L) and *Papilio polyxenes* Fabr. Ecol. Entomol., **4**: 393–400.
Jackson, R. R. and A. D. Blest.
1982a. The biology of *Portia fimbriata,* a web-building jumping spider (Araneae, Salticidae) from Queensland: utilisation of webs and predatory versatility. J. Zool. (London), **196**: 255–293.
1982b. The distances at which a primitive jumping spider, *Portia fimbriata,* makes visual discriminations. J. Exp. Biol., **87**: 441–445.
Kettlewell, H. B. D.
1955. Recognition of appropriate background by the pale and black phases of Lepidoptera. Nature, **175**: 943–944.
Lubin, Y. D., W. G. Eberhard, and G. G. Montgomery.
1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche, **85**: 1–23.
Malcom, W. M. and J. P. Hanks.
1973. Landing-site selection searching behavior in the micro-lepidopteran *Agonopteryx pulvipennella.* Anim. Behav., **21**: 45–48.
Opell, B. D.
1984. Phylogenetic review of the genus *Miagrammopes* sensu lato (Araneae: Uloboridae). J. Arachnol., **12**: 229–240.
Opell, B. D. and P. E. Cushing.
in press. Visual fields of orb-web and single-line-web spiders of the family Uloboridae. Zoomorphology.
Robinson, M. H.
1969a. Defense against visually hunting predators. Evol. Biol., **3**: 225–259.
1969b. The defensive behaviour of some orthopteroid insects from Panama. Trans. R. Soc. London, **121**: 281–303.
Sargent, T. D.
1966. Background selections of geometrid and noctuid moths. Science, **154**: 1674–1675.
1968. Cryptic moths: effects on background selection of painting circumocular scales. Science, **159**: 100–101.
1969. Behavioural adaptations of cryptic moths. III. Resting attitudes of two bark-like species, *Melanolophia canadaria* and *Catocala uttronia.* Anim. Behav., **17**: 670–672.

1984. Melanism in *Phigalia titea* (Lepidoptera: Geometridae) in southern New England: A response to forest disturbance? J. N. Y. Entomol. Soc., **93**: 1113–1120.

SARGENT, T. D. AND R. R. KEIPER.

1969. Behavioral adaptations of cryptic moths, I. Preliminary studies on bark-like species. J. Lepid. Soc., **23**: 1–9.

SIMS, S. R. AND A. M. SHAPIRO.

1983a. Pupal color dimorphism in California *Battus philenor* (Papilionidae): Morphology factors and selective advantage. J. Lepid. Soc., **37**: 236–243.

1983b. Pupal dimorphism in California *Battus philenor* (L): Pupation sites, environmental control, and diapause linkage. Ecol. Entomol., **8**: 95–104.

WEST, D. A. AND W. N. HAZEL.

1979. Natural pupation sites of swallowtail butterflies (Lepidoptera: Papilioninae): *Papilio polyxenes* Fabr., *P. glaucus* L. and *Battus philenor* (L.). Ecol. Entomol., **4**: 387–392.

1982. An experimental test of natural selection for pupation site in swallowtail butterflies. Evolution, **36**: 152–159.

NATAL NEST DISTRIBUTION AND PLEOMETROSIS IN THE DESERT LEAF-CUTTER ANT *ACROMYRMEX VERSICOLOR* (PERGANDE) (HYMENOPTERA: FORMICIDAE)

By Steven W. Rissing,* Robert A. Johnson,* and Gregory B. Pollock**

While most ant colonies are started by single queens, colony foundation by groups of queens, pleometrosis, also occurs (Wilson 1971, Hölldobler and Wilson 1977). Several extensively studied, highly pleometrotic species are notably similar with respect to important aspects of colony ontogeny and population dynamics. *Myrmecocystus mimicus, Solenopsis invicta* and *Veromessor pergandei* queens found colonies mutualistically without respect to relatedness (Bartz and Hölldobler 1982, Tschinkel and Howard 1983, Pollock and Rissing 1985, Rissing and Pollock 1986). Further, while adult colonies of these species are highly territorial (Hölldobler 1976a, 1981; Wilson et al. 1971; Went et al. 1972, Wheeler and Rissing 1975), natal colonies are clumped with brood raiding and subsequent worker defection from brood-raided colonies occurring (references cited above for *M. mimicus* and *S. invicta,* for *V. pergandei:* Rissing and Pollock, in press). Given such frequently deleterious natal colony interactions, adaptive value of habitat selection by founding queens resulting in clumping of natal nests is unclear. Natal nests of *M. mimicus* are generally clumped in areas devoid of adult nests (Bartz and Hölldobler 1982), yet still occur near such nests (B. Hölldobler, pers. comm.), and queens of *S. invicta* show some preference for microtopographic features (Tschinkel and Howard 1983). Here we present data relating habitat selection and clumping of natal nests of the highly pleometrotic leaf-cutter ant *Acromyrmex versicolor* (Pergande) directly to survival of founding queens. The only other report regarding any aspect of colony initiation in this species is a description of mating flights following summer rains in the Sonoran Desert by Wheeler (1917).

*Department of Zoology, Arizona State University, Tempe, AZ 85287
**School of Social Science; University of California, Irvine; Irvine, CA 92717
Manuscript received by the editor April 6, 1986.

Methods

A major flight of *A. versicolor* occurred on 19 September 1985 on a study area in North Scottsdale, AZ 5.6 km north of Maricopa County along Pima Rd, approximately 3.2 km west of the McDowell Mountains. The habitat in this area is typical of the Sonoran Desert with *Larrea tridentata* and *Franseria dumosa* dominant shrubs and *Olneya tesota* and *Cercidium microphyllum* dominant trees along numerous shallow washes in the gravel/sandy soil. A major storm front produced rain throughout the region the previous day; 2.6 cm of rain was recorded at the Arizona State Laboratory of Climatology located 32 km south of the study area.

Habitat choice by *A. versicolor* queens was examined by running a transect 20 m long and 2 m wide from the base of 10 haphazardly chosen trees on the study area. Transect direction was chosen haphazardly. Distance of each starting nest from base of tree was recorded and standardized into "canopy units" by dividing by distance from base of tree to outer canopy edge along each transect. This standardization was necessitated by variance in tree size and canopy extent. Distance to nearest neighboring tree was measured for 20 haphazardly chosen trees and converted to canopy units using the larger canopy extent of each pair. Number of queens per starting nest was determined by excavating 43 nests during this time. Additionally, 21 starting nests were excavated on 22 September on a study area of similar habitat in South Mountain Park, Phoenix, AZ, 38.5 km southwest of the main study area.

Effect of temperature in a starting nest on queen survivorship was determined by placing 18 queens (from the above excavated nests) in a large test tube plugged with cotton and containing a large ball of cotton saturated with water to prevent desiccation. Test tubes were placed in a darkened incubator at 20, 25,...45°C in random predetermined order; subsequently an additional tube was exposed to 42.5°C. To mimic late afternoon temperature exposures in the field, tubes remained at their given temperature for 2 hours. Queens incapable of righting themselves after 2 hours were considered dead. Likely temperatures in starting nests were determined by taking soil temperatures 5 and 10 cm below surface at the trunk base (0 canopy units), canopy edge (1 canopy unit) and in the open (> 1 canopy unit) on the main study area between 16:00 and 17:00 h on 24

September and 4 October 1985. All queens excavated 1–2 days following the mating flight were found 5–10 cm below the soil surface.

The possible importance of relatedness in formation of queen associations was tested according to the methods of Rissing and Pollock (1986). Eight plastic "choice boxes" (30 × 15 × 8 cm, half filled with sand moistened in each corner and at the midpoints along the long sides) were established with 2 sets of 4 queens, one set collected from each of the two study sites (38.5 km apart). In 5 boxes, queens were color marked according to collection locale; different patterns of the same two colors were used to avoid providing cues for recognition. As an additional control for possible paint odor, queens in the remaining 3 boxes were not marked. Boxes were excavated 24 hrs later when queens had dug below the surface; location of each queen was noted relative to the others.

Results

Acromyrmex versicolor queens strongly prefer to start nests immediately below the outer canopy of trees; while mean inter-tree distance was 6.10 ± 1.85 canopy units (= 21.37 ± 5.14 m between tree bases; N = 20), the average starting nest was .87 ± .53 canopy units (= 3.15 ± 1.88 m; N = 115) from a tree base (Fig. 1). Although measurements were not taken, the same distribution of starting nests was observed at South Mountain Park. All queens examined for temperature tolerance survived exposure to temperature up to and including 40°C for at least 2 hr; survivorship was 0, however, at 42.5°C and above. Temperatures above 40°C were found in the open between trees (>1 canopy units) at soil depths normally occupied by newly starting colonies ($\bar{x}_{5cm}$ = 42.0 (± 1.1)°C, N = 5; $\bar{x}_{10cm}$ = 36.9 (± 1.2)°C, N = 10); temperatures this high were not found at canopy edges (= 1 canopy unit) ($\bar{x}_{5cm}$ = 38.2 (± 5.5)°C, N = 5; $\bar{x}_{10cm}$ = 32.8 (± 3.7)°C, N = 9) or at tree bases (= 0 canopy units) ($\bar{x}_{5cm}$ = 28.91 ± 2.4), N = 2; $\bar{x}_{10cm}$ = 27.4 (± 0.8)°C, N = 5).

Acromyrmex versicolor is highly pleometrotic; 82.5% of all queens excavated (N = 160 queens from 64 nests) were from pleometrotic associations (Table 1). Relatedness appears unimportant in a queen's decision to enter a foundress association; five of the 8 "choice boxes" resulted in a single starting nest occupied by all 8 queens. The remaining 3 boxes had two starting nests each: of these 6 starting nests, 4 contained queens from both collection locales, 1

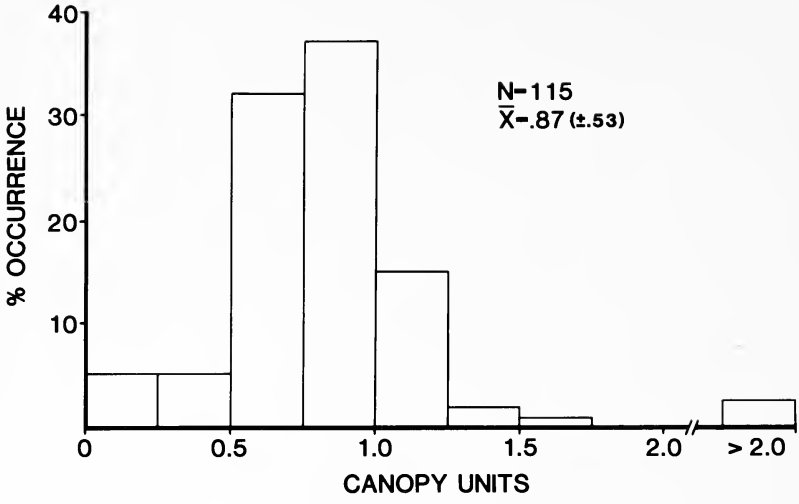


Figure 1. Habitat choice by *Acromyrmex versicolor* queens. "Canopy units" represent distance of a starting nest from the base of tree divided by distance from tree base to outer extent of canopy along that transect.

contained 3 queens from one site only, and the last contained a solitary foundress.

Discussion

The distinct habitat choice of *A. versicolor* queens (Fig. 1) seems a likely response to high soil temperatures in sunlit areas during the mid-late summer flight season of this species. Queens initiating nests in open areas will likely experience lethal temperatures even 5 cm below the soil surface. We routinely found queens at this depth 2–3 days following the mating flight. These nests, however, were located under trees where potentially lethal temperatures were never recorded. *Acromyrmex versicolor* queen death after 2 hours of exposure to temperatures 40–43°C is consistent with upper temperature tolerances of foragers of this species of 42–43°C (Gamboa 1976).

Queens of several other ant species display varying degrees of habitat choice. Queens of *Lasius niger* and *Lasius flavus* both prefer bare, sunlit soil where they establish colonies more successfully than

Table 1. Pleometrosis in *Acromyrmex versicolor.*

No. queens in nest	Collection frequency
1	28
2	16
3	6
4	7
5	3
7	2
9	1
16	1

in shaded soil (Pontin 1960). Queens of the tropical leaf-cutting ant *Atta cephalotes* appear capable of choosing between major habitat types (mature evergreen woodlands as opposed to deciduous forest or cultivated fields) (Rockwood 1973). Similar ability to choose between major habitat types (woods versus open fields) while flying occurs in *Lasius neoniger* and *Solenopsis molesta* (Wilson and Hunt 1966).

Preference by queens for the canopy edge (as opposed to anywhere under a tree) may represent a trade-off for shade while still being as warm as possible for rapid development of an initial worker force and eventual establishment of a foraging territory. This would be consistent with the high degree of pleometrosis in this species (see below) and with the "maxi-therm" hypothesis of Hamilton (1973). Location of a starting nest under a tree canopy (especially *O. tesota* whose branches frequently droop to the ground) would permit easy and safe access to vegetation for initiation and growth of the fungus garden characteristic of all leaf-cutters. Unlike most species of higher ants, queens of *Acromyrmex* spp., including *A. versicolor,* routinely forage for vegetation, especially at colony initiation (Weber 1972, Gamboa 1974). Trees, including *O. tesota,* are commonly harvested by *A. versicolor* (Gamboa 1975).

Of the several hundred adult colonies of *A. versicolor* we have observed within the vicinity of Phoenix, AZ, virtually all have been located directly under adult trees and never in the open between trees. *Acromyrmex, Atta* and related genera are a largely tropical, New World group of ants; *A. versicolor* is the northernmost of 24 *Acromyrmex* species and certainly one of the most desert-adapted of all the leaf-cutters (Creighton 1950, Weber 1972). Habitat choice by founding queens and location of adult nests under trees may be

an important behavioral adaptation permitting range extension into the Sonoran Desert. *Acromyrmex versicolor* queens clump around the essential resource of favorable nest sites (tree shade with ready access to lower canopy leaves). The mating system of this species may also permit "tracking" of this resource. Unlike some desert species that have massive mating swarms (e.g. *Pogonomyrmex* spp.: Chapman 1957; Nagel and Rettenmeyer 1973; Hölldobler 1976b, c; Davidson 1982), *A. versicolor* mates in small, localized groups at or near the ground in open areas between trees (Wheeler 1917; R. A. Johnson, pers. obs.). This behavior mimics closely the mating behavior of *M. mimicus* (M. Cazier, pers. comm.) and likely *V. pergandei* (Pollock and Rissing 1985), pleometrotic species with clumped natal nests. Whether such localized mating aggregations have led to a highly female biased sex ratio, as appears to have occurred in *V. pergandei* (Pollock and Rissing 1985), is currently unknown for these other pleometrotic species.

Some other ant species with clumped, natal nests engage in internest brood raiding in the process of establishing natal territories (references cited above). This may select for pleometrosis (Rissing and Pollock, in press) which generally results in more rapid production of a larger initial worker force (Waloff 1957; Stumper 1962; Markin et al. 1972; Taki 1976; Mintzer 1979; Bartz and Hölldobler 1982, Tschinkel and Howard 1983, Rissing and Pollock, in press). Colonies of these species are also territorial as adults. Brood raiding also seems likely in *Atta texana,* another pleometrotic desert leafcutter (Mintzer and Vinson 1985), which "merges" young colonies in the laboratory and field (Echols 1966). Adult colonies of *Acromyrmex versicolor* are territorial (Gamboa 1974). We suggest such territoriality, when coupled with natal nest clumping through habitat choice, makes brood raiding and associated forms of natal nest competition likely for this species as well.

A final similarity between *A. versicolor* and other pleometrotic ants with clumped natal nests discussed here is the apparent formation of foundress associations without respect to relatedness. Queens collected from distant locales readily associate. Similar observations exist for *M. mimicus* (Bartz and Hölldobler 1982), *A. texana* (Mintzer and Vinson 1985) and *V. pergandei* (Rissing and Pollock 1986); electrophoretic evidence indicates *S. invicta* queens also associate randomly (Ross and Fletcher 1985). This differs

dramatically from the close relatedness of cofoundresses in primitively eusocial wasps (Pfennig et al. 1983 and included references). Given the normally claustral method of colony foundation in ants, relatedness to potential cofoundresses should be unimportant in this essentially mutualistic process (Rissing and Pollock 1986). Colony foundation in leaf-cutters (including *A. versicolor*), however, is not claustral; foundresses forage (references cited above). This presents an opportunity to extend and examine the dynamics of the mutualistic process of colony foundation by unrelated females. Work in this area is currently planned.

Summary

Queens of the desert leaf-cutter ant, *Acromyrmex versicolor* exhibit distinct habitat choice during colony foundation; almost all natal nests are located directly under the canopy edge of large trees. Soil temperatures in these sites are conducive to queen survivorship during the first several days of colony initiation while those in open areas between trees are high enough to result in queen death. This habitat choice results in clumping of many natal nests under individual trees implying strong natal colony competition. Indeed, as with several other ant species exhibiting such competition, starting colonies are frequently pleometrotic; 82.5% of all queens excavated were from such multiple foundress associations. As with other pleometrotic ant species, mating aggregations of *A. versicolor* are small and localized, and relatedness appears unimportant in a queen's decision to enter a foundress association.

Acknowledgments

G. E. Walsberg provided advice regarding queen temperature tolerance tests.

Literature Cited

Bartz, S. H. and B. Hölldobler

1982. Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. Behav. Ecol. Sociobiol. **10**: 137–147.

Chapman, J. A.

1957. A further consideration of summit ant swarms. Canadian Entomol. **89**: 389–395.

Creighton, W. S.
1950. The ants of North America. Bull. Mus. Comp. Zool. **104**: 1–585.
Davidson, D. W.
1982. Sexual selection in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). Behav. Ecol. Sociobiol. **10**: 245–250.
Echols, H. P.
1966. Compatibility of separate nests of Texas leaf-cutting ants. J. Econ. Ent. **59**: 1299–1300.
Gamboa, G. J.
1974. Surface behavior of the leaf-cutter ant *Acromyrmex versicolor versicolor* Pergande (Hymenoptera: Formicidae). Masters Thesis; Arizona St. Univ., Tempe, Arizona.
1975. Foraging and leaf-cutting of the desert gardening ant *Acromyrmex versicolor versicolor* (Pergande) (Hymenoptera: Formicidae). Oecologia (Berl.) **20**: 103–110.
1976. Effects of temperature on the surface activity of the desert leaf-cutter ant, *Acromyrmex versicolor versicolor* (Pergande) (Hymenoptera: Formicidae). Amer. Midl. Natur. **95**: 485–491.
Hamilton, W. J.
1973. *Life's Color Code.* McGraw-Hill, New York, N.Y.
Hölldobler, B.
1976a. Tournaments and slavery in a desert ant. Science **192**: 912–914.
1976b. The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). Behav. Ecol. Sociobiol. **1**: 405–423.
1976c. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav. Ecol. Sociobiol. **1**: 3–44.
1981. Foraging and spatiotemporal territories in the honey ant *Mrymecocystus mimicus* Wheeler (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. **9**: 301–314.
Hölldobler, B. and E. O. Wilson.
1977. The number of queens: An important trait in ant evolution. Naturwissenschaften **64**: 8–15.
Markin, G. P., H. L. Collins, and J. H. Dillier.
1972. Colony founding by queens of the red imported fire ant, *Solenopsis invicta*. Ann. Entomol. Soc. Am. **65**: 123–124.
Mintzer, A.
1979. Colony founding and pleometrosis in *Camponotus* (Hymenoptera: Formicidae). Pan-Pacific Entomol. **55**: 81–89.
Mintzer, A. and S. B. Vinson.
1985. Cooperative colony foundation by females of the leafcutting ant *Atta texana* in the laboratory. J. New York Entomol. Soc. **93**: 1047–1051.
Nagel, H. G. and C. W. Rettenmeyer.
1973. Nuptial flights, reproductive behavior and colony founding of the western harvester ant, *Pogonomrymex occidentalis* (Hymenoptera: Formicidae). J. Kansas Entomol. Soc. **45**: 82–101.
Pfennig, D. D., G. J. Gamboa, H. K. Reeve, J. S. Reeve, and I. D. Ferguson.
1983. The mechanism of nestmate discrimination in social wasps (*Polistes*, Hymenoptera: Vespidae). Behav. Ecol. Sociobiol. **13**: 299–305.

Pollock, G. B. and S. W. Rissing.
1985. Mating season and colony foundation of the seed-harvester ant, *Veromessor pergandei.* Psych **92**: 125–134.

Pontin, A. J.
1960. Field experiments on colony foundation by *Lasius niger* (L.) and *L. flavus* (F.) (Hym., Formicidae). Ins. Soc. **7**: 227–230.

Rissing, S. W. and G. B. Pollock.
1986. Social interaction among pleometrotic queens of *Veromessor pergandei* (Hymenoptera: Formicidae) during colony foundation. Anim. Behav., **34**: 226–233.
Queen agression, pleometrotic advantage and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). Anim. Behav., in press.

Rockwood, L. L.
1973. Distribution, density and dispersion of two species of *Atta* (Hymenoptera: Formicidae) in Guanacaste Province, Costa Rica. J. Anim. Ecol. **42**: 803–817.

Ross, K. G. and D. J. C. Fletcher.
1985. Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. **17**: 349–356.

Stumper, R.
1962. Sur un effet de groupe chez les femelles de *Camponotus vagus* (Scopoli). Ins. Soc. **9**: 329–333.

Taki, A.
1976. Colony founding of *Messor aciculatum* (Fr. Smith) (Hymenoptera: Formicidae) by single and grouped queens. Physiol. Ecol. Japan **17**: 503–512.

Tschinkel, W. R. and D. F. Howard.
1983. Colony founding by pleometrosis in the fire ant, *Solenopsis invicta.* Behav. Ecol. Sociobiol. **12**: 103–113.

Waloff, N.
1957. The effect of the number of queens of the ant *Lasius flavus* (Fab.) (Hym., Formicidae) on their survival and on the rate of development of the first brood. Ins. Soc. **4**: 391–408.

Weber, N. A.
1972. Gardening ants the Attines. Mem. Amer. Phil. Soc. **92**: 1–146.

Went, F. W., G. C. Wheeler, and J. Wheeler.
1972. Feeding and digestion in some ants (*Veromessor* and *Manica*). Bioscience **22**: 82–88.

Wheeler, J. and S. W. Rissing.
1975. Natural history of *Veromessor pergandei.* II. Behavior. Pan-Pacific Entomol. **51**: 303–314.

Wheeler, W. M.
1917. Notes on the marriage flights of some Sonoran ants. Psyche **24**: 177–180.

Wilson, E. O.
1971. *The Insect Societies.* Cambridge, Massachusetts: Belknap Press of Harvard University Press.

WILSON, E. O. AND G. L. HUNT.
1966. Habitat selection by the queens of two field-dwelling species of ant. Ecology **47**: 485–487.
WILSON, N. L., J. H. DILLIER, AND G. P. MARKIN.
1971. Foraging territories of imported fire ants. Ann. Entomol. Soc. Amer. **64**: 660–665.

REVISION OF THE ONOCOSMOECUS UNICOLOR GROUP (TRICHOPTERA: LIMNEPHILIDAE, DICOSMOECINAE)

By Glenn B. Wiggins[1] and John S. Richardson[2]

Introduction

The genus *Onocosmoecus,* by current definition, comprises the *unicolor* group and the *frontalis* group (Schmid 1980, *occidentalis* group = *unicolor* group; Wiggins 1977). From a separate study of generic relationships within the Dicosmoecinae (G. B. Wiggins & O. S. Flint, in prep.), it is clear that *Onocosmoecus* in this broad sense is not monophyletic. The *frontalis* group will be considered in a subsequent paper, but in the interim the two western North American species of which it is composed, *O. frontalis* (Banks) and *O. schmidi* (Wiggins), remain nominally under *Onocosmoecus.* Thus, in final analysis, this study of the *unicolor* group will constitute a revision of the genus *Onocosmoecus s.s.,* and the generic name is used here in that restricted sense.

Among the genera of the limnephilid subfamily Dicosmoecinae, *Onocosmoecus s.s.* is one of the most widespread, represented across the whole of northern North America from Newfoundland to Alaska, south in the western mountains to California, and across the Bering Strait to Kamchatka. They are rather large caddisflies, not often found in abundance but by no means rare. Larvae occur in cool lotic habitats, and also in the littoral zone of cool lakes, where they are detritivorous. Seven species have been assigned to the genus in the past but reservations concerning their validity have been expressed by several authors (e.g., Schmid 1955, 1980; Flint 1960; Wiggins 1977). Because no analysis of types or of long series of specimens has been undertaken, identity of the putative species has always been doubtful. The purpose of the present study was to undertake that analysis.

[1]Department of Entomology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

[2]Department of Zoology, University of British Columbia, Vancouver, B.C. Canada.

Manuscript received by the editor June 17, 1986.

Materials and Methods

Extensive collections in the Department of Entomolgy, Royal Ontario Museum (ROM) provided the main basis for this study and were supplemented by material borrowed from other collections; deposition of all other specimens examined is given below. On the distribution map for *O. unicolor* (Fig. 14), not all records in the central part of the range are plotted. Since complete listing of all records for *O. unicolor* is too voluminous for inclusion here, an abbreviated citation is used; localities are listed under state or province and any other identifier, followed by the place of deposition of the material, and the range for adult flight records is given for each state or province. A complete listing of all records compiled is deposited in the Library of the Royal Ontario Museum. Records for larvae are included; instars are designated as LV (Larval instar V), LIV, LIII, P (Pupa), PP (Prepupa). Life history data for *O. unicolor* are grouped into weekly intervals for plotting (Fig. 10), with each dot representing a collection comprising one or more individuals at a given stage. Larvae were identified to the third instar, although some characters are not as well developed as in the final instar.

Observations on food are based on analysis of the contents of the entire gut from 10 LV, following the method of Cummins (1973). Food data were recorded on a percentage area basis using an eyepiece grid, and were classified under four categories: animal fragments, vascular plant pieces and filamentous algae, diatoms, and fine particulate organic material (FPOM) unidentifiable as to origin.

Location of specimens examined

CAS California Academy of Sciences, San Francisco
CNC Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, Ottawa
DGD D. G. Denning, Moraga, California
DJB D. J. Burdick, Department of Biology, California State University, Fresno
INHS Illinois Natural History Survey, Champaign
LACM Los Angeles County Museum
MCZ Museum of Comparative Zoology, Harvard University, Cambridge

NHA N. H. Anderson, Department of Entomology, Oregon State University, Corvallis
Oswood M. W. Oswood, Division of Life Sciences, University of Alaska, Fairbanks
SDS S. D. Smith, Central Washington University, Ellensburg
UA Strickland Museum, University of Alberta, Edmonton
UBC Spencer Entomological Museum, University of British Columbia
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.
Vienna Naturhistorisches Museum, Vienna
Z.I. USSR Zoological Institute, Academy of Sciences, Leningrad

Genus Onocosmoecus Banks

Dicosmoecus (Onocosmoecus) Banks 1943, p. 357; type-species by original designation *D. (O.) tristis* Banks 1900.
Onocosmoecus: Schmid 1955, p. 37.
Onocosmoecus: Flint 1960, p. 19.
Onocosmoecus: Wiggins 1977, p. 268.
Onocosmoecus: Schmid 1980, p. 83.

Originally recognized as a subgenus of *Dicosmoecus* (Banks 1943), *Onocosmoecus* was later elevated to full generic status by Schmid (1955) on the basis of characters of adults. Larval characters added to the generic diagnosis by Flint (1960) were augmented by Wiggins (1977).

Description. Adults (Fig. 1) over-all light to medium brown colour, legs uniformly light brown; fore wings yellow-brown with variable markings, corneous spots in cells R4 and M variably pigmented from dark brown to colourless, variable darkish pigmented areas around these spots and along apical and costal margins, ranging from complete absence to the condition where most of the wing is medium brown; these corneous points and surrounding pigmented areas sometimes show a range of expression in a series from a single locality; hind wings paler and without markings. Venation similar to *Dicosmoecus* except discoidal cell of forewing not more than three times longer than basal radial sector (petiole). Length of fore wing: male 14.5–22 mm; female 15–23 mm. Tibial spurs 1, 3, 4. Head and thorax with sparse brownish and pale setae; setal warts approximately same colour as surrounding cuticle; pleural setal

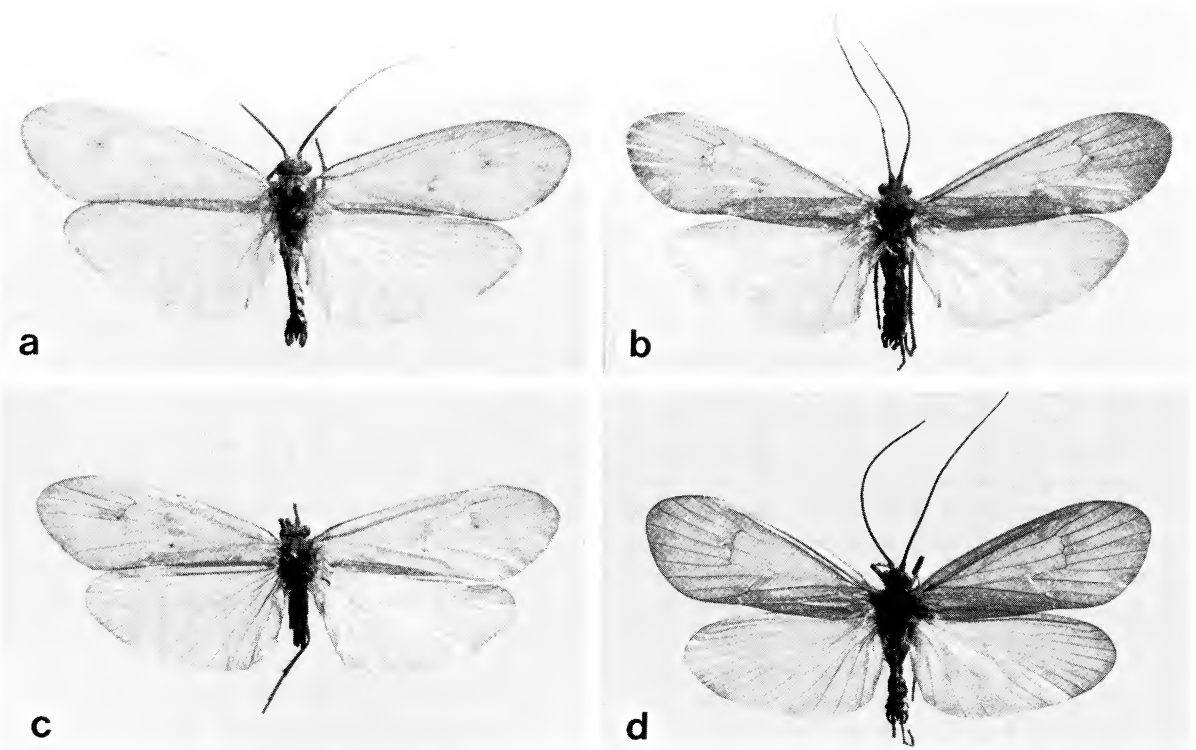


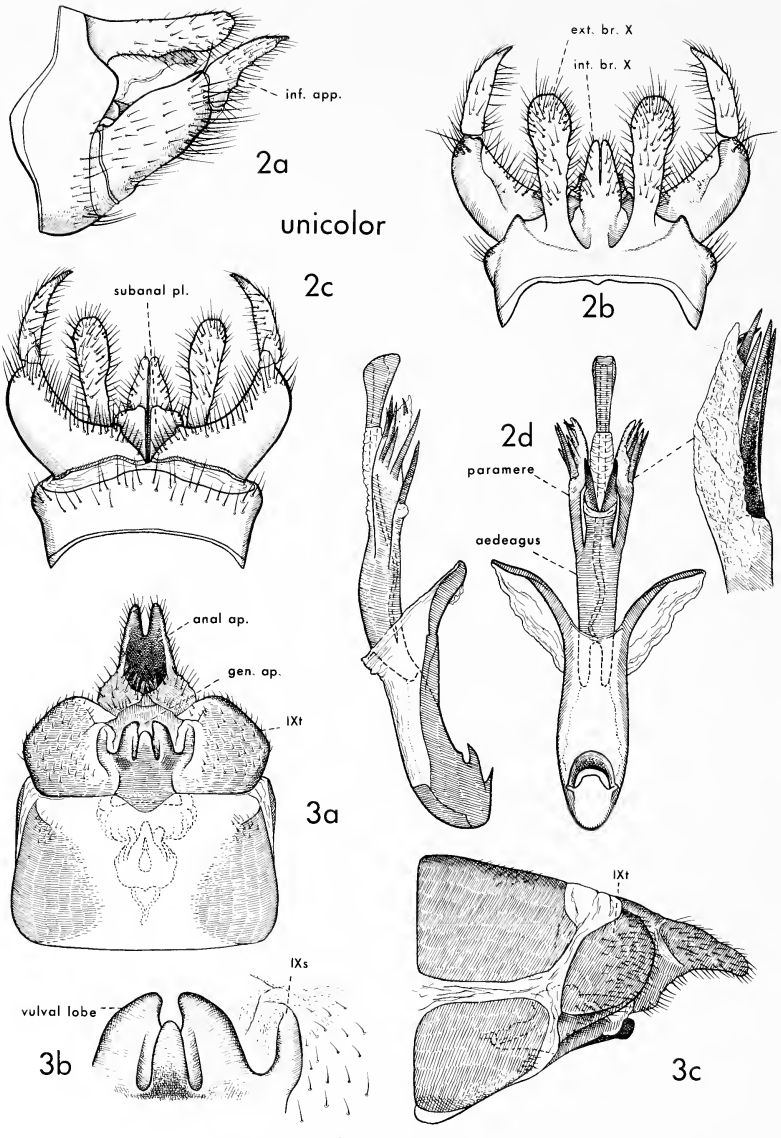
Fig. 1. *Onocosmoecus unicolor* (Banks), males. a, British Columbia, Vancouver Is.; b, Michigan, Houghton Co.; c, Kurile Isl, Chishima; d, Utah, Provo R.

warts with pale setae, not as dense or long as in *Dicosmoecus* spp. (except *D. obscuripennis* Banks); mesepisternum lacking second setal wart.

Male genitalia (Figs. 2, 4, 11, 12). Segment IX broader laterally than in *Dicosmoecus,* sternum not extended posteromesally. Segment X with external branches broad, flattened, longer than basal segment of inferior appendages, fused to segment IX close to mid-dorsal line dorsad of internal branches; internal branches variably fused together dorsally, inferior branches lacking or occasionally represented by small process, or well developed and prominent; subanal plate cleft mesally, truncate apically. Phallus bearing pair of stout spines ventrally at base of aedeagus; parameres partially and variably fused with aedeagus, each expanded into membranous apex bearing 1–6 stout spines, the arrangement, number and length of these spines extremely variable and in more than 50 per cent of specimens examined spines differ on each paramere of a single individual.

Female genitalia (Figs. 3, 5, 6, 7, 13). Highly variable in structural detail. Segment VIII variably sclerotized ventromesally. Segment IX with massive rounded tergal lobes extending ventrolaterally to sternum IX which is here interpreted as reduced to a very small lobe or fold on each side of flattened vulval lobe; vulval lobe subdivided into three parts apically but continuous basally, median part variable in shape, lateral parts concave mesally and variable in shape. Segment X elongate, forming anal tube, open ventrally, variably cleft dorsomesally; in ventral aspect, basal shoulders of segment X highly variable in shape even within single series, frequently extended into angulate ledge or tooth at each side.

Larva. (Fig. 8). Broad, light coloured median band extending from coronal suture, over pronotum and mesonotum; sclerites of head, pronotum and mesonotum with dense, minute spines. Pronotum lacking stout spines along anterior margin, but with row of 12–16 long, black setae just behind anterior margin, pair closest to mid-dorsal line distinctly shorter, space between these setae and next seta on either side narrower than that between remaining setae of row (character valid at least to LIII); pronotum and mesonotum with sparse, short yellowish and longer dark setae. Metanotal setae confined to setal areas, variable: sal 4–15, sa2 3–13, sa3 9–26; metepimera each with approximately 8–15 setae. Setae on or near ventral



Figs. 2–3. *Onocosmoecus unicolor* (Banks). 2, Male genitalia (specimen from Ontario, Durham Co.): a, lateral; b, dorsal; c, ventral; d, phallus, lateral and ventral. 3, Female genitalia (specimen from Ontario, Durham Co.): a, ventral; b, detail of vulval lobe; c, lateral. (anal op., anal opening; gen. op., genital opening; IXt & IXs, tergum and sternum of segment IX; inf. app., inferior appendage; ext. br. X, int. br. X, external and internal branches of segment X; subanal pl., subanal plate).

edge of femora: profemur 1–3, mesofemur 4–11, metafemur 6–13; tibiae with a single pair of stout spur-like setae; trochanteral brush present on all legs, density variable. Femora flattened and compressed, ventral edges blade-like. Abdominal segment VI with 1–4 setae posterodorsally on each side of median line; VII with 1–5, usually 4 setae in this position; VIII with dorsal transverse row of approximately 16–24 setae; dorsal sclerite on segment IX with 12–15 setae; lateral abdominal gills present on segments IV and V; abdominal gills: dorsal, II 1–2, 3–4; III 3, 3–4; IV 3, 3–4; V 2–3, 2–3; VI 2–3, 2–3; VII 2, 2–3; VIII 0–2; lateral, II 0, 2–3; III 2–3, 2–3; IV 2–3, 2; V 1–2; ventral, II 2, 4; III 3, 4; IV 3, 3–4; V 2–3, 4; VI 2–3, 3–4; VII 2, 2–3. Length of larva up to 25 mm.

CASE (Fig. 9). Constructed of fragments of leaves, wood and bark, walls rather thin and flexible; length of case up to 27 mm.

PUPA. Generally as in *Dicosmoecus* with dorsal hook plates on segments III-VII, dorsal sclerites on segment I with pronounced median notch, and setal tufts present on first two antennal segments; dorsum of segment VIII with approximately 30 setae, dorsum IX with approximately 14; anal processes slightly curved.

Onocosmoecus unicolor (Banks)

Anabolia unicolor Banks 1897, p. 27; holotype ♀, Washington, Mus. Comp. Zool. Harvard.

Asynarchus tristis Banks 1900, p. 254; cotypes 1♂, 2♀, Colorado, Mus. Comp. Zool. Harvard. NEW SYNONYMY.

Dicosmoecus coloradensis Ulmer 1905, p. 64, figs. 14–16; cotypes 2 ♂, 1♀, Colorado, Naturhistorisches Mus., Vienna. NEW SYNONYMY.

Anabolia quadrinotatus Banks 1908 *(Anabolia 4-notata),* p. 62, fig. 14; holotype ♂, Newfoundland, Mus. Comp. Zool. Harvard. NEW SYNONYMY.

Dicosmoecus flavus Martynov 1914, p. 253, cotypes 2♀, Kamchatka, Zool. Inst., Leningrad. NEW SYNONYMY.

Dicosmoecus (Onocosmoecus) occidentis Banks 1943, p. 362, figs. 104, 116, 124, 125, 128, 132, 136; holotype ♂, Idaho, Mus. Comp. Zool. Harvard. NEW SYNONYMY.

Dicosmoecus (Onocosmoecus) alascensis Banks 1943, p. 363, figs. 105, 123, 129; holotype ♂, Alaska, Mus. Comp. Zool. Harvard. NEW SYNONYMY.

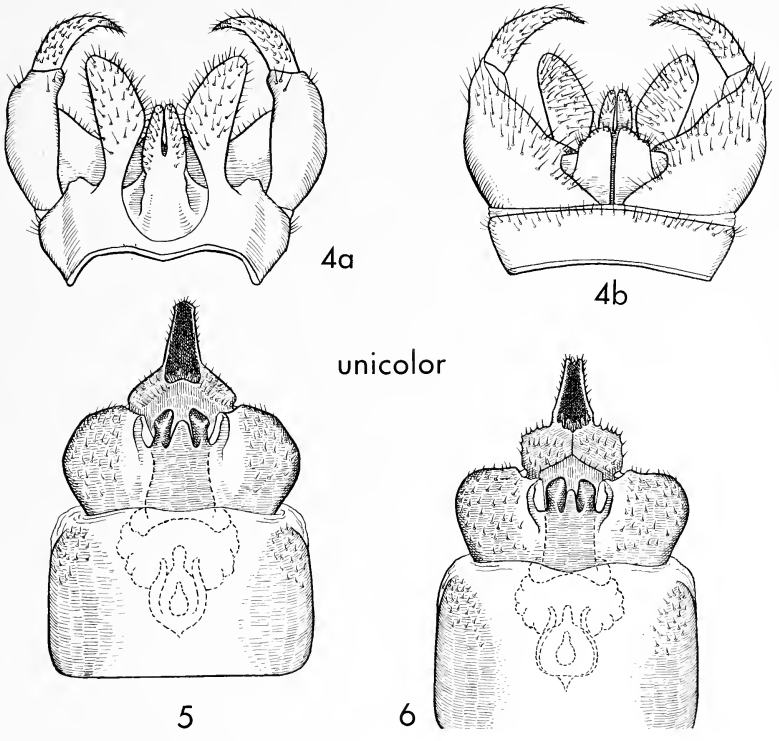
In 1943 Banks reviewed the characters used to distinguish the four Nearctic species then assigned to *D. (Onocosmoecus),* and at the same time described two additional species, *D. (O.) occidentis* and *D. (O.) alascensis.* After studying more than 1000 adult specimens,

we conclude for reasons outlined below, that all of these names are best treated as synonyms of the original species *O. unicolor;* also included in the synonymy is the Palaearctic *O. flavus.*

In distinguishing species within the *unicolor* complex, Banks (1943) utilized characters derived from colour of the fore wings and genitalic morphology. The corneous points on the fore wings of most Trichoptera in cells R4 and M (thyridial cell) are usually darkly pigmented in species of *Onocosmoecus* and contrast strongly with the light to medium brown fore wings. Around these points the membrane often has indefinite darkened areas, and the extent of these "clouds" was used by Banks as a diagnostic character (Fig. 1). Although the darkened areas show some differences among type series, we found that variation prevented their use as effective diagnostic characters. We have been unable to find in genitalic structures of either males or females throughout the *unicolor* complex discrete or discontinuous character states signifying genetic groups and taxonomic species. Differences in shape of the branches of segment X or segments of the inferior appendages to which Banks (1943) also referred seem valid for a few male specimens but blend into a seemingly continuously variable range when more series are studied. Particular importance as diagnostic characters was given by Banks to the number and arrangement of spines on the parameres. We found inordinate variability in these spines, ranging from one to six on each paramere throughout the range of the *unicolor* complex and frequently with a range in number exhibited within a series from one locality; size and arrangement of the spines was equally variable. Frequently on the two parameres of a single individual the spines differed in both number and arrangement, sometimes exhibiting conditions said to be diagnostic for two of the putative species.

Diagnosis of the females was based mainly on characters of the shape of the tapered posterior extremity of segment X (Banks' sheath of the ovipositor) and presence of a basolateral tooth or ledge, and shape of the three parts of the vulval lobe. Using these features Banks characterized the females in rather general terms but not with precise diagnoses. We found, as with the males, that because of many intermediate conditions in the characters proposed we were unable to establish discrete groups for females within the *unicolor* complex.

We have been cognizant of the possibility that species might be definable within the *unicolor* complex on the basis of other



Figs. 4–6. *Onocosmoecus unicolor* (Banks). 4, Male genitalia (specimen from Alaska, Admiralty Is.): a, dorsal; b, ventral. 5, Female genitalia (specimen from Alaska, Admiralty Is.), ventral. 6, Female genitalia (specimen from Oregon, Baker Co.), ventral.

characters, including those from other body structures, but we have not been able to recognize discontinuities in any other characters. Thus we conclude from our study of this material that the entire *unicolor* complex is best treated as a single, variable taxonomic species. Conclusions from study of the type specimens of the species placed in synonymy follow.

O. unicolor (Banks). We have examined the holotype female (Skokomish R., Washington) in the Museum of Comparative Zoology. The wings are torn and the apical lobes of segment X broken. The two corneous points on the fore wing are only lightly pigmented, and the surrounding membrane only slightly darker than

the rest of the wing. Banks (1943) stated that the apical lobes of segment X are longer in *O. unicolor* than in the other species; in females of the *unicolor* complex that we have examined these lobes are elongate but variable, and discontinuously longer in none. In the holotype there is a distinct tooth or ledge at the base of each lobe of segment X on the lateral margin (e.g. Fig. 6); expression of this character also shows continuous variability in our material and the ledge is lacking in most specimens (e.g. Fig. 3a). The median and lateral vulval lobes of the holotype taper to rounded points, which blend continuously with a range of conditions in our material.

The male has not been clearly identified in the literature. The illustration of male genitalia labeled as *unicolor* by Ross (1938, fig. 48) was given only the status of the "supposed male of '*unicolor*'" by Banks (1943); and although no locality data were given for the specimen illustrated by Ross, Banks (1943: 364) stated that it came from Inyo Co., California. Banks himself (1943) referred to specimens from Banff and Alaska that "may be males of this species," offering as a diagnostic character that the third and fourth spines of the paramere are not widely separated. Our material shows such a very wide range of variation in arrangement of the spines of the parameres that this character cannot be regarded as distinctive.

O. tristis (Banks). We have examined the three specimens (South Park, Colorado) in the type series from the Museum of Comparative Zoology. From these specimens Ross (1938) designated a lectotype male (17 Aug. 1899) and lectoallotype female (20 Aug. 1899); the remaining female (20 Aug. 1899) is identical to the lectoallotype. Ross (1938) placed *O. tristis* in synonymy with *O. unicolor,* but Banks (1943) maintained that the two were distinct species. Although the females in the type series were characterized by a pronounced basolateral tooth or ledge on segment X (Banks 1943), there seems little difference between these specimens and what remains of this character in the holotype of *O. unicolor* (see above). The apices of the posterior lobes of segment X are closely appressed in both females of the type series, and all three parts of the vulval lobe are truncate. This latter character contrasts with somewhat more rounded lobes in the holotype of *O. unicolor,* but we have many specimens showing intermediate conditions. The male in the type series of *O. tristis* was distinguished by narrower external branches of segment X (superior appendages of Banks), but

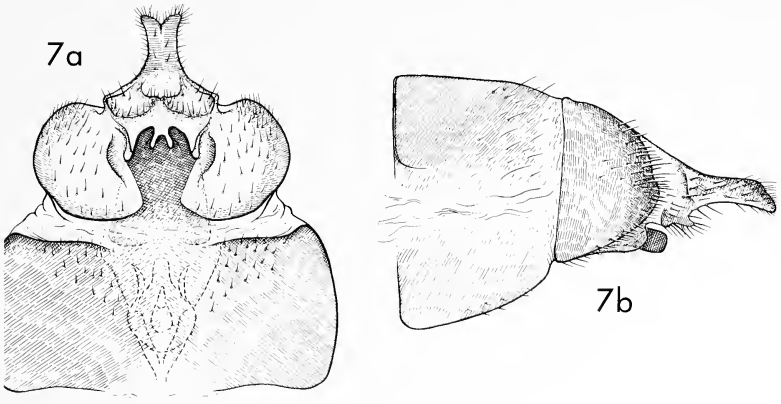
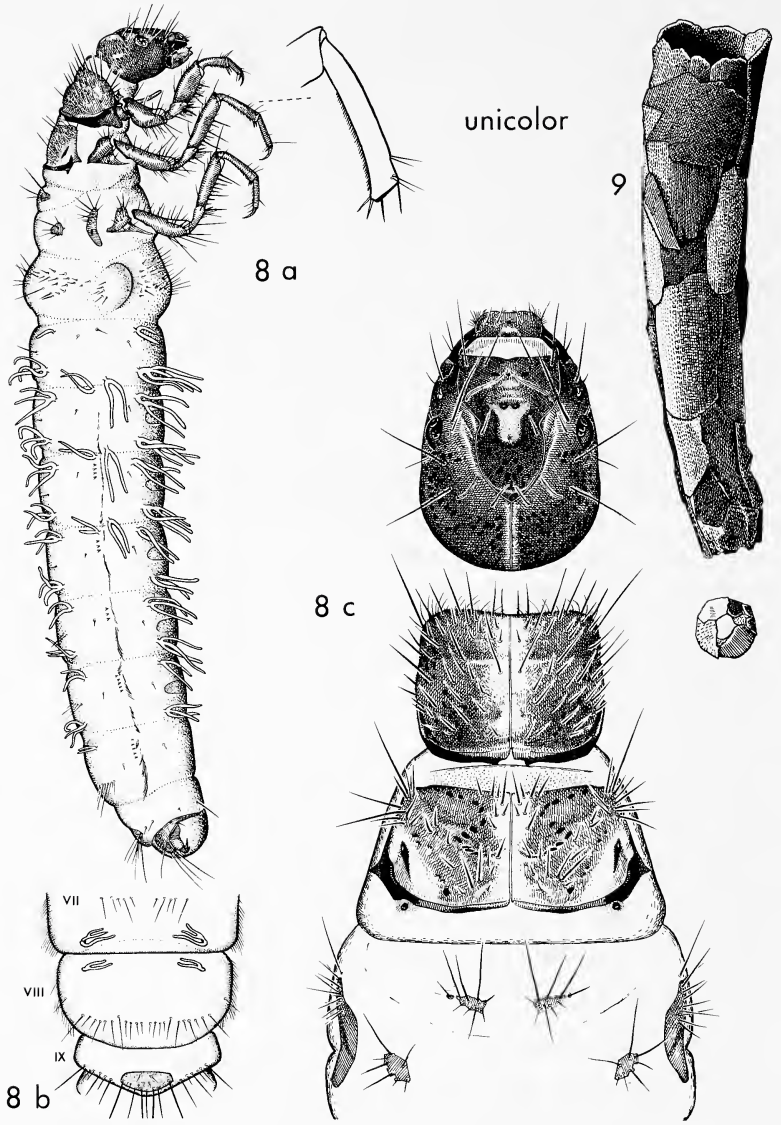


Fig. 7. *Onocosmoecus unicolor* (Banks), female genitalia (specimen from Kamchatka, U.S.S.R.; Syntype of *O. flavus* (Martynov)): a, ventral; b, lateral.

we find little distinction in this character and considerable variation in our material generally (cf. Figs. 2 and 4). The five spines of the parameres, offered as a diagnostic character for *O. tristis* by Banks, have little value in view of the wide variability in number, size and arrangement in our material of the *unicolor* complex. The three specimens in the type series show slightly different degrees of pigmentation of the corneous points of the fore wing.

Although Ross (1938) designated both lectotype male and lectoallotype female for *O. tristis,* there is no male specimen bearing a lectotype label, and it must be concluded either that the specimen was not labelled, or that the label or labelled specimen has been lost. Since among the three remaining specimens of the type series there is only one male, that specimen is here designated lectotype, an assignment which would of course lapse should Ross' lectotype be found.

O. coloradensis (Ulmer). In the original description Ulmer offered no diagnostic characters for separating *O. coloradensis* from closely related forms, but he later commented in a re-description of *O. flavus* (Ulmer 1927: 6) that his *O. coloradensis* was the same as *Asynarchus tristis* Banks, the genital appendages resembling in turn those of *O. flavus* Martynov. Diagnosis on the basis of only two spines on each paramere was later proposed by Banks (1943), who



Figs. 8–9. *Onocosmoecus unicolor* (Banks), larva (specimen from British Columbia). 8a, larva with detail of mesofemur, lateral; b, abdominal segments VII, VIII, IX, dorsal; c, head and thorax, dorsal. 9, case, detail of posterior end.

cited an illustration by Ross (1938, fig. 48) as an example. It is not clear what basis there was for this character; no reference was made to it in Ulmer's original description (no genitalic preparations had been made from the type series), and Ross' figure actually shows a third small apical spine on the paramere. Origin of the specimen on which Ross' figure 48 was based was not given, although Banks (1943: 364) stated that it came from Inyo Co., California; furthermore, although designated as *O. unicolor* by Ross, the specimen was not accepted by Banks as the male of that species (see above), evidently because he regarded it as *O. coloradensis.*

We have examined the three co-types (2♂, 1♀, S. Colorado, 1879) in the collection of the Naturhistorisches Museum, Vienna. The parameres of one male each have three spines and those of the other, four spines. We find no other features of these males that are distinctive. In the female of the type series, the apical lobes of segment X are rather long and slender, lacking the basal ledge or tooth of the holotype of *O. unicolor* or the females in the type series of *O. tristis.* The two corneous points in the fore wing are dark in all specimens, which in the males particularly are surrounded by a relatively large dark area.

O. quadrinotatus (Banks). We examined the holotype male (Grand Lake, Newfoundland, 28 July 1906) in the Museum of Comparative Zoology. This is the only name based on material from eastern North America, and was distinguished from the western forms by uniformly dark fore wings (Banks 1943). The holotype displays this character, but in some eastern populations there is a tendency for slighty darkening around the spot in cell R4 (Fig. 1b). Moreover, some specimens from western North America also have uniformly dark fore wings, e.g. Fig. 1d. Some of these have several spines on the parameres (e.g., California, Nevada Co., Sagehen Cr., 4 Aug. 1985, 1♂, ROM), but in others the spines are reduced to one or two (Utah, Summit Co., E. Fork Bear R., ca. 2 mi. above confluence with Bear R., 4–5 Aug. 1985, 7 ♂, ROM; Idaho, Teton Co., Darby Cr., 6–7 Aug. 1985, 6♂, ROM). The holotype male has five and six spines respectively on the two parameres, distinguished by the basal spine being little longer than the others and not reaching the tip of the paramere (Banks 1943). Within the eastern part of North America where no western species has ever been recorded in the literature, we found spines of the parameres

ranging from three to six, with the basal spine in some extending to the end of the paramere; and within a single series (Province of Quebec, Wacouno R., n. Sept. Iles, 10 Aug. 1973, ROM) all conditions from three to six are represented.

No precise diagnosis was offered for the female by Banks, but only the general characters of rather short apical lobes (Banks' sheath of the ovipositor) and absence of a basal ledge on segment X, and a broad median vulval lobe (Fig. 3). Our sample of females from eastern populations comprises only six specimens (Ont., P.Q., N.H., Mich.), but genitalic structures differ considerably among them: shape of the vulval lobes, and on segment X, the length and taper of the apical lobes and development of the basolateral ledge. These variations concern the same characters proposed by Banks for diagnosis of the western species of *Onocosmoecus,* and we find no other basis for identification of *O. quadrinotatus* as a separate species.

O. occidentis (Banks). We examined the holotype male (Wallace, Idaho, 1 October) in the Museum of Comparative Zoology. Diagnosis was based solely on genitalic characters. In the male the internal branch of segment X (Banks' superior plate) was said to be broadened toward the base and to have a median separation extending to the basal fourth; our examination of the holotype reveals no distinctive broadening in the shape of these combined internal branches and the median separation extends no more than half the length, which is generally characteristic of males of the *unicolor* complex. Spines of each paramere are four in number as stated, but the arrangement attributed to them holds true only for one paramere of the holotype, spines of the other being quite different. The female was distinguished by characters of segment X—short apical lobes with slightly divergent tips and lacking the basolateral tooth or ledge; over the range of characters in *O. unicolor s.l.*. none of these characters is unique as described, and we find nothing that would serve to distinguish this species.

O. alascensis (Banks). We have examined the holotype male (1 Aug. 1917) and single male paratype (29 July 1917), both from Iditarod, Alaska, from the collection of the Museum of Comparative Zoology. Among the diagnostic characters proposed by Banks (1943) was four spines on the parameres, which the holotype has, but the paratype has three and five spines respectively on the two

parameres. The external branches of segment X (superior appendages of Banks) are slightly narrowed at the base, but this feature is variable and appears not to be of diagnostic value. The two corneous points on the fore wings are darkly pigmented and each is surrounded by a fairly well defined dark area. Within the material of the *unicolor* complex that we have examined none of these characters is distinctive, and we find no reliable basis for identifying this species.

O. flavus (Martynov). Recognition of this Palaearctic species was somewhat irregular in that the description of the female appeared as *Dicosmoecus* sp. (sp.n.?) (Martynov 1913: 477), with the name proposed later (Martynov 1914: 253). To the original description, Martynov (1913: 478) added the comment: "This species resembles *D. unicolor* Banks from Washington Territory. But having seen no specimens of the last named species, and the structure of its genital appendages being entirely unknown, I cannot identify my specimens with *D. unicolor.*" Judging by the illustrations, the female appears to have been described again as *Dicosmoecus* sp. (Martynov 1925, figs. 1, 2). The male was described and illustrated by Ulmer (1927) along with the female; Ulmer mentioned the surprising similarity between *flavus* and the North American *coloradensis* [= *unicolor*] which he had described earlier. We have examined from the Zoological Institute, Academy of Sciences, Leningrad, one of the two female syntypes (Pushino, Kamchatka R., 19 July 1908) and a male evidently identified by Martynov; and in the ROM are additional specimens from two localities in Kamchatka (Dalneje Lake, 1♂, 1♀, and Ponomarskaya R., 1♂), and from the Kurile Islands (Chishima, 1♂) (Fig. 1c). The syntype female (Fig. 7) fits readily into the range exhibited by our Nearctic material, and we found no unique genitalic characters; the dorsal lobes of segment X lack a basolateral tooth and the median vulval lobe is narrow and well separated from the lateral lobes. In genitalic characters this *flavus* syntype is very close to females from Washington (Olympic National Park, 29 June–1 July 1969, ROM #690148) and from the Yukon (Dempster Hwy., km. 72, 1 Aug 1979, ROM #791191b); other Washington females (Minotaur Cr., Chelan Co., Sept.–Oct. 1976, S. D. Smith coll.) have several similar characters. By contrast, in the Dalneje Lake female, segment X has a basolateral tooth and the median vulval lobe is broad with its sides largely

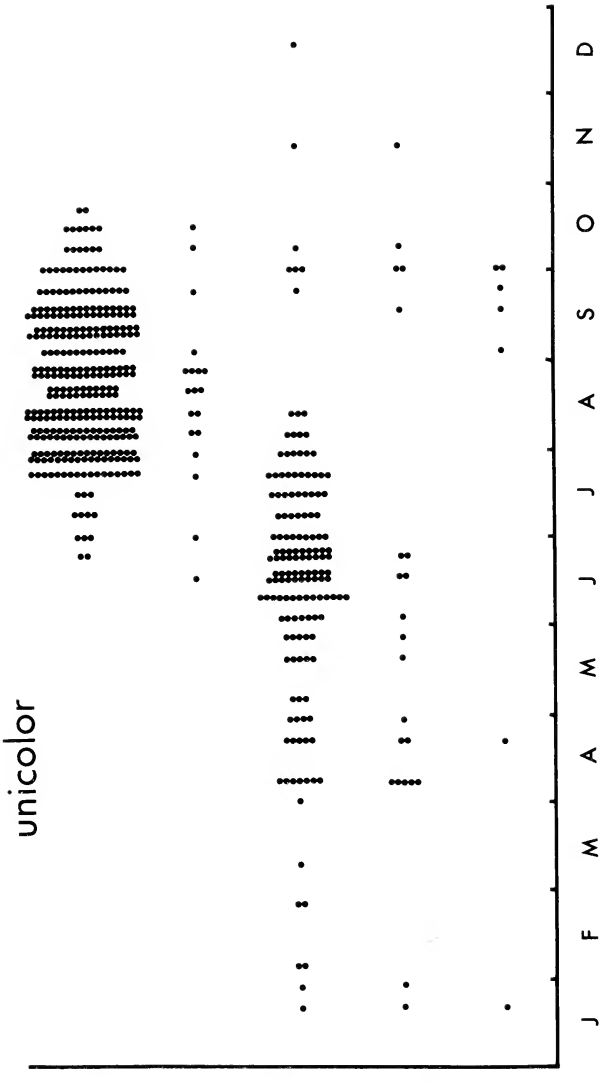


Fig. 10. Life cycle data for *Onocosmoecus unicolor* (Banks). Dots grouped vertically in weekly intervals, each dot representing collection of 1 or more individuals at 1 site.

fused to the lateral lobes, demonstrating a tendency for variation similar to that which is so widespread among Nearctic specimens. All four male specimens are generally consistent in genitalic characters with the external branches of segment X expanding rather broadly at mid-length and tapering toward a rounded apex, but this condition also occurs widely in Nearctic material; two of the specimens have four spines on each paramere, but the Dalneje Lake male shows three and five spines respectively on each paramere, and the Chishima male five and six spines. The fore wings of the syntype female have dark corneous points surrounded by faint darkish areas of moderate size, similar to the type specimens of the Nearctic *O. occidentis, alascensis,* and *coloradensis;* and these darkish areas are somewhat variable in size in the other specimens. The few specimens we have seen are smaller [length of fore wing male 14.5–16 mm (n = 4), female 15–17.5 (n = 2)] than most of our North American specimens, although specimens of that size are represented in our material. Finding no characters to separate these representatives of *O. flavus* from the Nearctic populations of *O. unicolor,* we extend our interpretation of *O. unicolor* as a widespread and highly variable species to include the Palaearctic *O. flavus.*

Other variants. One of the extreme variants encountered occurs in Alaska (Admiralty Island, Young Bay, 23 July 1981, 1♂, 1♀, ROM). The male of this series (Fig. 4) shows both pronounced narrowing at the base of the external branch of segment X and broadening toward the apex, as well as a strong tooth on the mesal edge of the basal segment of the inferior appendage (Fig. 4b). In the female (Fig. 5), segment X forms a slender tubular ovipositor lacking any dorsomedian subdivision, and the basal shoulders of X are not produced as a ledge. By contrast, in a female from Oregon (Baker Co., Pine Cr., 14 July 1967, 1♂, 1♀, ROM), segment X has the form of a slender ovipositor (Fig. 6), but the base of X is strongly produced as a sharp dentate ledge. While these are representative of the extreme variation, we found intermediates between them and less extreme genital structures. In a single series from Oregon (Lane Co., 12 mi. SE Eugene, 22 Sept. 1968, 2♂, 2♀, ROM) segment X in ventral aspect of one female forms an elongate ovipositor similar to that in Figure 5, but in the other female the ovipositor is extremely wide; in one of these females the lateral vulval lobes are enlarged apically into a thick truncate knob, very unlike the more usual flattened condition in Figure 3b.

Diagnosis for adults of O. unicolor *(Banks) s.l.* Fore wings ranging in colour from light yellow brown to dark brown; length of fore wing: male 14.5–18.5 mm; female 15–21 mm.

Male genitalia (Figs. 2, 4). Segment IX not unusually short; inferior appendages variable in shape of segments, ventromesal angle of basal segment in ventral aspect ranging from obtuse (Fig. 2c) to sharply pointed (Fig. 4b). Segment X with external branches tending to be orientated in an oblique to horizontal plane, usually narrowed basally and broader toward the apex; internal branches fused together into a flattened, somewhat pointed median lobe variably cleft at the apex; inferior branches usually absent, occasionally represented by a small protuberance or angulate vertical lobe. Phallus with parameres variably fused to aedeagus, ranging from little separation (Fig. 2d) to almost complete separation (as in Fig. 11d); spines at apex of parameres extremely variable, ranging from 1 to 6, usually straight and singlepointed.

Female genitalia (Figs. 3, 5, 6, 7). Segment IX with enlarged tergal lobes uniformly bulbous; sternum IX reduced to a small sclerotized lobe at each side of the vulval lobe. Segment X in ventral aspect tapered and tubular, broadly open ventrally, dorsally entire or with a narrow median cleft, base of X extended into a lateral shoulder in ventral aspect, variable in shape and frequently dentate.

Biology. Larvae of *O. unicolor* live in slow water and pool areas of cool rivers and streams, and also in the littoral zone of cool lakes. There appears to be little preference in substrate since larvae occur in stony streams and organic sediments of lake margins. Larvae usually burrow into bottom sediments for pupation, fixing the case to some larger object such as a rock. Collection records plotted by week for specimens examined (Fig. 10) are interpreted as a univoltine life cycle. Most adults emerge in the period 15 July–15 September. Early larval development proceeds quickly, third instars appearing at least by early September, fourth instars by mid-September, with fourth and fifth instars overwintering. In contrast to *Dicosmoecus* (Wiggins & Richardson 1982, figs. 33, 34), no diapausing fifth instar larvae were found in *O. unicolor.* Pupae were collected from June to the middle of October. These data are similar to those from an intensive study of a population in Marion Lake, B.C. (Winterbourn 1971), except that most larvae overwintered there as instars III and IV; egg masses (4.5–5 mm diam., approx. 150 eggs each) were found 9–24 September.

Larvae are shredders, vascular plant pieces and filamentous algae combined accounting for over 71% of the total gut content in material (10 LV) we sampled. Animal fragments averaged 9.7% but in one individual accounted for 97% of the gut content. Diatoms were present in small numbers in most guts, averaging 12.2%, although one specimen contained approximately 77 percent diatoms. Fine particulate organic matter averaged 6.9%. Our data contrast strongly with those of Winterbourn (1971) who reported only sediment and animal fragments in the guts of this species in a lake habitat.

Head widths for the last three instars have been established as follows (n = 204): LV, 1.62 mm (range 1.25–2.0); LIV, 1.12 mm (1.025–1.125); LIII, 0.725 mm.

Range. (Fig. 14). As defined here, *O. unicolor* is transcontinental through northern North America, extending throughout the western mountains and into eastern Asia. In North America the species is recorded from Alaska, Alberta, British Columbia, California, Colorado, Idaho, Maine, Manitoba, Massachusetts, Michigan, Montana, Nevada, Newfoundland, New Hampshire, New Mexico, New York, Northwest Territories, Nova Scotia, Ontario, Oregon, Quebec, Saskatchewan, South Dakota, Utah, Vermont, Washington, Wisconsin, Wyoming, and Yukon.

Material examined and other records. **ALASKA.** 24 June–27 September. Mile 140, Hwy. 3 (CNC). Admiralty Is. (ROM). Anchorage (ROM). Angel Cr. (ROM). Bear Cr. (CNC). Byers Cr. (ROM). Chatanika R. (Oswood). Chena R. (Oswood). Chichagof Is. (ROM). Chilkoot R. (ROM). Circle (ROM). Delta (CNC). Eklutna Lk. (INHS). Etolin Is. (ROM). Fairbanks (CNC). Glenallen (ROM). Gulkana R. (ROM). Haines (ROM). Hood Bay Cr. (ROM). Iditarod (MCZ, USNM). Juneau (ROM). Kenai Peninsula (ROM). Kodiak Is. (ROM). Lk. Iliamna (ROM). Lowe (Oswood). Lower Summit Lk. (ROM). Moon Lk. (ROM). Palmar (USNM). Parks Hwy., mp. 128.5 (ROM). Port Heiden (ROM). Portage (CNC). Prince of Wales Is. (DGD). Reflection Lk. (ROM). Sadlerochit Spring (USNM). Squirrel Cr. Cpgrd. (CAS, DGD). Steese Hwy., ml. 35–97.2 (ROM). Tolsona R. (ROM). Trapper Cr. (CNC). Turner Lk. (ROM). Ugak Bay (ROM). Umnak Is. (ROM). Upper Gulkana R. (INHS). Wasilla (INHS). Wrench Cr. (ROM). **ALBERTA.** 16 July–12 October. Banff (INHS, ROM, UA, USNM). Calgary (INHS). Canmore (ROM, UA). Coleman (UA).

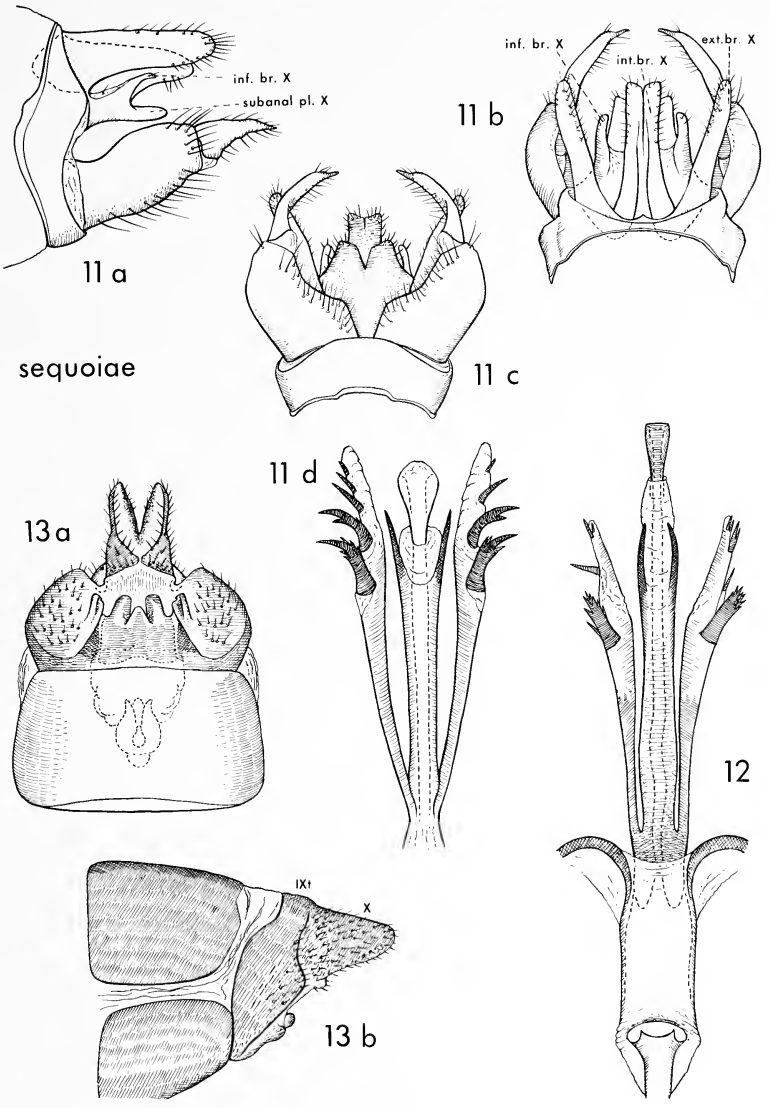
Crowsnest R. (UA). Cypress Hills Prov. Pk. (ROM). Dungarvan Cr. (ROM). Edson (ROM, UA). Fairview (ROM). Fawcett (UA, USNM). Ft. McMurray (USNM). Ft. Vermilion (ROM). Galwey Brook (ROM). Gorge Cr. (UA). Hinton (UA). House R. (ROM). Jasper Nat. Pk. (ROM, UA). Kananaskis (UA). LaBiche R. (ROM). Longview (UA). Lundbreck Falls (ROM, UA). McLeod R. (UA). Nojack (ROM, UA). Nordegg (ROM, UA). N. Ram R. (ROM). Red Deer Crossing (ROM). Sheep R. (UA). Ware Cr. (UA). Waterton Nat. Pk. (ROM, UA). Whitecourt (ROM). Wildhorse Camp (ROM). Yara Cr. (ROM). **BRITISH COLUMBIA**. 2 July–14 November. Atlin (CNC). Babine R. (INHS). Beaverdell (CNC). Cassiar Jct. (CNC). Clinton (ROM). Creston (CNC). Cultus Lk. (CNC, INHS, ROM). D'Arcy (ROM). E. C. Manning Prov. Pk. (ROM). Edgewood (INHS). Fernie (INHS, ROM). Fraser Lk. (CNC). Galena Bay (CNC). Glacier (ROM). Golden (ROM). Haney (ROM). Harrison Lk. (CNC, INHS). Highland R. Prov. Pk. (ROM). Invermere (ROM). Jesmond (CNC). Kamloops (ROM). Knutsford (ROM). Langley (ROM). Lillooet (CNC, USNM). Little Fort (CNC). Lower Post (CNC). McBride (CNC). Miledge Cr. (CNC). Mt. Robson Prov. Pk. (ROM). New Denver (CNC). Nicola (CNC). Pemberton (CNC). Princeton (CNC). Prophet R. Prov. Pk. (ROM). Queen Charlotte Islands (USNM). Revelstoke (USNM). Rolls (INHS). Rosebery (CNC). Salmon Arm (INHS). Sandon (USNM). Sicamous (CNC). Squamish (CNC). Stanley (CNC). Summerland (CNC). Terrace (CNC, INHS, USNM). Topley (CNC). Trutch (CNC). Valemount (CNC). Vancouver (INHS). Vancouver Is. (CNC, ROM). Vavenby (USNM). Walhachin (ROM). Wycliffe (ROM). Yellowhead Pass (ROM). **CALIFORNIA.** 23 July.–11 October. Alpine Co. (INHS). Fresno Co. (DJB). Inyo Co. (DJB, INHS). Modoc Co. (CAS, CNC, USNM). Napa Co. (ROM). Nevada Co. (ROM). Placer Co. (DGD, LACM). Plumas Co. (DJB). Santa Cruz Co. (INHS). Sequoia Nat. Pk. (INHS). Siskiyou Co. (CAS, USNM). Trinity Co. (CNC). Yosemite Nat. Pk. (LACM). **COLORADO**. 2 August–1 October. Cameron Pass (INHS). Chaffee Co. (CAS). Custer Co. (USNM). El Paso Co. (INHS). Jefferson Co. (USNM). Larimer Co. (INHS, ROM). Park Co. (USNM). Routt Co. (CAS). Saquache Co. (ROM). S. Colorado (Vienna). S. Park (MCZ). **IDAHO**. 5 July–1 October. Bannock Co. (ROM). Bonner Co. (CAS, ROM). Idaho Co. (ROM,

USNM). Latah Co. (ROM). Teton Co. (ROM). Valley Co. (CAS, ROM). Wallace (MCZ). **MAINE**. 4 August–15 September. Cumberland Co. (USNM). Oxford Co. (INHS). Piscataquis Co. (USNM). **MANITOBA**. 27 August. Flin Flon (ROM). God's R. (ROM). Hayes R. (INHS). **MASSACHUSETTS**. No adults. Berkshire Co. (USNM). **MICHIGAN**. 28 August–29 August. Emmet Co. (ROM). Houghton Co. (ROM). Lake Co. (fide Flint 1960). **MONTANA**. 7 August–28 September. Carbon Co. (ROM). Cascade Co. (ROM). Flathead Co. (ROM). Gallatin Co. (CNC). Glacier Nat. Pk. (DGD, ROM, USNM). Missoula Co. (INHS, ROM). Ravalli Co. (ROM). **NEVADA**. 31 July. Washoe Co. (USNM). **NEWFOUNDLAND**. Grand Lake, 28 July, (MCZ). Cartwright (Labrador) 2 August (ROM). **NEW HAMPSHIRE**. 4 August–10 September. Coos Co. (INHS, ROM, USNM). **NEW MEXICO**. 4 September. Rio Arriba Co. (INHS). **NEW YORK**. 7 September. Ulster Co. (INHS). **NORTHWEST TERRITORIES**. 6 July–24 August. Aklavik (CNC, ROM). Great Slave Lk. (UA). Norman Wells (ROM). **NOVA SCOTIA**. 12 August, Baddeck (fide Banks 1943). **ONTARIO**. 9 August–18 September. Algoma Dist. (ROM). Belfountain (ROM). Cochrane Dist. (ROM). Durham Co. (ROM, USNM). Kenora Dist. (ROM). Lk. Superior (ROM). Midland (ROM). Oro Station (ROM). Rainy R. Dist. (ROM). Thunder Bay Dist. (ROM). Wellington Co. (ROM). **OREGON**. 21 June–13 November. Baker Co. (ROM, USNM). Benton Co. (INHS, NHA, ROM). Blue Mtns. (ROM). Clackamas Co. (ROM). Clatsop Co. (INHS, ROM, USNM). Crook Cr. (ROM). Deschutes Co. (NHA, ROM). Douglas Co. (ROM). Grant Co. (ROM). Harney Co. (ROM). Hood River Co. (ROM). Jefferson Co. (ROM). Klamath Co. (NHA). Lake Co. (DGD, ROM). Lane Co. (ROM). Lincoln Co. (DGD, ROM). Linn Co. (ROM). Umatilla Co. (ROM). Union Co. (NHA, SDS). Wallowa Co. (INHS, NHA, ROM). Wasco Co. (ROM). Wheeler Co. (ROM). Yamhill Co. (INHS). **QUEBEC**. 29 June–23 September. Brebeuf (ROM). Cascapedia (INHS). Harrington (ROM). Matamek R. (fide Williams and Williams 1979). Mt. Lyall (INHS). Wacouno R. (ROM). Other records fide Roy and Harper 1979. **SASKATCHEWAN**. 22 August–2 September. N. Battleford (ROM). Pierceland (ROM). Prince Albert (INHS, ROM). **SOUTH DAKOTA**. No adults. Lawrence Co. (ROM). **U.S.S.R.** 19 July–17 September. Kamchatka (ROM). Kurile Islands,

Chishima (ROM). Pushino (Z.I. USSR). **UTAH**. 23 July–16 September. Cache Co. (INHS, ROM). Carbon Co. (USNM). Daggett Co. (ROM). Garfield Co. (ROM). San Juan Co. (USNM). Summit Co. (CAS, ROM, USNM). Wasatch Co. (INHS, ROM). Washington Co. (USNM). **VERMONT**. 11 September–23 September. Bennington Co. (ROM). Windham Co. (DGD). **WASHINGTON**. 1 June–9 October. Chelan Co. (ROM, SDS, USNM). Jefferson Co. (ROM, USNM). King Co. (ROM). Kittitas Co. (ROM, SDS, USNM). Mt. Rainier Nat. Pk. (ROM). Okanogan Co. (USNM). Pacific Co. (ROM). Snohomish Co. (MCZ). Whatcom Co. (CNC, ROM, USNM). Whitman Co. (INHS). Yakima Co. (ROM). **WISCONSIN**. (fide Longridge and Hilsenhoff 1972). **WYOMING**. 6 August–1 September. Albany Co. (ROM). Carbon Co. (ROM). Teton Co. (INHS). Uinta Co. (USNM). Yellowstone Nat. Pk. (INHS). **YUKON**. 26 June–29 August. Alaska Hwy. At Aishihik R. (CAS) and at Koidern R. (ROM). Bearfeed Cr. (ROM). Blackstone (ROM). Burwash Landing (CNC). Champagne (CNC). Christmas Cr. (ROM). Clear Cr. (ROM). Dawson (CNC). Dempster Hwy., kmp 72, 140.5 (ROM). Dezadeash Lk. (ROM). Eagle Plain (ROM). Eagle R. (ROM). Engineer Cr. (ROM). Flat Cr. (ROM). George's Gorge (CNC). Haines Jct. (CNC). Haines Rd., kmp 175 (ROM). Klondike Hwy., kmp 476, 562, 572, 626 (ROM). Kluane (UBC). Lake Laberge (UBC). Lapie R. Canyon (ROM). Lower Rancheria R. (ROM). Mayo Rd., kmp 14 (ROM). McQuesten R. (ROM). Money Cr. (ROM). Pelly Crossing (ROM). Pine Cr. (ROM). Quiet Lk. (ROM). Rancheria (UBC). Rose Lk. (UBC). South Canol Rd., kmp 22, 39.5, 154, 172 (ROM). Sulphur Lk. (ROM). Tagish (UBC). Takhanne R. (ROM). Tatchun Cr. (ROM). Teslin (CNC). Watson Lk. Cpgrd. (ROM). Whitehorse (CNC). Willow Cr. (CNC, ROM).

Onocosmoecus sequoiae n.sp.
Figs. 11–13

Almost all of the several hundred adult specimens examined fall within the bounds of continuous variation described above in the *O. unicolor* complex, except some from a few localities for the most part in the Sierra Nevada Mountains of California. Because these specimens show clear structural differences from *O. unicolor* as defined above, and because intermediate forms have not been



Figs. 11–13. *Onocosmoecus sequoiae* n.sp. 11, Holotype male, Tulare Co., California, genitalia: a, lateral; b, dorsal; c, ventral; d, phallus. 12, Variant male, Shasta Co., California, phallus. 13, Allotype female, Tulare Co., California, genitalia: a, ventral; b, lateral. (ext. br. X, int. br. X., inf. br. X, external, internal, & inferior branches of segment X; subanal pl. X, subanal plate of segment X; IXt, tergum of segment IX; X, segment X).

found, we consider them to represent a distinct and previously unrecognized species.

Adult. Similar to *O. unicolor* in general body characters and venation, but distinguished by characters of the male and female genitalia as outlined in the key to species. Colour more similar to yellowish variants of *O. unicolor* than to the darker brown specimens; dark markings on the fore wings around the corneous spot in cell R4 and around the thyridium variable. Length of the fore wing: ♂ 18–20 mm; ♀ 20–21 mm.

Male genitalia (Fig. 11). Segment X with external branches in lateral aspect broad at the base, usually somewhat tapered toward the apex, orientation mainly in a vertical plane; internal branches in dorsal aspect with a double-edged median crest; subanal plate in dorsal aspect extending beyond the periphery of the internal branches; inferior branch of X prominent as a flattened tongue between the external branch and the subanal plate. Phallus with parameres entirely separate from the aedeagus except at the basal articulation, spines fewer than in *O. unicolor* and bent, proximal spines cusped with small accessory points, apex of each paramere a prominent membranous lobe.

Female genitalia (Fig. 13). Segment IX with tergum consisting of enlarged lateral lobes as in *O. unicolor,* but the lobes concave ventrolaterally; sternum of IX somewhat folded and less sclerotized than in *O. unicolor.* Segment X in ventral aspect shorter and broader than in *O. unicolor,* and more widely divided dorsally, prominent basal shoulder lacking. Vulval lobe in ventral aspect with median portion wider and more pointed than is usually so in *O. unicolor.*

Larva. Unknown for this species, and consequently *Onocosmoecus* larvae from the general range of *O. sequoiae* cannot yet be assigned to species.

Types. Holotype male (pinned): CALIFORNIA, Tulare Co., Salmon Cr., trib. Kern R., Horsemeadow Campground, Sequoia National Forest, approx. 7000 ft., 10 mi. NE Kernville, 7 August 1985, black light trap, R. W. Wisseman; Allotype female (pinned), same data as holotype; Paratypes 48♂ 17♀, same data as holotype, specimens pinned and in alcohol. These specimens are deposited in the Department of Entomology, Royal Ontario Museum, Toronto.

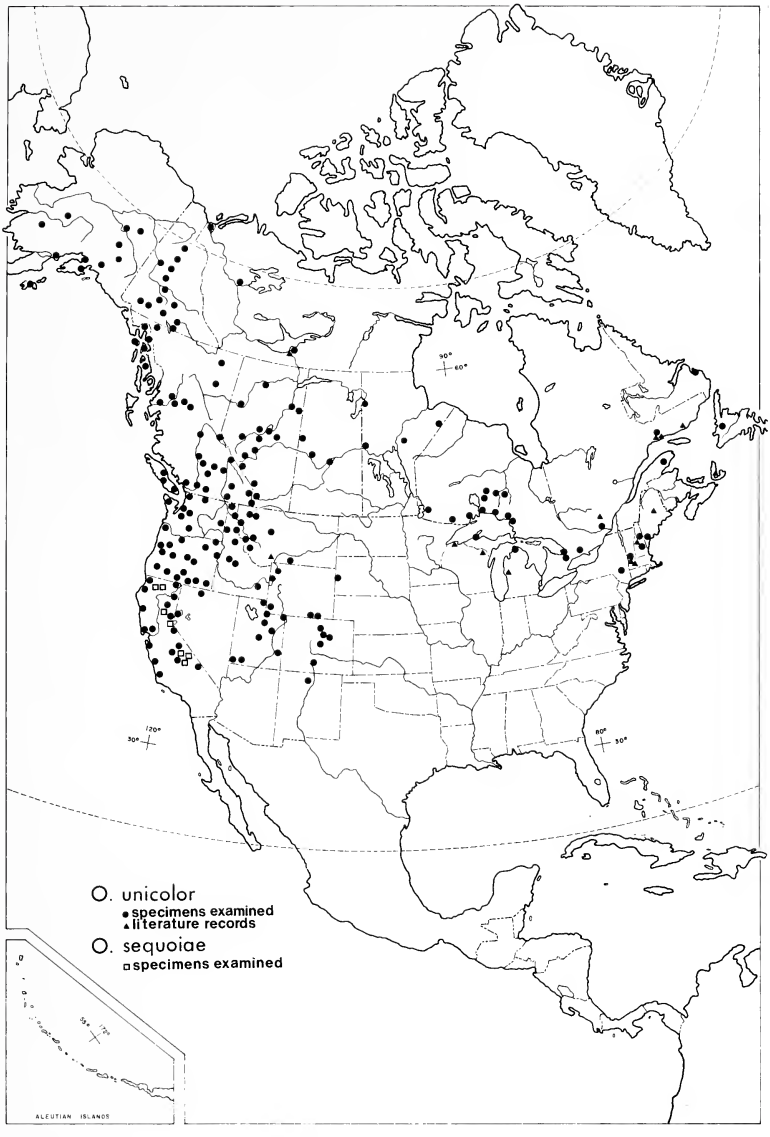


Fig. 14. Nearctic distribution of *Onocosmoecus* spp.

Additional Paratypes. CALIFORNIA: El Dorado Co., Tahoe Paradise, 5–13 August 1985, 4♂, W. H. Tyson, DGD; 1 mi. SW Meyers, 13 July 1984, 1♀, W. H. Tyson, DGD. Madera Co., Red's Meadow, 16 August 1941, 3♂ 1♀, M. V. Hood, LACM; Nelder Cr. Camp, 4600 ft., 25 August 1973, 1♀, W. H. Tyson, USNM; Central Camp, 5500 ft., 30 July 1983, 3♂, J. Larson, DGD. Siskiyou Co., Shadow Cr., 7 mi. E Cecilville, 5 September 1968, 1♀, USNM. Tulare Co., Salmon Cr. at Horsemeadow Campground, Sequoia National Forest, 31 July 1965, 2♂, W. P. Vann, DGD; Johnsondale, Aug.–Sept. 1985, many ♂♂ ♀♀, uvl, D. J. Burdick, CAS, DJB, USNM, ROM.

From extensive u.v.l. collections made by D. J. Burdick, we have been able to examine long series of adults of *O. sequoiae.* There is no evidence of intergradation between *O. sequoiae* and *O. unicolor,* and both species were represented in two of the series examined: Madera Co., Lewis Cr., 16–22 September 1983; El Dorado Co., 1 mi. SW Meyers, 30 August 1984 (specimens in collection of D. J. Burdick). In two male specimens of *O. unicolor* from Fresno Co. (Friant) the inferior branch of segment X was an angulate vertical plate, but not the flattened tongue of *O. sequoiae;* and the parameres of these specimens were typical of *O. unicolor.*

Range and Habitat. Adults of this species have been collected in the vicinity of streams mainly in the Sierra Nevada Mountains of California in El Dorado, Inyo, Madera, Plumas, Shasta, Siskiyou, and Tulare Counties (Fig. 14). In the absence of information on larvae of *O. sequoiae,* any difference in habitat between the two species remains unknown.

Variation. Another form, provisionally considered a variant of *O. sequoiae,* has been found in collections from Shasta County (Castle Cr., approx. 3 mi. w. Hwy. I-5, 9 August 1985, 18♂ 7♀, uvl, ROM; Indian Cr., Castle Crags State Park, 9 August 1985, 1♂, uvl, ROM; Hat Cr., 25 June 1947, 1♂, CAS) and Plumas County (Thompson Cr., 0.6 mi. above Thompson Meadows, s.w. Quincy, 16–17 July 1985, 1♂, uvl, ROM). These specimens are larger than most *O. unicolor* and typical *O. sequoiae* (length of fore wing: ♂ 21–22 mm; ♀23 mm), but the principal difference is in the parameres of the males (Fig. 12) where the proximal spine is a long, stout straight process with a cluster of short denticles at the apex. The distal spines on the parameres are reduced in size and nearly

straight, and the apical membranous lobe is also reduced. The fused internal branches of segment X are more flattened than in the typical form and the median crest less distinct; the external branches of X tend to be straight-sided and less tapered than in the typical form, but are enlarged apically in one specimen in the Shasta County series. Females of this variant are similar to the typical form.

None of these variant specimens is included in the type material of *O. sequoiae,* and in the continued absence of intermediates, they could be considered as representing a distinct species.

Key to adults of *Onocosmoecus s.s.* species

1 Males 2
Females 3

2(1) In lateral aspect, inferior branches of segment X large and well developed into a flattened tongue between the external branch and subanal plate, external branches of X largely orientated in a vertical plane, frequently broadest at the base and tapering apically (Fig. 11a). Known only from the Sierra Nevada Mountains of eastern California (Fig. 14) ..... *sequoiae*
In lateral aspect, inferior branches of segment X usually lacking, occasionally present but very small, external branches of X oriented more horizontally, frequently narrow at the base and broadened apically (Fig. 2a). Widely distributed in North America including California (Fig. 14) and also far eastern USSR ..... *unicolor*

3(1) Segment IX with terga enlarged and bulbous, segment X in ventral aspect a tapered tube, open ventrally but closed dorsally for the most part or with a narrow apical cleft (Figs. 3, 5, 6, 7) ..... *unicolor*
Segment IX with terga enlarged but concave ventrolaterally, segment X in ventral aspect tubular but tapered apically little if at all, and cleft both dorsally and ventrally in a broad V-shape (Fig. 13) ..... *sequoiae*

Acknowledgments

This study was completed under financial support (to GBW) from the Natural Sciences and Engineering Research Council of Canada. Field studies were supported by previous grants (to GBW) from the

National Research Council of Canada (A5707), the U.S. National Science Foundation (G22135) and the Canadian National Sportsmen's Show. For the loan of type specimens and of general collections, we acknowledge the assistance of N. E. Woodley, A. F. Newton and N. D. Stone, Museum of Comparative Zoology, Harvard University; A. Kaltenbach, Naturhistorisches Museum Wien; O. S. Flint, United States National Museum of Natural History; D. G. Denning, Moraga, California; D. J. Burdick, California State University, Fresno; J. D. Unzicker, Illinois Natural History Survey; S. D. Smith, Central Washington State College; A. P. Nimmo, University of Alberta; N. H. Anderson and R. W. Wisseman, Oregon State University; I. M. Levanidova, Institute of Biology and Pedology, Vladivostok; M. W. Oswood, University of Alaska; F. Schmid, Biosystematics Research Institute, Ottawa; L. Zhiltzova, Zoological Institute, USSR Academy of Sciences, Leningrad; W. J. Pulawski, California Academy of Sciences, San Francisco. For assistance with field collections we are indebted to G. W. Courtney, H. E. Frania, E. R. Fuller, R. Jaagumagi, L. H. Kohalmi, B. D. Marshall, C. R. Parker, R. S. Scott, I. M. Smith, R. N. Vineyard, R. W. Wisseman, and T. Yamamoto.

Line drawings were prepared by Anker Odum and Zile Zichmanis of the Royal Ontario Museum. Photographs were made by Brian Boyle, ROM Photography. Susan Pasch, Shakilah Mehrunnisa and E. R. Fuller assisted with the preparation of the manuscript.

Summary

From analysis of type specimens of the seven putative species of the *Onocosmoecus unicolor* group and of extensive collections from many localities in North America, six names (*Asynarchus tristis* Banks, *Dicosmoecus coloradensis* Ulmer, *Anabolia quadrinotatus* Banks, *Dicosmoecus (O.) occidentis* Banks, *Dicosmoecus (O.) alascensis* Banks all from North America, and *Dicosmoecus flavus* Martynov from Kamchatka) are proposed as junior subjective synonyms of *Onocosmoecus unicolor* (Banks). Other variables are discussed and it is concluded that existing evidence shows *O. unicolor* to be a highly variable and widespread species ranging through northern and montane North America to eastern Asia. A new species *Onocosmoecus sequoiae* is recognized from several localities, mainly in

the Sierra Nevada Mountains of California. These two species con titute *Onocosmoecus s.s.;* geographic distribution is summarized and observations on biology are included.

References

Banks, N. 1897. New North American neuropteroid insects. *Trans. Am. ent. Soc.* **24:** 21–31.

———. 1900. New genera and species of Nearctic neuropteroid insects. *Trans. Am. ent. Soc.* **26**: 239–259.

———. 1908. Some Trichoptera, and allied insects, from Newfoundland. *Psyche* **15:** 61–67.

———. 1943. Notes and descriptions of Nearctic Trichoptera. *Bull. Mus. comp. Zool.* **92:** 341–369.

Cummins, K. W. 1973. Trophic relations of aquatic insects. *Ann. Rev. Entomol.* **18:** 183–206.

Flint, O. S. 1960. Taxonomy and biology of Nearctic limnephilid larvae (Trichoptera), with special reference to species in eastern United States. *Entomologica am.* **40:** 1–120.

Longridge, J. L. and W. L. Hilsenhoff. 1972. Trichoptera (Caddisflies) *In* Aquatic Insects of the Pine Popple River, Wisconsin by W. L. Hilsenhoff et al. Wisconsin Dept. Nat. Resources, Tech. Bull. **54**, pp. 1–44.

Martynov, A. V. 1913. Trichoptera of the Kamtshatka expedition. *Russk. ent. Obozr.* **13**: 476–481.

———. 1914. Les Trichoptères de la Sibérie et des régions adjacentes. IV-e partie. Sousfam. Limnophilinae (fam. Limnophilidae). *Ezheg. zool. Muz.* **19**: 173–285.

———. 1925. Trichoptera recueillis au Kamtshatka par l'expédition de Mr. Th. Riabusinskij en 1908–1909. *Ezheg. zool. Muz.* **26**: 10–26.

Ross, H. H. 1938. Lectotypes of North American caddis flies in the Museum of Comparative Zoology. *Psyche* **45**: 1–61.

Roy, D. and P. P. Harper. 1979. Liste préliminaire des Trichoptères (insectes) du Québec. *Ann. Soc. ent. Québec* **24**: 148–171.

Schmid, F. 1955. Contribution à l'étude des Limnophilidae (Trichoptera). *Mitt. schweiz. ent. Ges.* **28**.

———. 1980. Genera des Trichoptères du Canada et des États adjacents. Les Insectes et Arachnides du Canada, Partie 7. *Can. Agric. Publ.* **1692.** 296 pp.

Ulmer, G. 1905. Neue und wenig bekannte aussereuropäischeTrichopteren, hauptsächlich aus dem Wiener Museum. *Annln naturh. Mus. Wien* **20**: 59–98.

———. 1927. Entomologische Ergebnisse der schwedischen Kamtchatka-Expedition 1920–1922. 11. Trichopteren und Ephemeropteren. *Ark. Zool.* **19**: 1–17.

Wiggins, G. B. 1977. Larvae of the North American Caddisfly Genera (Trichoptera). University of Toronto Press, Toronto and Buffalo. 401 pp.

Wiggins, G. B. and J. S. Richardson. 1982. Revision and synopsis of the caddisfly genus *Dicosmoecus* (Trichoptera: Limnephilidae; Dicosmoecinae). *Aquat. Insects* **4**: 181–217.

WILLIAMS, N. E. AND D. D. WILLIAMS. 1979. Distribution and feeding records of the caddisflies (Trichoptera) of the Matamek River region, Quebec. *Can. J. Zool.* **57**: 2402–2412.

WINTERBOURN, M. J. 1971. The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. *Can. J. Zool.* **49**: 623–635.

POPULATION FLUIDITY IN *LEPTOTHORAX LONGISPINOSUS* (HYMENOPTERA:FORMICIDAE)*

By Joan M. Herbers and Carol W. Tucker

Department of Zoology, University of Vermont
Burlington VT 05405

Introduction

Although social insect colonies are commonly conceived as stable entities in time and in space, considerable information exists to demonstrate that population fluidity can be pronounced. Data on ants show that workers can be exchanged between nests (Kannowski 1959; Scherba 1965; Chauvin and Leconte 1965; Alloway *et al* 1982; Del Rio Pesado and Alloway 1983; MacKay and MacKay 1983); a colony can undergo budding (Scherba 1958; Talbot 1961; Brian 1965; Cherix *et al* 1980; Stuart 1985; Pamilo *et al.* 1985); and entire nests can move from one site to another (Van Pelt 1976; Smallwood and Culver 1979; Smallwood 1982; Droual 1984; Herbers 1985). These observations lead to the conclusion that in some species the colony is not a fixed entity, but rather a shifting collection influenced by ecological contingencies.

That a given colony can occupy more than one physical nest site, a condition known as polydomy, deserves particular attention (Fletcher and Ross 1985). Evolutionary dynamics under conditions of colony fractionation are poorly understood, even though the consequences for eusocial evolution may be profound. There is surprisingly little information to document and measure the extent of population fluidity for any species, a gap we help to fill in this paper.

Recent work demonstrates that some species of leptothoracine ants are polydomous (Alloway *et al* 1982; Del Rio Pesado and Alloway 1983; Stuart 1985). These inconspicuous temperate species are well-suited for detailed studies of polydomy because they are small and easy to culture. Here we quantify nest fission, fusion, migration, and other features of polydomy for *Leptothorax longispinosus* kept under semi-natural conditions in the laboratory. While

Manuscript received by the editor May 12, 1986

a complete understanding of population fluidity must be predicated on work conducted in the field, our results provide insight into the evolutionary ecology of this ant.

Population structure in *L. longispinosus*

Many ants of the genus *Leptothorax* are polygynous (Buschinger 1968, 1974), and *L. longispinosus* is no exception (Talbot 1957; Headley 1943; Alloway *et al* 1982). Previous work on the E. N. Huyck Preserve (Albany County, New York) showed the population to be facultatively polygynous: some nests contain no queen, others have one, and still others have multiple queens (Herbers 1984). Moreover, there was a strong winter-summer dichotomy in queen distribution. Many nests in summer are queenless, whereas in winter such groups are rare (Herbers 1986a); similarly, the average number of queens per nest is lower in summer. Finally, nests are considerably more spread out in summer than in winter (Herbers 1985). These results are best explained as correlates of a seasonal shift in spatial structure: colony fractionation in summer and condensation for overwintering. It appears that, for the most part, overwintering nests are independent colonies that become polydomous in summer when they fractionate to occupy several nest sites (Herbers 1986a). This cyclic polydomy hypothesis is supported by behavioral evidence reported below.

Methods

Nests of *L. longispinosus* were excavated from the New York site in late October 1983, when they exhibited spatial relationships and a distribution of queens among nests that is typical of winter. Each nest was returned to the laboratory and removed from its stick, acorn, or root. The ants were then resettled into glass tubes 10 cm long and 4 mm in diameter. Each nest was put into a separate box and incubated at 4° C for overwintering. In March the temperature and light-dark cycles were slowly incremented to match outside conditions. On May 8, 1984 the conditions were stabilized at 14 hours of light. On that date, we positioned 17 nests on 4 artificial forest floors to duplicate their spatial positions in nature the previous fall (Figure 1). Observations and censuses were then conducted until August 27, 1984, when the experiments were terminated.

The artificial forest floors were 1m × 1m in size. Each had a red glass base upon which autoclaved pine needles, leaf fragments and other debris typical of the habitat were scattered. The sides of the floor were coated with petroleum jelly to prevent worker escapes, and the entire structure was enclosed in mosquito netting to restrict alate fights. Lights above and below the red glass base provided illumination. The temperature was maintained at 18–20° C and relative humidity at 60–90%. Periodically water was sprinkled on the floor to simulate rainfall. In addition to placing nests on the floor according to where they had been collected, we supplied additional tubes so that each floor had a total of 10 nesting sites. Nests were supplied with water *ad libidum* and solid food (both frozen fruitflies and a formula based on Bhatkar and Whitcomb's (1970) recipe) three times weekly. Detailed observations of behavior were taken for the first 3 weeks (2 hours of continuous observation daily from 9:00–11:00 as well as periodic checks), after which the intensity of observation was reduced to 2 hours per week. Nests were censused daily for the first two weeks and weekly for the rest of the period.

Results

The initial contents of nests are given in Table 1. Four nests on 1A (all polygynous), three nests on 1B (one queenless, one monogynous, one polygynous) and five nests on 2B (two queenless, one monogynous, two polygynous) were positioned to duplicate their natural locations with respect to each another (Figure 1).

Direct observations of the ants showed that initially aggression was common: workers engaged in fighting behavior, wherein two workers would interlock mandibles, attempt to sting each other, push or pull by the mouthparts, and so on. These encounters sometimes resulted in death of one or both participants. Not all interactions were aggressive, however; workers were observed to carry other workers, brood, and in one case a queen outside the nest. Several occasions of tandem running (which usually precedes a colony migration (Möglich 1978) were observed. In addition to interacting with other ants, workers were often observed to explore, forage, and manipulate pieces of detritus and food.

Particularly striking was exploration of the empty tubes which represented potential new nesting sites. This exploratory behavior is

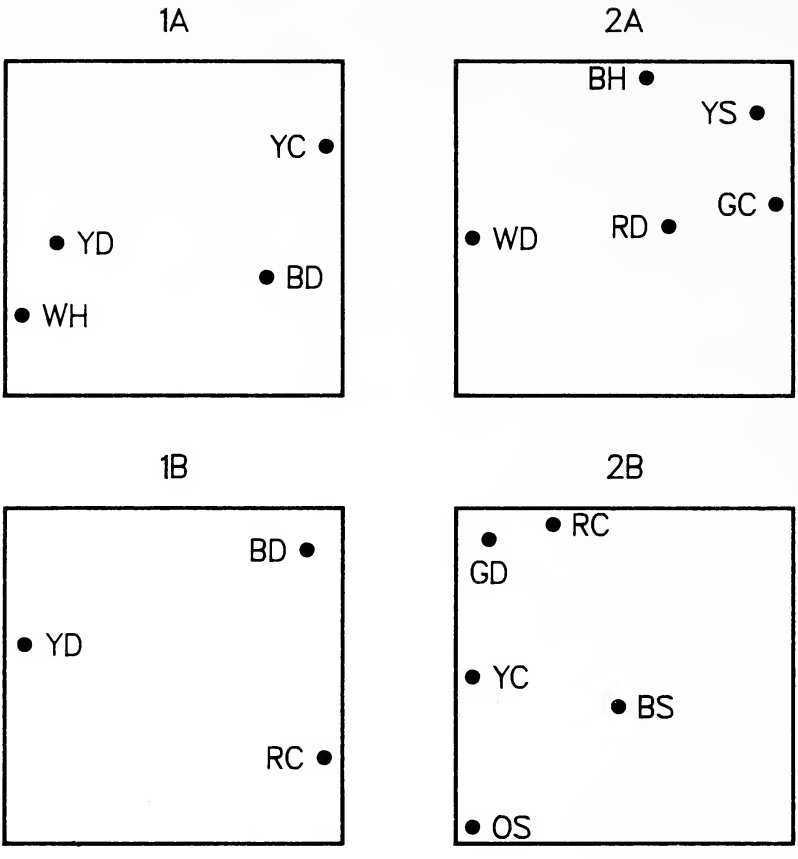


Fig. 1. Spatial relationships of nests placed on floors (each 1m × 1m). Additional nesting tubes were supplied to give a total of 10 on each floor.

apparent from censuses when one or two workers were observed within a tube (cf. Table 2). Sometimes this exploration was followed by immigration, but more often there was no apparent result.

The time scale within which population changes occurred is given in Figure 2. Fighting between workers was most frequent in the first three weeks of the season, and virtually nonexistent after 8 weeks. Similarly, observations of workers carrying other workers were clustered in the first few weeks of the experiments. Exploration of new nesting sites was quite high initially, then fell off by the second

Table 1. Occupants of nests positioned on forest floors in early May

	Marker	Queens	Workers	Eggs	Larvae
Floor 1A	BD	22	91	10	178
	YC	4	30	2	73
	WH	2	24	0	28
	YD	7	80	0	99
Floor 1B	YD	1	20	14	11
	BD	5	13	0	28
	RC	2	28	5	19
Floor 2A	BH	0	13	0	18
	WD	0	9	0	8
	RD	3	9	0	47
	GC	4	63	0	64
	YS	2	39	0	67
Floor 2B	GD	1	12	5	29
	OS	3	11	0	15
	YC	0	101	0	66
	BS	3	29	13	15
	RC	0	21	0	39

week. Moreover, the five observations of tandem running behavior were restricted to the first 2 weeks. Workers and/or brood moved between existing nests primarily within the first four weeks. By mid-June there was little activity on the floors other than routine foraging.

The first month of census data for nests on floor 2B are given in Table 2. From these data we can infer the following: a group of workers moved from RC to GD on May 9. On the 10th, a queen and some workers moved from GD to RC, and the fusion of GD and RC continued over the following three days. On May 28 the YC nest split, with 47 workers moving to GD and 35 remaining behind. At about this time members of the RC site started to explore OH; this tentative exploration continued for about two weeks more. Thus a great deal of information about population fluidity can be gleaned from census data alone.

The census data also showed striking differences in activity between the first few weeks and the rest of the summer. Wholescale migration, fission into subunits, and fusion of nests occurred most often early in the experiments (Figure 3). Of three migration events, two occurred in the first two weeks. Of four fission events, two

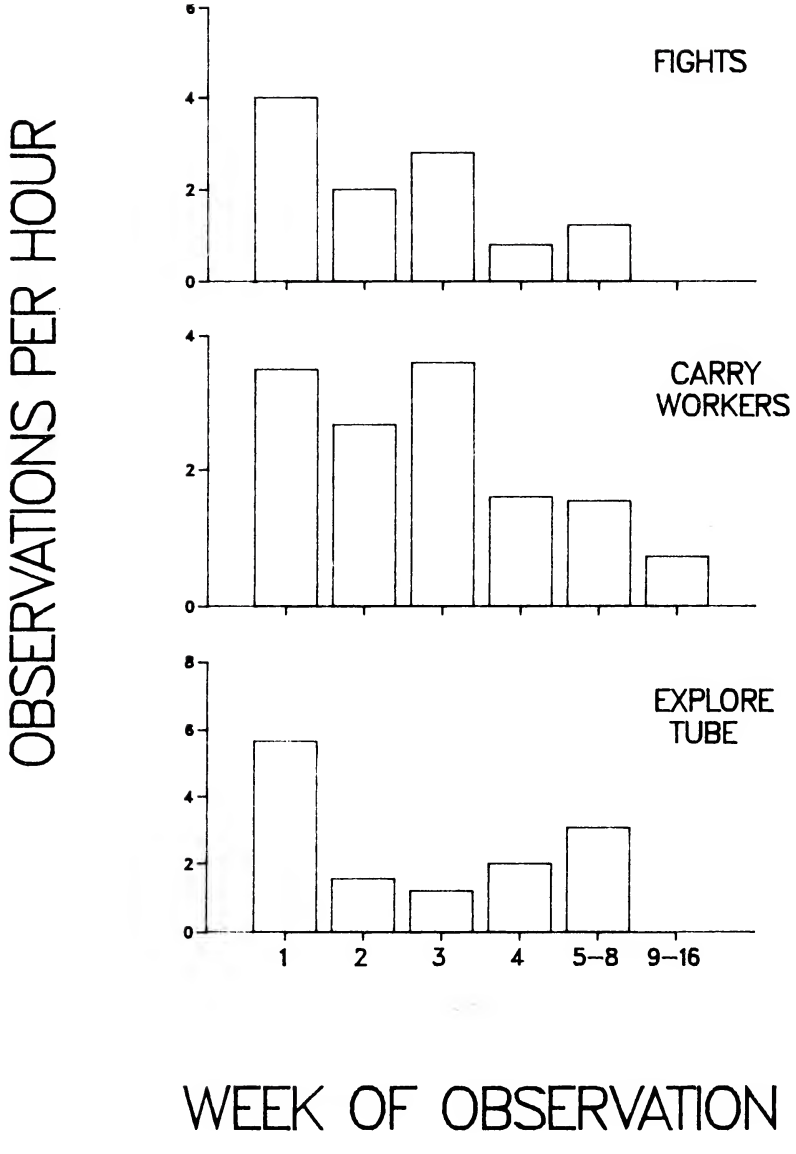


Fig. 2. Frequencies of certain events associated with population changes. The time scale is irregular to indicate how activity dropped off in summer.

occurred in the second week, and one in the fourth week. Of two fusions, one occurred on the third day of observation. The remaining events occurred in late July, and involved ants only on Table 1A (Figure 4): one nest moved and split within the next week; one of those subunits was apparently joined by a second nest immediately thereafter. Thus, although the two nests had not interacted in any discernible way prior to the end of July, they demonstrated a remarkable fluidity after being in place for eight weeks.

Fission rates may be a function of nest size (Stuart 1985). Nests that underwent fractionation tended to have more queens than those which failed to subdivide during this study (average ranks of 10.4 and 8.6, respectively), but this difference was not significant (Mann-Whitney U-test; $P \gg .05$). Similarly, nests that underwent fission tended to have more workers ($\bar{R} = 12.8$) than those which failed to subdivide ($\bar{R} = 7.9$), but again the differences were not significant ($U = 40.6$, $P = .07$). Although the small number of fissions reduced the power of our analysis, nonetheless out results are consistent with Stuart's observations.

Most nests in this experiment reared sexuals. Since it is extremely difficult to mimic the naturally-occurring reproductive flights of this species in the laboratory and thus our observations of reproductive behavior may not be indicative of natural activity, we give only a brief account: males eclosed in late July, and after staying in the nesting tubes for a week or so, they started to emerge onto the forest floor. There they explored and took a few preliminary hops before returning to their natal nests (at which point they were not always allowed reentry). By late August, all males left their nests permanently, and many were dead. Female alates, however, were much more reclusive, and came outside the nest rather infrequently. As a rule, these females were reaccepted into their natal nests readily. In only two cases was a gyne from one nest accepted into a second nest; thus acceptance of non-natal new queens may be rare in nature as well. These observations suggest that polygyny develops in *L. longispinosus* nests primarily when daughters rejoin their nest of origin.

Discussion

Like all laboratory studies, our work can be criticized on the grounds that behavior of disturbed nests in seminatural conditions

Table 2. Census data for nests on Floor 2B. Only ants inside nesting tubes were counted, which produced some variation in worker numbers from day to day.

Site Marker	5/8/84		5/9		5/10		5/11		5/12		5/13		5/14		5/15		5/16	
	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W
GD	1	12	1	25	0	16	0	6	0	1	0	1	0	0	0	0	0	0
OS	3	11	3	9	3	9	3	8	3	9	3	7	3	6	3	7	3	7
YC	0	101	0	95	0	91	0	92	0	94	0	81	0	100	0	95	0	86
BS	3	29	3	26	3	26	3	23	3	16	3	16	3	10	3	15	3	13
RC	0	21	0	7	1	11	1	16	1	24	1	26	1	28	1	19	1	19
OH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Nest Tube	5/17		5/18		5/21		5/28		6/4	
	Q	W	Q	W	Q	W	Q	W	Q	W
GD	0	1	0	0	0	0	0	47	0	37
OD	3	6	3	6	3	7	3	5	3	2
YC	0	88	0	85	0	76	0	35	0	24
BS	3	12	3	9	3	5	0	3	0	6
RC	1	23	1	19	1	14	1	8	0	4
OH	0	0	0	0	0	0	0	2	1	0

bears no resemblance to field behavior. While sensitive to this argument, we nonetheless maintain that our data can be extended to evolutionary and ecological considerations. There were no gross differences between lab and field behavior; indeed a striking feature of these *Leptothorax* ants is how readily they adapt to laboratory conditions (e.g. Wilson 1975). Comparable studies of polydomy in these tiny ants cannot be conducted in the field. Given that this species adjusts well to captivity and no other avenue of investigation is possible currently, we proceed to interpret results of our laboratory studies.

When the ants were first introduced to the artificial forest floor, they not only encountered a new environment that required exploration, but also met members of other nests. Thus the effects of exploring new habitat and encountering new ants were initially confounded in this study. However, we argue that, within a week, the behavior of these ants came to reflect what might be observed in the field. *Leptothorax* workers seem to become familiar with their surroundings quickly; certainly when these ants are placed into a new nest box the initial intense exploration wanes within 2–3 days. Moreover, the ants would have encountered each other in nature under spring conditions, just as they did in the lab. Therefore, while the effects of exploring a new habitat cannot be separated out, we feel they are relatively inconsequential after the first week of our observations.

The most striking aspect of this study was how critical spring activity is in determining a population structure that remains relatively stable throughout the rest of the summer. The vast majority of aggressive encounters (which may result in intraspecific dulosis (Alloway 1980)), exploration of new nesting sites, apparent recruitment of nestmates (tandem running), and colony subdivision occurred within three weeks of the arrival of "spring". In fact, very little behavior of interest to this study was observed after June 15. Most ants emerging from the nest in summer were apparently searching for food or water; when two individuals met, they usually antennated briefly and then went their separate ways. This pattern is consistent with their natural history. The only field observations of queens walking alone and of workers carrying other workers or brood have been recorded in early May. Extra-nest worker activity from June–August appears restricted to individual foraging (Herbers, pers. obs.).

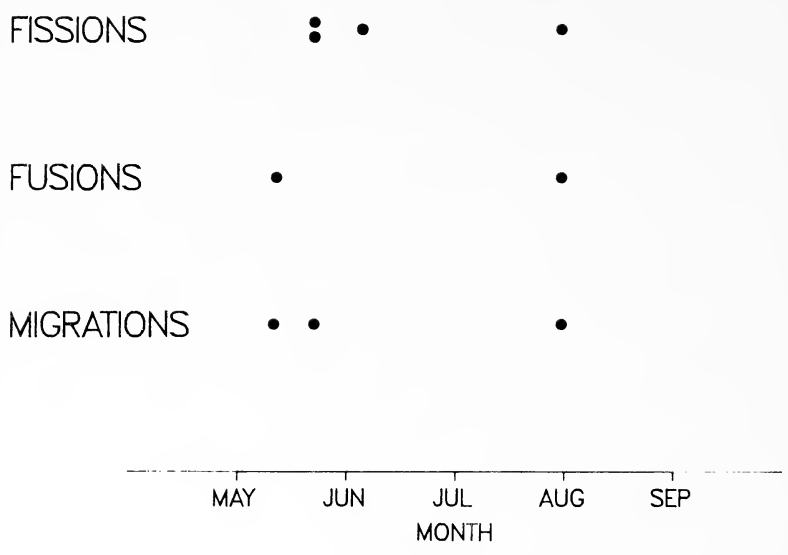


Figure 3. Large-scale events occurred infrequently over the season and were clustered in early spring.

These behavioral observations accord well with inferences made about population structure that are based on spatial distributions of nests and queen distribution among nests (Herbers 1986a). If the cyclic polydomy hypothesis is correct, then the nests used in this study, which had been collected in late fall, had already undergone colony coalition for overwintering. The units that were set out on the floors, then, were presumably functional, independent colonies. When ants from different colonies came back into contact after overwintering, they re-established dominance relations through aggressive encounters and perhaps staked out territories. Likewise, under spring conditions, colonies fractionated to occupy empty nesting sites. After a period of fusions, fissions, brood exchange, and the like, a spatial pattern was achieved that was largely maintained throughout the rest of the summer. We expect that, had we been able to expose the floors to more autumn-like conditions, we would have observed nest fusions and colony condensations to increase.

This seasonal cycle makes comparisons to other studies difficult. Alloway et al (1982) reported that fusion resulted in each of three

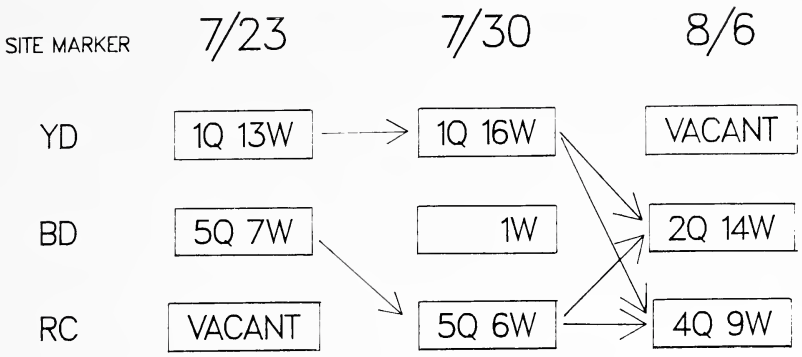


Figure 4. Schema of changes on floor 1A in late July.

separate experiments where 2 nests of *L. longispinosus* were positioned naturally on floors. They also examined the closely related *L. ambiguus,* for which fusions occurred in 16 of 21 replicates. Their experiments were apparently conducted on nests collected from spring through mid-summer, which probably included parts of polydomous colonies. That we observed only 2 fusions in a comparable study may reflect the fact that we placed functional colonies on our floors; a lower fusion rate would be expected for entire colonies than for subunits of polydomous colonies.

In contrast to fusion events, reports of spontaneous polydomy show rough similarity between species. Stuart (1985) found that 12 of 57 nests of *L. curvispinosus* underwent fission in the laboratory, events that were dispersed throughout the season. Our fission rate (4 events for 17 nests) is quite comparable, although we observed spontaneous polydomy primarily in spring. Thus fission events may not be as strongly seasonal as our results imply.

The above data are entirely consistent with the cyclic polydomy hypothesis, since activities associated with colony fractionation (brood transport, tandem running, fissions, worker exchange) occurred mainly in early spring. The fluid nature of this *L. longispinosus* population is quite evident, and can help to explain summer-winter differences in queen and worker distribution (Herbers 1986a). The causes of cyclic polydomy are obscure at present. Colony fission during spring and summer may serve to alleviate competition for food (Herbers 1985), but nest coalition in fall is more

difficult to explain. Condensation for overwintering might serve important social functions. Alternatively, a tantalizing suggestion based on laboratory data is that nest survivorship in winter is a function of resident queen number (Herbers 1986b). If the same relation holds in nature, then nests subunits may have higher survivorship in concert than they would alone. Whatever the proximate and ultimate causes, the seasonal cycle in polydomy deserves closer scrutiny.

Acknowledgments

This study was supported by grants from the National Academy of Sciences and the National Science Foundation (DEB 82-02361 and BSR-8516639).

References

Alloway, T. M. 1980. The origins of slavery in leptothoracine ants (Hymenoptera: Formicidae). Amer. Nat. **115**: 247–261.

Alloway, T. M., A. Buschinger, M. Talbot, R. Stuart, and C. Thomas. 1982. Polygyny and polydomy in three North American species of the ant genus *Leptothorax* Mayr (Hymenoptera: Formicidae). Psyche **89**: 249–274.

Bhatkar, A. & W. H. Whitcomb. 1970. Artificial diet for rearing various species of ants. Fla. Ent. **53**: 271–232.

Brian, M. V. 1965. Social insect populations. London: Academic Press.

Buschinger, A. 1968. Monogynie und Polygynie bei Arten der Gattung *Leptothorax* Mayr. Ins. Soc. **15**: 217–226.

Buschinger, A. 1974. Monogynie und Polygynie in Insektsozietäten. *In:* G. H. Schmidt, ed. Sozialpolymorphismus bei Insekten. Stuttgart: Wissenschaftliche Verlagsgesellschaft.

Chauvin, R. and J. LeComte. 1965. Evolution des Echanges entre differentes colonies-filies de *Formica polyctena.* Mesuree a l'aide des radio-isotopes. Ins. Soc. **12**: 197–200.

Cherix, D., P. Werner, and F. Catzeflis. 1980. Organisation spatial d'un systeme polycalique chez Formica (Coptoformica) exsecta Nyl. (Hymenoptera: Formicidae). Bull. Soc. Ent. Suisse **53**: 163–172.

Del Rio Pesado, M. G. and T. M. Alloway. 1983. Polydomy in the slave-making ant *Harpagoxenus americanus* (Emery) (Hymenoptera: Formicidae) Psyche **90**: 151–162.

Droual, R. 1984. Anti-predator behaviour in the ant *Pheidole desertorum:* the importance of multiple nests. Anim. Beh. **32**: 1054–1058.

Fletcher, D. J. C. and K. G. Ross. 1985. Regulation of reproduction in eusocial hymenoptera. Ann. Rev. Entomol. **30**: 319–343.

Headley, A. E. 1943. Population studies of two species of ants, *Leptothorax longispinosus* Roger and *Leptothorax curvispinosus* Mayr. Ann. Ent. Soc. Amer. **36**: 743–753.

HERBERS, J. M. 1984. Queen-worker conflict and eusocial evolution in a polygynous ant species. Evol. **38**: 631–643.

HERBERS, J. M. 1985. Seasonal structuring of a northeastern ant community. Ins. Soc. **32**: 224–240.

HERBERS, J. M. 1986a. Nest site competition and facultative polygyny in *Leptothorax longispinosus*. Beh. Ecol. Sociobiol. **19**: 115–122.

HERBERS, J. M. 1986b. Effects of ecological parameters on queen number in *Leptothorax longispinosus* (Hymenoptera: Formicidae). J. Kans. Ent. Soc. (in press)

KANNOWSKI, P. 1959. The use of radioactive phosphorus in the study of colony distribution of the ant *Lasius minitus*. Ecol. **40**: 162–165.

MACKAY, W. AND E. MACKAY. 1983. Analysis of internest movement in *Formica haemorrhoidalis* Emery. Southwest. Natur. **28**: 295.

MÖGLICH, M. 1978. Social organization of nest emigration in *Leptothorax* (Hym., Form.) Ins. Soc. **25**: 205–225.

PAMILO, P., R. H. CROZIER, AND J. FRASER. 1985. Inter-nest interactions, nest autonomy, and reproductive specialization in an Australian arid-zone ant, *Rhytidoponera* sp. 12. Psyche **92**: 217–236.

SCHERBA, G. 1958. Reproduction, nest orientation, and population structure of an aggregation of mound nests of *Formica ulkei* Emery (Formicidae) Ins. Soc. **2**: **201**–213.

SCHERBA, G. 1965. Analysis of inter-nest movement by workers of the ant *Formica opaciventris* Emery. Anim. Behav. **12**: 508.

SMALLWOOD, J. 1982. Nest relocations in ants. Ins. Soc. **29**: 138–147.

SMALLWOOD, J. AND D. C. CULVER. 1979. Colony movements of some North American ants. J. Anim. Ecol. **48**: 373–382.

STUART, R. J. 1985. Spontaneous polydomy in laboratory colonies of the ant *Leptothorax curvispinosus* Mayr (Hymenoptera: Formicidae). Psyche **92**: 71–81.

TALBOT, M. 1957. Population studies of the slave-making ant *Leptothorax duloticus* and its slave *Leptothorax curvispinosus*. Ecology **38**: 449–456.

TALBOT, M. 1961. Mounds of the ant *Formica ulkei* at the Edwin S. George Reserve, Livingston County, Michigan. Ecol. **42**: 202–205.

VAN PELT, A. 1976. Nest relocation in the ant *Pogonomyrmex barbatus*. Ann. Ent. Soc. Amer. **69**: 493.

WILSON, E. O. 1975. *Leptothorax duloticus* and the beginnings of slavery in ants. Evol. **29**: 108–119.

GEOGRAPHIC VARIATION IN THE CAVE BEETLE *NEAPHAENOPS TELLKAMPFI* (COLEOPTERA: CARABIDAE)

By Thomas C. Kane[1] and George D. Brunner

Department of Biological Sciences, University of Cincinnati
Cincinnati, OH 45221 USA

Introduction

More than 200 species of cave limited (i.e., troglobitic) trechine carabid beetles are known from caves of the eastern United States (Barr, 1979b, 1981). These species are generally considered to be derived from ancestral surface species which were widespread during the cold, moist climates associated with glacial maxima (Barr, 1968). Subsequent warming and drying of these regions, as glaciers retreated, led ultimately to the extirpation of surface populations, with only some of the cave limited stocks surviving. Available evidence suggests that for trechines cave isolation is irreversible (Barr, 1968, 1979a). Therefore, geographic spread of and gene flow in troglobitic trechines will be restricted to subterranean routes (Barr, 1968). The interconnectivity of caves and the presence of geological barriers (e.g., noncavernous strata and large rivers) become important factors in determining the geographic extent of and degrees of gene flow within these troglobitic taxa.

In extensive and highly continuous limestone cave systems, such as those of the Mississippian plateaus, interpretation of evolutionary relationships between closely similar taxa becomes especially complicated (Barr, 1979b). One question which arises is whether such taxa represent multiple isolations of a common surface dwelling ancestor or are the product of more recent divergence in a common troglobitic ancestor. Even when the latter scenario appears to be the case, divergence may only involve subtle, although generally consistent, differences in minor morphological characters. Thus, inferences about such factors as the amount of gene flow, if

[1]Author to whom all editorial correspondence and reprint requests should be addressed.

Manuscript received by the editor March 25, 1986.

any, still occurring among the taxa, the relative degree of differentiation between the various taxa, and the manner in which the present geographic pattern has been produced may be strengthened by the availability of genetic data such as those obtained through gel electrophoresis (Barr, 1979b; Turanchik and Kane, 1979).

As Barr (1979b) has indicated, the large geographic distribution and abundance of *Neaphaenops tellkampfi* populations present an excellent opportunity to assess the extent of gene flow between local populations of a troglobitic trechine using both morphological and electrophoretic data. Among the many species of troglobitic trechine carabid beetles in the United States, *Neaphaenops tellkampfi* is noteworthy for having the most extensive geographic range and being one of the most abundant species of the group (Barr, 1979b, 1981). The species is distributed (Fig. 1) from just south of the Ohio River in the north to its southern limit near the Tennessee border, in the highly cavernous Mississippian limestones of the Pennyroyal Plateau in west central Kentucky (Barr, 1979b). The western extent of its range is delimited by the noncavernous Big Clifty sandstone, and the eastern and southeastern limits of the range correspond roughly with the contact with the Salem and Warsaw limestones (Barr, 1979b).

Neaphaenops tellkampfi, like other cave trechines, is an important predator in terrestrial cave communities (Barr and Kuehne, 1971; Kane and Poulson, 1976). Unlike other troglobitic trechines in the Pennyroyal Plateau, however, *N. tellkampfi* has evolved specialized behaviors which allow it to prey on the eggs and early instar nymphs of the common cave "cricket" *Hadenoecus subterraneus* (Orthoptera: Rhaphidophoridae), resources which are energy rich and seasonally abundant (Kane and Poulson, 1976; Hubbell and Norton, 1978). This predator-prey interaction has evolved to the extent that no *N. tellkampfi* populations occur outside the range of *H. subterraneus* (Hubbell and Norton, 1978). In fact, Barr (1979b) has suggested that at least part of the eastern limits of the *N. tellkampfi* range may be determined by the absence of *H. subterraneus* further east, rather than to the presence of any extrinsic geological barrier.

Using morphological and geological criteria, Barr (1979b) has recognized four subspecies of *N. tellkampfi.* The nominate subspecies, *N. t. tellkampfi,* on which most of the ecological studies dis-

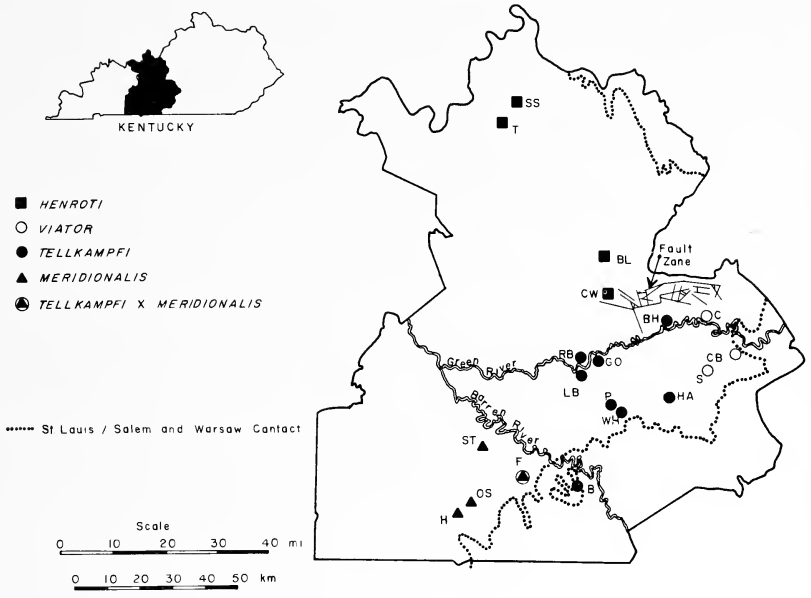


Figure 1. Map of west central Kentucky showing locations sampled for *Neaphaenops tellkampfi* in this study. Taxonomic designations of populations at these sites (after Barr, 1979b) are as follows: *N. t. henroti:* BL; CW; SS; T; *N. t. meridionalis:* H; OS; ST; *N. t. tellkampfi:* B; BH; GO; HA; LB; P; RB; WH; *N. t. viator:* C; CB; S; *N. t. meridionalis* × *N. t. tellkampfi* hybrid: F.

cussed previously have been done, is distributed in the central portion of the range to include the caves of Mammoth Cave National Park. *Neaphaenops t. meridionalis,* the southern subspecies, is limited to the north by the noncavernous sandstones near the Barren River. However, two populations are known in the southeastern part of the range which are morphologically intermediate between nominate *tellkampfi* and *meridionalis* for six of nine diagnostic characters, suggesting a narrow zone of hybridization between the two subspecies. Barr (1979b) points out, however, that despite the limited gene flow, *meridionalis* is morphologically the most distinct of the four subspecies. Morphological evidence (Barr, 1979b) suggests a broad zone of hybridization between nominate *tellkampfi* and the eastern subspecies *N. t. viator,* with gradual intergradation between the two subspecies over approximately an

eight km. distance. The eastern extent of the *viator* range is delimited by the contact of the St. Louis/Salem and Warsaw limestones and, perhaps more directly, by the absence of *H. subterraneus* further east (Barr, 1979b). As is the case with nominate *tellkampfi,* populations of *viator* are known from caves on both the north and south sides of the Green River. The northern limits of the *viator* range are set in large part by a sandstone ridge and extensive fault zone across Hart County. This geological feature also appears to be a complete barrier to gene flow between the northern subspecies *N. t. henroti* and either nominate *tellkampfi* or *viator* to the south (Fig. 1) (Barr, 1979b). Despite the absence of any known hybrid populations, *tellkampfi* and *henroti* are the most similar subspecies morphologically, and *henroti* also shows a large degree of morphological affinity with *viator* as well (Barr, 1979b).

Previous studies using gel electrophoresis (Giuseffi et al., 1978; Turanchik and Kane, 1979) have shown that genetic variability in local populations of *N. t. tellkampfi* approach those observed in similar surface dwelling invertebrates. These results, coupled with similar subsequent findings in other species (e.g., Dickson et al., 1979), suggest that cave adaptation does not necessarily result in a reduction in genetic variation. Further, genetic similarity values (I) (Nei, 1972) among eight local populations of nominate *tellkampfi* fall in the range (i.e., 0.90–1.00 (Turanchik and Kane, 1979)) commonly reported for populations of continuously distributed surface dwelling species. These results substantiate the contention that continuous limestone expanses can act as underground dispersal highways for cave limited species (Barr, 1968).

The purpose of the present study was to examine electrophoretically several local populations of each of the other three subspecies of *N. tellkampfi.* We were interested in determining how infrasubspecific variation in these subspecies compared with that of nominate *tellkampfi.* Further, we wished to use these electrophoretic data to quantitatively assess relationships among subspecies and also to gain some insight to how the present distributional pattern of the species has been produced. In these regards, Barr's (1979b) morphological and biogeographic work provides a model against which the electrophoretic data can be examined.

Methods

Electrophoretic data gathered from a total of 18 populations (Fig. 1) of *Neaphaenops tellkampfi* were analyzed in this study. All of the electrophoretic data for ten of these populations were gathered during the course of the present study, between 1980 and 1983. These ten populations include three each of *N. t. henroti* (BL, CW and T/SS; Fig. 1), *N. t. meridionalis* (H, OS and ST; Fig. 1) and *N. t. viator* (C, CB and S; Fig. 1) as recognized by Barr (1979b). The tenth population (F; Fig. 1) is a purported *meridionalis* × *tellkampfi* hybrid on morphological grounds (Barr, 1979b). Most, but not all, of the electrophoretic data on the eight populations of *N. t. tellkampfi* (B, BH, GO, HA, LB, P, RB and WH; Fig. 1) were collected in 1977–78 and reported by Turanchik and Kane (1979). Modifications of and additions to the nominate *tellkampfi* data set will be discussed in appropriate sections below. All 18 of the populations sampled, with the exception of the SS and T sites of *henroti,* represent a single cave location. During the course of the study permission to sample the SS site was rescinded before a sample adequate for complete electrophoretic survey could be obtained. Subsequently the nearby T site was located but it harbored a much smaller *henroti* population and failed to yield a large enough sample to obtain data on all electrophoretic loci. Pooling of the data from the two sites, which appears to be justified by their geographic proximity, did produce a complete set of electrophoretic data.

Beetles were maintained alive at 5° C or frozen at -80° C prior to electrophoresis. All electrophoresis was conducted on vertical polyacrylamide slab gels using an Ortec Model 4200 Electrophoresis System or a Hoefer Scientific SE600 System. Sample preparation and run procedures used in this study were similar to those discussed by Giuseffi et al. (1978) and Turanchik and Kane (1979). Each animal provided enough homogenate for two assays.

Six enzyme systems provided a total of seven consistently scorable loci. These included: alkaline phosphatase (ALP) (1); esterase (EST) (1); malate dehydrogenase (MDH) (2); phosphoglucomutase (PGM) (1); phosphoglucose isomerase (PGI) (1); and, xanthine dehydrogenase (XDH) (1). In addition a general protein (GP) stain revealed two sets of consistently scorable bands which are also

included in the data. The more complete data of this study suggested interpretational changes at two loci from those reported by Turanchik and Kane (1979). The present data show that the ALP bands are properly interpreted as a single variable locus rather than as two separate loci. Also, we have chosen a more conservative interpretation of the XDH data. Electrophoretic analysis of XDH in *N. tellkampfi* populations produces a single band per beetle with slight differences in mobility between some individuals. Initially these data appeared to be consistent with data reported by Singh et al. (1976) for a variable XDH locus in *Drosophila pseudoobscura.* However, application of additional techniques which Singh et al. (1976) used to reveal multiple bands in *D. pseudoobscura* heterozygotes, failed to reveal any multiple banded *N. tellkampfi* individuals at the XDH locus. More recently, Finnerty and Johnson (1979) have shown that data such as these may be the result of post-translational modification of an enzyme encoded by a monomorphic locus. We have chosen this interpretation of the XDH locus in the present study. PGM was not assayed in previous studies of *N. tellkampfi* (Giuseffi et al., 1978; Turanchik and Kane, 1979) and therefore populations of *N. t. tellkampfi* were re-collected and surveyed for this enzyme. The majority of the data analysis was accomplished using a Fortran 77 version of the BIOSYS-1 program developed by Swofford and Selander (1981).

Results

Of the nine putative genetic loci examined in this study, five were polymorphic and the remaining four were monomorphic with the same variant fixed in all populations of the four taxa (Table 1). Genetic variability in *N. tellkampfi* populations has been estimated as the proportion of polymorphic loci per population (P) and the average frequency of heterozygous loci per individual (H) (Table 2). The average *N. tellkampfi* population is polymorphic at approximately 30% of its loci and the average individual in such a population is heterozygous at 9.4% of its loci (Table 2). These values are somewhat lower than those reported previously by Turanchik and Kane (1979) as a result of the addition of another invariant locus (PGM) and the more conservative interpretation of the XDH locus. However, these values of P and H still approach values typically reported for many surface invertebrates (Selander, 1976). Therefore,

Table 1. Gene frequencies for 18 populations of *Neaphaenops tellkampfi*. N = Sample size.

		Cave																	
Locus		CW	BL	T/SS	H	OS	ST	F	B	BH	GO	HA	LB	P	RB	WH	C	CB	S
1. Monomorphic loci with the same variant fixed in all populations—4 loci (GP-2; MDH-1; PGM; XDH)																			
2. Loci coding for monomorphic and/or polymorphic proteins.																			
ALP	N	27	29	10	25	42	11	7	15	20	14	10	11	13	16	10	21	9	22
	a	0.41	0.43	0.45	0.48	0.39	0.55	0.57	0.67	0.78	0.54	0.30	0.46	0.58	0.59	0.70	0.52	0.33	0.61
	b	0.59	0.57	0.55	0.52	0.61	0.45	0.43	0.33	0.22	0.46	0.70	0.54	0.42	0.41	0.30	0.48	0.67	0.39
EST	N	20	27	11	30	25	12	8	21	22	40	31	29	33	21	15	21	9	22
	a	0.00	0.00	0.00	1.00	1.00	1.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00
	c	1.00	1.00	1.00	0.00	0.00	0.00	0.25	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00
GP-1	N	30	29	18	28	23	15	17	8	13	6	13	22	10	19	15	23	13	17
	a	0.08	0.22	0.11	0.29	0.33	0.00	0.29	0.06	0.08	0.00	0.23	0.00	0.10	0.08	0.07	0.02	0.31	0.26
	b	0.92	0.78	0.89	0.71	0.67	1.00	0.71	0.94	0.92	1.00	0.77	1.00	0.90	0.92	0.93	0.98	0.69	0.74
MDH-2	N	33	36	10	59	33	11	18	23	28	26	20	24	29	37	20	22	18	30
	a	0.91	0.93	1.00	0.89	0.95	1.00	1.00	0.94	0.79	0.83	0.90	0.96	0.91	0.77	0.93	0.93	1.00	0.97
	b	0.09	0.07	0.00	0.11	0.05	0.00	0.00	0.06	0.21	0.17	0.10	0.04	0.09	0.23	0.07	0.07	0.00	0.03
PGI	N	38	43	9	29	30	13	18	20	22	42	30	24	20	24	22	30	23	27
	a	0.00	0.00	0.00	1.00	1.00	1.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00
	c	1.00	1.00	1.00	0.00	0.00	0.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00

these data continue to support the contention that cave isolation does not necessarily result in a permanent reduction in genetic variability for a species (Barr, 1968; Giuseffi et al., 1978; Dickson et al., 1979; Turanchik and Kane, 1979).

Estimates of P and H by subspecies (Table 2) indicate no differences in genetic variability between the four taxa. Of the five polymorphic loci examined, two, EST and PGI, are diagnostic of subspecific differentiation (Table 1). Three variants have been detected at each of these loci, with all *meridionalis* populations fixed for a slow migrating electromorph at both loci, all *viator* populations fixed for electromorphs of intermediate mobility at each locus, and all *henroti* and nominate *tellkampfi* populations being fixed for the fast migrating electromorphs at both loci. The only local population that is polymorphic at these two loci is population F (Fig. 1 and Table 1). This population, which is morphologically intermediate between *meridionalis* and *tellkampfi* and a purported hybrid of the two subspecies (Barr, 1979b), contains both the slow and fast electromorphs at both the EST and PGI loci. The fact that these electromorphs are alternatively fixed in *meridionalis* and *tellkampfi* populations respectively provides biochemical evidence of the hybrid nature of this population. By contrast, all three of the *viator* populations are fixed for the intermediate mobility electromorphs at both the EST and PGI loci even though two of these populations, C and S, lie in the zone of morphological intergradation between *tellkampfi* and *viator* (Barr, 1979).

Rogers' (1972) estimate of genetic similarity (S) was used for pairwise comparisons of the 18 populations (Table 3). Rogers' distance values were used in a UPGMA clustering procedure to produce a biochemical dendrogram (Fig. 2). Infrasubspecific genetic identities are all greater than 0.90. This includes some populations, such as the C population of *viator,* separated from other populations of the same subspecies by shallow rivers such as the Green River. This finding is consistent with earlier work (Turanchik and Kane, 1979) on populations BH, RB and B of nominate *tellkampfi* and with findings on at least one other cave limited species in the same area (Laing et al., 1976), and serves to reconfirm the fact that rivers per se are not necessarily dispersal barriers for cave limited forms. Genetic differentiation between subspecies is substantial in some cases (Fig. 2). *Neaphaenops t. meridionalis* and *N. t. viator*

Table 2. Genetic variability in four subspecies of *Neaphaenops tellkampfi*. P = average proportion of polymorphic loci per population; H = average proportion of heterozygous loci per individual.

Subspecies	Site	P	H OBS.	H EXP	Avg. Alleles/ Locus
henroti	CW	0.333	0.088	0.091	1.145
	BL	0.333	0.117	0.110	1.182
	T/SS	0.222	0.091	0.081	1.187
	AVG	0.296	0.099	0.094	1.171
meridionalis	H	0.333	0.133	0.124	1.216
	OS	0.333	0.119	0.113	1.201
	ST	0.111	0.040	0.058	1.109
	AVG	0.259	0.097	0.098	1.175
tellkampfi	B	0.333	0.058	0.079	1.116
	BH	0.333	0.077	0.094	1.132
	GO	0.222	0.088	0.086	1.153
	HA	0.333	0.107	0.111	1.166
	LB	0.222	0.070	0.067	1.119
	P	0.333	0.076	0.092	1.152
	RB	0.333	0.073	0.112	1.184
	WH	0.333	0.076	0.079	1.114
	AVG	0.305	0.078	0.090	1.142
viator	C	0.333	0.093	0.075	1.132
	CB	0.222	0.101	0.102	1.171
	S	0.333	0.101	0.104	1.177
	AVG	0.296	0.098	0.094	1.160
mer. × *tell.* hybrid	F	0.444	0.192	0.167	1.265
		Neaphaenops tellkampfi			
	AVG	0.302	0.094	0.097	1.162
	OVERALL	0.556			

show levels of similarity to each other and to the other two subspecies in the range of 0.69–0.78 (Fig. 2). Genetic similarity between *henroti* and nominate *tellkampfi* ($S > 0.96$; Table 3) is as great as similarity values among local populations within a subspecies. Although these two subspecies are the most similar of the four

Table 3. Rogers' (1972) coefficients of genetic similarity (S) for comparisons of four subspecies of *Neaphaenops tellkampfi.* Values shown are averages of pairwise comparisons of appropriate populations. Values in parentheses are the ranges of similarity values appropriate to each comparison.

		Subspecies			
Subspecies	No. of Pops.	*N. t. h.*	*N. t. m.*	*N. t. t.*	*N. t. v.*
henroti	3	0.975 (0.971–0.978)			
meridionalis	3	0.748 (0.732–0.766)	0.956 (0.942–0.983)		
tellkampfi	8	0.963 (0.928–0.982)	0.730 (0.689–0.763)	0.963 (0.917–0.995)	
viator	3	0.741 (0.714–0.758)	0.740 (0.727–0.766)	0.737 (0.713–0.765)	0.963 (0.945–0.984)
mer. × *tell.* hybrid	1	0.878 (0.863–0.886)	0.833 (0.828–0.836)	0.865 (0.844–0.883)	0.770 (0.750–0.781)

morphologically, this large a genetic similarity is somewhat unexpected given the presence of the Hart Co. Ridge, an apparent geological barrier between these two subspecies.

Genetic differentiation within and between subspecies was examined using F-statistics (Wright, 1978) and a Chi-square contingency analysis of heterogeneity (Workman and Niswander, 1970). Allozyme phenotype frequencies for the 18 populations were used to calculate genetic differentiation (i.e., F-statistics) in a hierarchichal manner (Wright, 1978). The two hierarchical levels are subspecies within species and local populations within subspecies. Since the hybrid F population could not be unequivocally assigned to either *tellkampfi* or *meridionalis,* it was considered as a fifth "subspecies" at that level of the hierarchy. Three loci (ALP; GPT-1; MDH-2) are variable in some or all local populations of each subspecies. Significant heterogeneity in gene frequencies (Chi-square) was observed among *N. t. tellkampfi* populations at the ALP and MDH-2 loci but not at the GPT-1 locus (Table 4). Significant heterogeneity in gene frequencies at the GPT-1 locus was observed among local populations of *viator* and among local populations of *meridionalis,* but no differentiation was observed among local populations of either subspecies at the ALP or MDH-2 loci (Table 4). No heterogeneity in gene frequency was observed among *henroti* populations at any of

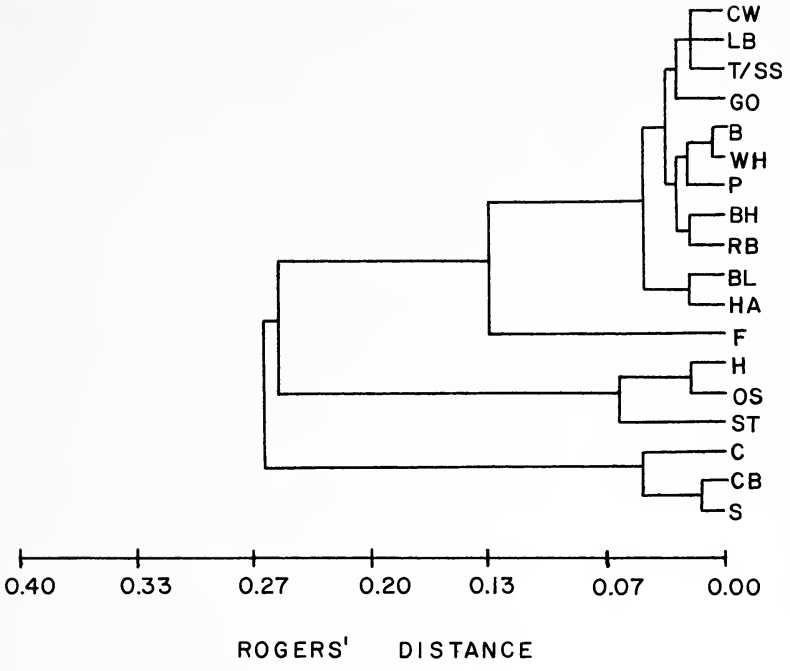


Figure 2. UPGMA dendrogram of 18 populations of *Neaphaenops tellkampfi*, generated from Rogers' genetic distance values for nine biochemical loci.

the three variable loci. The slightly greater differentiation observed among *tellkampfi* populations may be due to the fact that this subspecies has a somewhat larger geographic range than any of the other three subspecies, or simply to the fact that more populations (8) were examined for nominate *tellkampfi* than for any of the other three subspecies.

Whereas genetic differentiation between infrasubspecific populations is slight to moderate, differentiation between subspecies is very great (Table 5). At the level of subspecies, variation is observed at the EST and PGI loci in addition to the three loci discussed above. Significant heterogeneity in allele frequency between subspecies was observed at all five loci (Table 5) and overall genetic differentiation is very great (Fst = 0.528), with the EST and PGI loci essentially fixed for alternative alleles in three of the four subspecies.

Table 4. F-statistics and heterogeneity chi-square values for four subspecies of *N. tellkampfi.*

	F_{IT}	F_{IS}	F_{ST}	X^2
SUBSPECIES		ALP LOCUS		
henroti	-0.007	-0.013	0.006	0.510ns
meridionalis	0.098	0.083	0.016	1.690ns
tellkampfi	0.217	0.150	0.080	16.416*
viator	-0.183	-0.201	0.015	1.291ns
		GPT-1 LOCUS		
henroti	-0.166	-0.207	0.034	5.613ns
meridonalis	-0.004	-0.154	0.130	12.145***
tellkampfi	-0.083	-0.157	0.064	13.810ns
viator	0.193	0.105	0.098	12.465***
		MDH-2 LOCUS		
henroti	-0.007	-0.089	0.006	1.958ns
meridionalis	-0.055	-0.100	0.042	4.549ns
tellkampfi	0.209	0.176	0.041	17.605*
viator	-0.034	-0.058	0.022	2.539ns

ns = $P > 0.05$; * = $P < 0.05$; *** = $P > 0.005$

F_{IT} = correlation between uniting gametes relative to the gametes of the total population

F_{IS} = average correlation over subdivisions of uniting gametes relative to those of their own subdivision

F_{ST} = correlation of random gametes within subdivisions relative to gametes of the total population

Slatkin (1981) has proposed a method to estimate overall gene flow in natural populations in a qualitative manner from gene frequency data. Using computer simulation, Slatkin (1981) has demonstrated a dependence between gene flow and the conditional average frequency of an allele, $\bar{p}(i)$ where:

d = number of demes sampled

i = number of demes in which the allele occurs

$\bar{p}$ = average frequency of the alleles in those demes

Caccone (1985) used Slatkin's technique to assess gene flow in several species of cave animals, based on her own data for *H. subterraneus,* the data of Laing et al. (1976) for the scavenger beetle *Ptomaphagus hirtus* and Turanchik and Kane's (1979) data for the

Table 5. Hierarchichal F-statistics and heterogeneity chi-square analyis of allelic frequencies between subspecies of *Neaphaenops tellkampfi*

Locus	F_{CT}	F_{CS}	F_{ST}	X^2
ALP	0.022	0.023	-0.001	16.224**
EST	0.958	0.000	0.958	1564.120***
GPT-1	0.081	0.074	0.007	22.227**
MDH-2	0.044	0.035	0.009	17.900**
PGI	0.988	0.000	0.988	1841.171***
TOTAL	0.546	0.038	0.528	

** = $P < 0.01$; *** = $P < 0.005$

F_{CT} = correlation of random gametes in local populations relative to the gametes of the total population

F_{CS} = average correlation over subspecies of uniting gametes relative to those of their own subspecies

F_{ST} = correlation of random gametes within subspecies relative to gametes of the total population

subspecies *N. t. tellkampfi.* Thus, an analysis of gene flow in all four *N. tellkampfi* subspecies is appropriate since both *H. subterraneus* and *P. hirtus* are sympatric with *N. tellkampfi.* Further, the range of *H. subterraneus* examined by Caccone (1985) is more comparable to that of *N. tellkampfi* (s.l.) than simply to that of nominate *tellkampfi.*

The Slatkin analysis suggests that *N. tellkampfi* may be qualitatively described as a species in which gene flow level is low. Alleles with low incidence values (i/d) have high conditional frequencies ($\bar{p}$) (Fig. 3). Caccone (1985) showed that *P. hirtus* is also a species with low gene flow levels. By contrast, *H. subterraneus* is seen to be a species with intermediate gene flow levels (Caccone, 1985). As indicated earlier, the range of *H. subterraneus* is larger than and includes the entire range of *N. tellkampfi.* Unlike *N. tellkampfi* and *P. hirtus,* however, *H. subterraneus* is troglophilic (facultative cave dweller) and thus is capable of some dispersal on the surface in addition to the subterranean routes available to troglobites. Analysis of the eight nominate *tellkampfi* populations indicates a high level of gene flow within this subspecies (Fig. 3) despite some heterogeneity in gene frequencies among these populations (Table 4). The overall pattern of gene flow is generally consistent with the pattern of genetic differentiation obtained from the F-statistics.

Discussion

The patterns of variation described here for *N. tellkampfi* provide a basis for understanding some of the factors which cause genetic differentiation in cave limited species. Barr (1979b) suggested that three different patterns of gene flow were indicated by the morphological and geological data on the four subspecies. These include: (1) no gene flow (*henroti* with either *tellkampfi* or *viator*); (2) very limited gene flow (*meridionalis* with *tellkampfi*); and, (3) moderate gene flow (*tellkampfi* with *viator*). Initially the biochemical data seem to support only pattern (2) with population F clearly containing *meridionalis* × *tellkampfi* hybrids and with other *meridionalis* and *tellkampfi* populations examined in this study showing no biochemical evidence of hybridization. Thus, the morphological data (Barr, 1979b) and now the biochemical data suggest that hybridization is restricted to a very narrow geographic area.

The allozyme data directly support only part of pattern (1). The relatively large genetic distance between *henroti* and *viator* ($D = 0.289$) and the lack of any biochemical, as well as morphological (Barr, 1979b), evidence of hybridization support the assertion that the Hart Co. Ridge is acting as a complete barrier to gene flow between these two subspecies. The large genetic similarity between *henroti* and *tellkampfi* ($S > 0.96$) does not lend support to the conclusion that these two subspecies are also extrinsically isolated from each other. However, allozyme studies on the scavenger beetle *P. hirtus* (Laing et al., 1976) show that a population north of the Hart Co. Ridge has a genetic similarity (I) of approximately 0.75 with two populations south of the Ridge in caves GO and RB, which are also occupied by nominate *tellkampfi*. Further, the Hart Co. Ridge coincides with the southern range limit of *Orconectes inermis* (Decapoda: Astacidae) and the northern range limit of *O. pellucidus,* two species of troglobitic crayfish whose ranges are almost completely separate (Hobbs and Barr, 1972). Thus the evidence for the Hart Co. Ridge as a dispersal barrier is overwhelming.

The close genetic similarity between *henroti* and *tellkampfi* is consistent with Barr's (1979b) supposition that all four subspecies of *N. tellkampfi* are descended from a common ancestral stock that became isolated in caves in the southern portion of the present range. Barr argues that *henroti* was derived from a peripheral population of nominate *tellkampfi* which penetrated north of the Hart

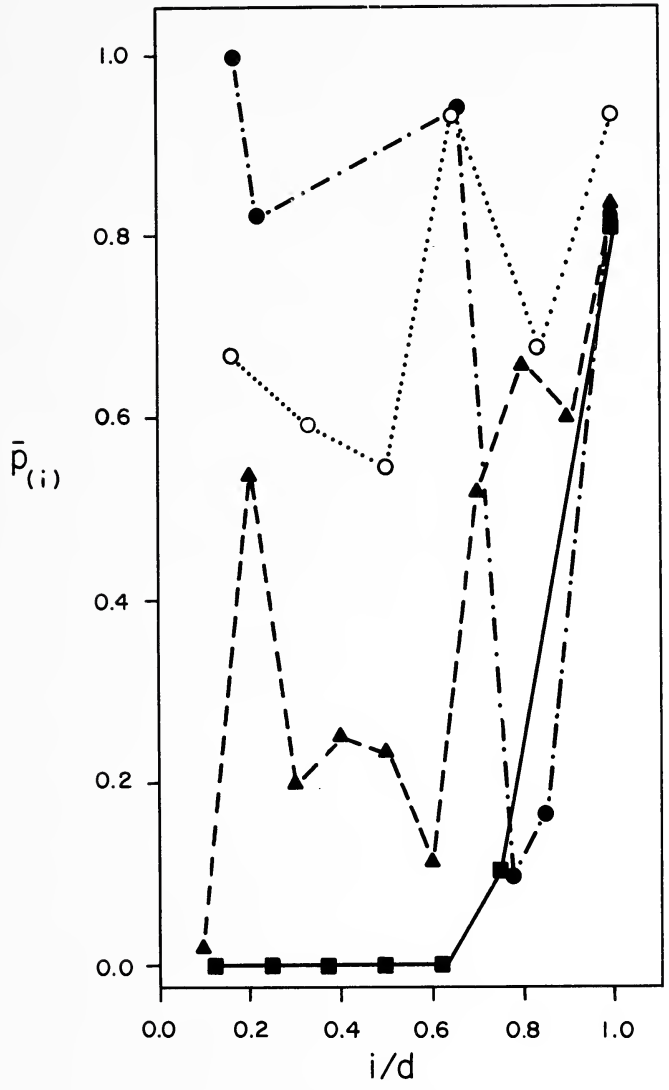


Figure 3. Conditional allele frequencies (p(i)) as a function of their incidence (i/d) in four taxa of cave-dwelling organisms. Three qualitative patterns of gene flow are inferred: low gene flow: *Neaphaenops tellkampfi* (filled circles) and *Ptomaphagus hirtus* [open circles (data from Laing et al., 1976)]; intermediate gene flow: *Hadenoecus subterraneus* [triangles (data from Caccone, 1985)]; and, high gene flow: *Neaphaenops tellkampfi tellkampfi* (squares).

Co. Ridge through some of the scattered cave systems known in the area. The close biochemical similarity of *henroti* and *tellkampfi* support this view over the alternative hypothesis that *henroti* represents a separate isolation of the surface dwelling ancestral species. Furthermore, Barr (1979b) notes that *henroti* has apparently not extended its range as far northward and westward as the geological evidence and the distribution of *Hadenoecus subterraneus* would suggest is possible. This observation, coupled with the evidence of high genetic similarity between *henroti* and *tellkampfi,* is supportive of a southern origin for *N. tellkampfi* with the range of *henroti* representing the most recent northward dispersal.

The allozyme data fail to demonstrate a broad zone of hybridization between *tellkampfi* and *viator* (pattern (3) above). Moreover, inclusion of additional information fails to explain the discrepancy between the biochemical distinctness of the two taxa, on the one hand, and the independent evidence for a broad zone of hybridization on the other. The lack of any geological barrier between *tellkampfi* and *viator* and the large degree of morphological intergradation between the two taxa (Barr, 1979b) give great support to the hypothesis of hybridization. Two of the *viator* populations examined in this study (i.e., C and S) lie within the zone of morphological intergradation, making the lack of biochemical hybridization even more puzzling.

Genetic differentiation in *N. tellkampfi* occurs primarily between subspecies, with high genetic similarity ($S > 0.90$) and only slight ($Fst < 0.05$) to moderate ($0.05 < Fst < 0.15$) genetic differentiation among infrasubspecific populations. Culver (1982) reanalyzed Laing et al.'s (1976) data on *P. hirtus* and found that the average between area Nei index for *P. hirtus* populations in the ranges of different *N. tellkampfi* subspecies was $I = 0.794$. The average I between *N. tellkampfi* subspecies from the present study is 0.791. Further, analysis based on conditional allele frequencies indicates that gene flow level in both species can be qualitatively described as low. Interestingly the two species differ greatly in their ecological and demographic characteristics (Kane, 1982) and a substantial amount of evidence suggests that *N. tellkampfi* has a longer evolutionary history of cave isolation than does *P. hirtus* (Laing et al., 1976; Barr, 1979b).

Caccone (1985) suggests that gene flow levels and degree of genetic differentiation in cave species may be influenced by their

degree of dependence on the cave environment. Troglobitic species such as *N. tellkampfi* and *P. hirtus,* which are restricted to subterranean routes of dispersal, might be expected to show lower gene flow levels and greater genetic differentiation than cave dwelling species which are still capable of some dispersal on the surface. Although its distribution is restricted to cave regions, *H. subterraneus* emerges from caves on warm humid evenings to feed. Thus, the intermediate levels of gene flow inferred for *H. subterraneus,* as opposed to low levels for the two troglobites, may result from limited surface dispersal. Morphological evidence (Hubbell and Norton, 1978) also suggests a lesser degree of geographic differentiation in *H. suberraneus* than in *N. tellkampfi* over approximately the same area. Morphological differences occur between southwestern populations of *H. subterraneus* (i.e., in the range of *N. t. meridionalis*) and those to the north. However, there is no significant morphological differentiation among the northern populations of *H. subterraneus* (Hubbell and Norton, 1978), whereas in the same region *N. tellkampfi* is morphologically differentiated into three distinct subspecies (i.e., *henroti, tellkampfi* and *viator*). Trogloxenes show less cave dependence than troglophiles. Such species often use caves only sporadically and only for shelter. Unfortunately no genetic data are available for trogloxenes which are partially or wholly sympatric with the species described above. Caccone (1985) does report genetic data for *Euhadenoecus puteanus,* a relative of *H. subterraneus,* which is a forest dweller and a sporadic trogloxene over a range from southern New York to Georgia. She finds relatively high levels of gene flow between five cave populations of *E. puteanus* which is at least consistent with the expectations for a trogloxene.

Although degree of cave dependence appears to play a major role in determining the degree of gene flow and genetic differentiation over the geographic range of cave dwelling species, ecological differences between species may also influence their genetic characteristics. *Neaphaenops tellkampfi* and *P. hirtus* are both troglobites and show similar biogeographic patterns of genetic differentiation. However, ecologically the two species are dissimilar. Whereas *N. tellkampfi* is a specialized predator which tends to establish large permanent populations (Kane and Ryan, 1983), *P. hirtus* is more opportunistic. Local populations may develop on small isolated patches of organic matter such as carrion or feces from reproduction by a few founders (Peck, 1973) and such populations are often

ephemeral. Thus, stochastic events may have a greater influence on the genetic characteristics of local *P. hirtus* populations than on those of *N. tellkampfi.* In fact, genetic variability in local *P. hirtus* populations (P = 0.154; H = 0.048 (Laing et al., 1976)) appears to be about half that of local *N. tellkampfi* populations (P = 0.302; H = 0.094). Further, the average Nei index between local *P. hirtus* populations in the range of *N. t. tellkampfi* is I = 0.874 (Culver, 1982), whereas the average I between local nominate *tellkampfi* populations is 0.981. Thus, if ecological differences influence genetic patterns of similarly cave dependent species, the effects appear to be manifested at the level of local populations.

Acknowledgments

We would particularly like to thank Dr. Thomas C. Barr, Jr. for valuable discussions throughout the study, including a critical review of the manuscript. In addition, Dr. Barr kindly provided us with locations for several of the cave sites and in one case (ST site) provided us with material for electrophoresis. We would also like to acknowledge and thank Curtis Meininger for field assistance and useful discussions and Kevie Vulinec for drafting the figures. The National Part Service, Mammoth Cave National Park, KY, kindly provided access to several of the sites used in this study. This research was partially supported by a National Speleological Society Research Grant to GDB and by grants from the American Philosophical Society (Penrose Fund No. 8718) and the National Science Foundation (DEB-8202273) to TCK.

Summary

An understanding of patterns of geographic variation is important in interpreting evolutionary relationships between closely similar taxa and in inferring levels of gene flow between geographic populations. For obligate cave dwelling (i.e., troglobitic) species, dispersal and gene flow are restricted to subterranean routes. Thus, the interconnectivity of caves and the presence of geological barriers become important factors in determining the geographical distribution and the degree of gene flow among populations of troglobitic species.

Neaphaenops tellkampfi, a troglobitic trechine beetle, has the most extensive geographic range and is one of the most abundant of

the approximately 200 species of cave trechines in the eastern United States. Four morphological subspecies of *N. tellkampfi* have been described over its range in west central Kentucky. In the present study, electrophoretic data were collected on a total of 18 populations to include all four subspecies. These data support the hypothesis that *N. tellkampfi* has been derived from a single isolation of a surface dwelling ancestor. The present distribution has apparently resulted from a northward movement of the troglobitic stock through subterranean routes. Morphological (i.e., subspecific) differentiation appears to be directly related to the presence of partial and/or complete geological barriers to dispersal in certain portions of the range.

Comparison of genetic data on *N. tellkampfi* with those on other sympatric cave dwelling species suggests that level of gene flow and degree of genetic differentiation may be related to the degree of cave dependence of such species. Troglobites show lower levels of gene flow and greater genetic differentiation over their geographic ranges than do more facultative cave dwellers (e.g., troglophiles and trogloxenes) in which intermediate to high levels of gene flow have been reported. Ecological differences between species with similar degrees of cave dependence do not appear to produce differences in genetic patterns on a biogeographic scale. There is some evidence to suggest, however, that ecological differences between such species may affect genetic variability and genetic distance at the level of local populations.

References

Barr, T. C. 1968. Cave ecology and the evolution of troglobites. In: T. Dobzhansky, M. K. Hecht and W. C. Steere (eds.) Evolutionary Biology, Plenum Press, New York pp. 35–102.

Barr, T. C. 1979a. Revision of Appalachian *Trechus* (Coleoptera: Carabidae). Brimleyana **2**: 29–75.

Barr, T. C. 1979b. The taxonomy, distribution, and affinities of *Neaphaenops* with notes on associated species of *Pseudanophthalmus* (Coleoptera: Carabidae). American Museum Novitates: No. 2682 pp. 20.

Barr, T. C. 1981. The cavernicolous carabid beetles of North America. Proceedings of the Eighth International Congress of Speleology **1**: 343–344.

Barr, T. C. and R. A. Kuehne. 1971. Ecological studies in the Mammoth Cave ecosystem of Kentucky. II. The ecosystem. Annales de Speleologie **26**: 47–96.

Caccone, A. 1985. Gene flow in cave arthropods: a qualitative and quantitative approach. Evolution **39**: 1223–1235.

Culver, D. C. 1982. Cave life: evolution and ecology. Harvard University Press, Cambridge, Mass.

Dickson, G. W., J. C. Patton, J. L. Holsinger and J. C. Avise. 1979. Genetic variability in cave-dwelling and deep-sea organisms with emphasis on *Crangonyx antennatus* (Crustacea: Amphipoda) in Virginia. Brimleyana **2**: 119–130.

Finnerty, V. and G. Johnson. 1979. Post-translational modification as a potential explanation of high levels of enzyme polymorphism: xanthine dehydrogenase and aldehyde oxidase in *Drosophila melanogaster*. Genetics **91**: 695–722.

Giuseffi, S., T. C. Kane and W. F. Duggleby. 1978. Genetic variability in the Kentucky cave beetle *Neaphaenops tellkampfi* (Coleoptera: Carabidae). Evolution **32**: 679–681.

Hobbs, H. H., Jr. and T. C. Barr. 1972. Origins and affinities of the troglobitic crayfishes of North America (Decapoda: Astacidae). II. Genus *Orconectes*. Smithsonian Contributions to Zoology: No. 105 pp. 84.

Hubbell, T. H. and R. M. Norton. 1978. The systematics and biology of the cave crickets of the North American Tribe Hadenoecini (Orthoptera Saltatoria: Ensifera: Rhaphidophoridae: Dolichopodinae). Miscellaneous Publications Museum of Zoology, University of Michigan, Ann Arbor: No. 156 pp. 124.

Kane, T. C. 1982. Genetic patterns and population structure in cave animals. In: D. Mossakowski and G. Roth, eds. Environmental adaptation and evolution. Gustav Fischer, Stuttgart, West Germany, pp. 131–149.

Kane, T. C. and T. L. Poulson. 1976. Foraging by cave beetles: spatial and temporal heterogeneity of prey. Ecology **57**: 793– 800.

Kane, T. C. and T. Ryan. 1983. Population ecology of carabid cave beetles. Oecologia (Berlin). **60**: 46–55.

Laing, C. D., G. R. Carmody and S. B. Peck. 1976. Population genetics and evolutionary biology of the cave beetle *Ptomaphagus hirtus*. Evolution **30**: 484–498.

Nei, M. 1972. Genetic distance between populations. American Naturalist **106**: 283–292.

Peck, S. B. 1973. A systematic revision and the evolutionary biology of the *Ptomaphagus* (Adelops) beetles of North America (Coleoptera: Leiodidae), with emphasis on cave-inhabiting species. Bulletin of the Museum of Comparative Zoology (Harvard). **145**: 29–162.

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics, University of Texas Publications 7213: 145–153.

Selander, R. K. 1976. Genic variation in natural populations. In: F. J. Ayala (ed.) Molecular Evolution, Sinauer, Sunderland, Mass. pp. 21–45.

Singh, R. S., R. C. Lewontin and A. A. Felton. 1976. Genetic heterozygosity within electrophoretic "alleles" of xanthine dehydrogenase in *Drosophila pseudoobscura*. Genetics **84**: 609–629.

Slatkin, M. 1981. Estimating levels of gene flow in natural populations. Genetics **99**: 323–335.

Swofford, D. L. and R. B. Selander. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. The Journal of Heredity **72**: 281–283.

TURANCHIK, E. J. AND T. C. KANE. 1979. Ecological genetics of the cave beetle *Neaphaenops tellkampfi* (Coleoptera: Carabidae). Oecologia (Berlin) **44**: 63–67.

WORKMAN, P. L. AND J. D. NISWANDER. 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. American Journal of Human Genetics **22**: 24–49.

WRIGHT, S. 1978. Evolution and the genetics of populations, vol. 4. Variability within and among natural populations. University of Chicago Press, Chicago.

BIOSYSTEMATIC REVISION OF *EPIMYRMA KRAUSSEI, E. VANDELI,* AND *E. FORELI* (HYMENOPTERA: FORMICIDAE)

By Alfred Buschinger[1], Karl Fischer[1], Hans-Peter Guthy[1], Karla Jessen[1], and Ursula Winter[2]

Introduction

The myrmicine genus *Epimyrma* Emery 1915 presently comprises 11 described species, inhabiting central and southern Europe and North Africa. They all are living as social parasites together with host species of the genus *Leptothorax* (subgenera *Myrafant* Smith 1950 and *Temnothorax* Mayr 1861), some as active slavemakers, e.g. *E. ravouxi* (André 1896) (Winter 1979), others as "degenerate slavemakers" (*E. kraussei* Emery 1915 (Buschinger & Winter 1982)), and *E. corsica* (Emery 1895) as a workerless permanent parasite (Buschinger & Winter 1985).

The taxonomy of the genus is not yet completely consolidated. Thus, in the most recent revision, Kutter (1973) comes to the conclusion that *E. kraussei, E. vandeli* Santschi 1927, and *E. foreli* Menozzi 1921, are so similar that a future comparison of larger series presumably would reveal their synonymy. It is the object of this paper to provide evidence for the accuracy of Kutter's prediction. *E. kraussei* was described by 2 ♀♀ and 1 ♀ (Emery 1915) from Sorgono, Sardegna. Menozzi (1921) established *E. foreli* on the basis of 4 colonies from the vicinity of Sambiase di Calabria, S'Italy, and *E. vandeli* was described after 6 colonies collected by A. Vandel near Miramont-de-Quercy and Touffailles, Dept. Tarn-et-Garonne, in S'France (Santschi 1927, Vandel 1927). The most distinctive characters of the 3 species were slightly different shapes of the petioli, different grades of coloration from light, yellow-brown in *E. foreli* to a nearly black in *E. vandeli,* and the lack of ♀♀ in the latter as opposed to *E. foreli* and *E. kraussei.*

[1]FB Biologie, Institut für Zoologie, der Technischen Hochschule, Schnittspahnstr. 3, D-6100 Darmstadt, FRG
[2]FB 2 (Biologie), Universität Bremen, Postfach 330440, D-2800 Bremen, FRG
Manuscript received by the editor December 23, 1985.

During the past years, we have collected *E. kraussei* from numerous localities in the mediterranean area, including the type localities of *E. vandeli* and *E. foreli.* We were studying their populations, ♂♀ ♀-production in the lab and in the field, their reproductive behavior, colony foundation behavior, and karotypes. Crossbreeding of several populations including *E. vandeli* and *E. foreli* was possible. All observations pointed towards a synonymy of the 3 species. Finally, the types were examined, and morphological studies including the ♂♂ of the 3 species were carried out. This considerable body of evidence now clearly demonstrates that *E. foreli* and *E. vandeli* represent but junior synonyms of *E. kraussei.*

Material Collected and Range of *Epimyrma kraussei*

A total of 337 colonies of *E. kraussei* (including *E.v.* and *E.f.*) have been collected between 1975 and 1984 (table 1). Populations are numbered for an easier identification in the following text. Fig. 1 may provide a visual impression of the range of *E. kraussei;* it also contains a few additional localities from the literature, mainly those from North Africa (Cagniant 1968). Nests usually are found in crevices between flat stones, most easily in old dry walls of terraced vineyards and olive orchards, but also in rocky slopes underneath shrubs (Buschinger & Winter 1983). Colonies are small and can thus be aspirated almost completely. In the type locality of *E. vandeli,* we did not find the species in the exact sites of Vandel; however, we could collect a sample of 11 colonies near Lauzerte, only 5 km W of the original site, in the limestone slopes of the Barguelonne valley (table 1, no 5). *E. foreli* had been found near Sambiase di Calabria, in moss covering the bark of olive trees (Menozzi 1921). We tried in vain to find Leptothoracini in such sites, presumably because the ants have been decimated there by pesticide treatment of the trees. However, in several localities around Sambiase (table 1, no 19), we found 22 colonies of a yellowish *Epimyrma* with *Temnothorax* hosts, again in terrace walls. We are convinced that they represent members of the same population as that studied by Menozzi. Unfortunately, the search for *E. kraussei* in its type locality, Sorgono in Sardegna, Italy, in April 1985, remained unsuccessful. Even the host species was quite rare in this area. From the map (Fig. 1) we may conclude that both the type localities of *E. vandeli* and *E. foreli* are situated well within the area of *E. kraussei.*

Table 1. Localities and numbers of colonies collected of *Epimyrma kraussei* Emery 1915 (no 5a: Type locality of *E. vandeli* Santschi 1927, no 19: Type locality of *E. foreli* Menozzi 1921).

population no.		locality	n colonies
1	1981/07/14-30	Calpe (Spain, E'coast)	16
2 a	1981/03/30	Banyuls (S'France)	36
b	1984/04/03	Puig de Pani (NE'Spain)	2
c	1984/04/03	Selva de Mar (NE'Spain)	5
d	1984/04/03	Faro de Sarnella (NE'Spain)	16
3 a	1984/04/05	Pont de Bar/Seo de Urgel (Span. Pyrenees)	8
b	1984/04/05	Tremp/Tolva (Span. Pyr.)	6
c	1984/04/06	Ainsa (Span. Pyr.)	1
d	1984/04/06	Broto (Span. Pyr.)	5
4	1984/04/10	Chapelle St. Pons (S Bouleterne, French Pyrenees)	2
5 a	1981/03/31 1981/04/01	Lauzerte/Quercy (S'France)	11
b	1978/08/10	Cabrespine/Aude (S'France)	1
6	1981/03/23	La Couronne/Bouches-du-Rhône (S'France)	1
7	1981/04/02	Nyons/Drôme (S'France)	4
	1984/04/11	Suze-la-Rousse/Vaucluse (S'France)	5
8	1983/05/07-08	Ste. Maxime, Puget Ville/Alpes Maritimes (S'France)	10
9	1982/03/25	Venaco/Haute Corse (France)	5
10	1983/05/03-06	Alassio. Albenga, Ranzo, Toirano Ventimiglia/Prov. Imperia and Savona (N'Italy)	45
11	1975/05/29	Aosta (N'Italy)	2
12 a	1978/05/02	Ossuccio/Lago di Como (N'Italy)	1
b	1978/10/14 1980/10/13	Biolo/Valtelino (N'Italy)	11
13	1980/10/12	Lovere (Lago d'Iseo, N'Italy)	2
14	1979/04/09 1980/05/05-06 1980/10/11	Tignale (Lago di Garda, N'Italy)	113

Table 1, continued.

population no.		locality	n colonies
	1981/03/26 1982/10/12		
15	1974/06/15	Salorno (Adige, N'Italy)	1
16	1981/09/23-26	Krk (Dalmatia, Yugoslavia)	4
17	1983/09/29	Pag (Dalmatia, Yugoslavia)	1
18	1978/08/22	Nacionalni park Paklenica (Dalmatia, Yugoslavia)	1
19	1982/10/03-10	Gizzeria, Rogliano, near Sambiase (Calabria, S'Italy)	22
			337

Morphological Studies

Comparison of the type material of *E. kraussei, E. vandeli,* and *E. foreli* with new material

The types of *E.v.* and *E.f.* are deposited in the Naturhistorisches Museum Basel, Switzerland. We could study 1♀ *E. foreli,* and 1♀ *E. vandeli,* both from the type series. The Museo Civico di Storia Naturale "Giacomo Doria" in Genova, Italy, has provided us with the types (1♀, 1☿) of *E. kraussei.*

With a close examination of these types we could only confirm the similarity of all 3 "species" as was already stated by Kutter (1973). We therefore refrain from a detailed presentation of measurements and structures compared. We also did not find any constant differences between the types and specimens from our newly collected material, with respect to size, shape of petioli, head and thorax, length of body hairs etc.; just the coloration was slightly variable between different populations. Thus, the population from Calabria (*E. foreli*), and one from Spain (pop. no. 3) exhibit a quite light, yellowish brown coloration of ♀ and ☿. Other *E.k.* populations appear brownish, whereas a dark brown or nearly black is typical for ♀ *E. vandeli* (pop. no. 5), for a colony from La Couronne (no. 6), and for population no. 9 from Corsica. Young ♀ ♀ are darker in coloration than old queens, and callow ♀ ♀ usually exhibit some darker spots in the thorax, and a yellow base of the gaster,

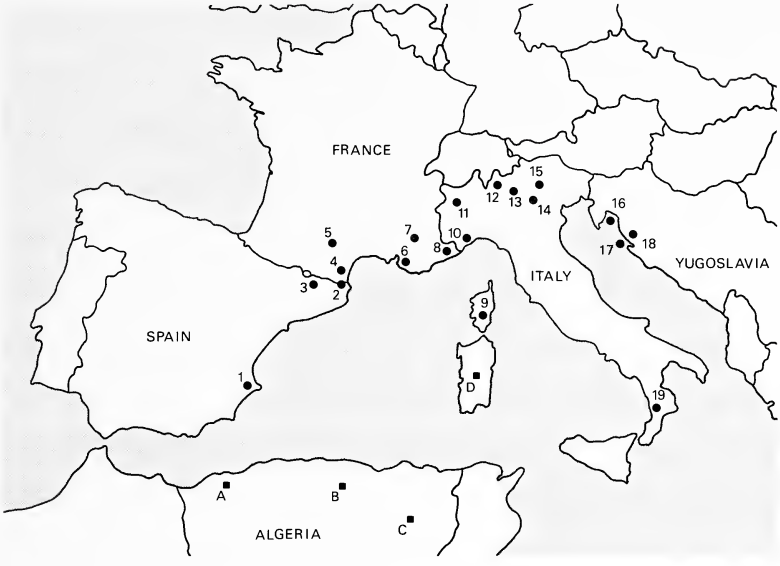


Fig. 1. Distribution of *Epimyrma kraussei* Emery 1915. ●: Our collecting sites listed in Table 1. No. 5: Type locality of *E. vandeli* Santschi 1927; no. 19: Type locality of *E. foreli* Menozzi 1921. A and C: Localities of *E. vandeli* in N'Africa cf. Cagniant (1968), B: Locality of *E. kraussei* cf. Cagniant (1968); D: Type locality of *E. kraussei* in Sardegna.

whereas the coloration in old queens is usually uniform. This age-dependent color variation is also typical for *E. ravouxi* (André 1896) (Buschinger 1982).

Male genitalia, wing venation, and shape of ♀♀ petioli

We studied wing venation and genitalia of *E.k.* ♂♂, and the outlines of the ♀ and ♀ petioli of specimens from Tignale and Biolo (Italian Alps), Calpe (Spanish Mediterranean coast), Calabria (S'Italy, *E. foreli*), and Lauzerte (S'France, *E. vandeli*). The same characters were investigated in *E. ravouxi* from several distant populations [Taubertal: Bavaria (D), Swiss Valley (CH), S'France, Corsica (F)], in order to compare their variation within and between the species. *E.r.* is clearly distinct from *E.k.* (Buschinger & Winter 1983, Winter and Buschinger 1983), and thus may serve as a reference species. Males preserved in alcohol were dissected, and permanent

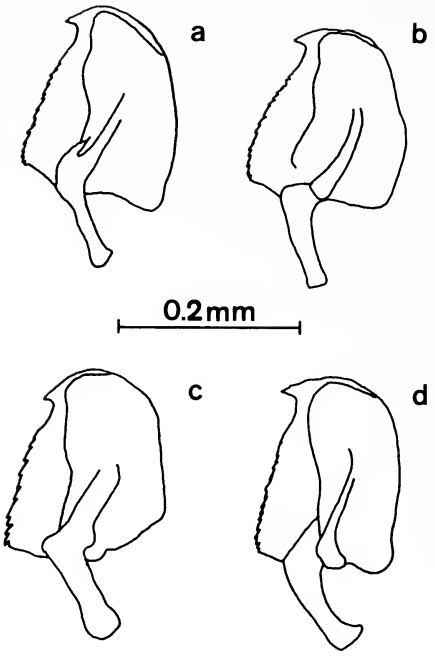


Fig. 2: Sagittae of *Epimyrma* ♂♂. a: Pop. no. 19 (*E. forelí*); b: Pop. no. 14 (*E. kraussei*); c: *E. ravouxi* from Corsica: d: Pop. no. 5a (*E. vandeli*).

mounds were made of the subgenital plate, the sagittae, and volsellae with laciniae, as well as the forewings and antennae. The outlines of ♀ and ♀̃ petioli were drawn and superimposed following a slightly modified method of Wehner (1983). As far as possible we always studied 10 ♂♀♀̃ from each of the populations mentioned above.

Male genitalia

Table 2 reveals that the numbers of sagittal teeth (Fig. 2) vary both within *E.k.* and *E.r.,* but with higher mean values in *E.k.,* including the populations of *E.v.* and *E.f.*.

The volsellae and laciniae (Fig. 3, table 3) exhibit a high conformity in *E.k.* and the two populations of *E.v.* and *E.f.,* in that the cuspis (tip of lacinia) rarely reaches, and never overlaps the digitus (terminology following Bitsch 1979). In *E. ravouxi,* on the contrary,

Table 2. Numbers of sagittal teeth in ♂♂ of *Epimyrma kraussei* Emery 1915 (= *E. vandeli* Santschi 1927, = *E. foreli* Menozzi 1921), and of *E. ravouxi* André 1896) from different populations.

species/population	*n teeth* min	$\bar{x}$	max	n sagittae checked
E. kraussei				
no 14 Tignale	11	13.9	16	19
no 12b Biolo	10	13.6	16	18
no 1 Calpe	10	14.3	19	20
no 19 Calabria (*E.f.*)	12	14.4	18	19
no 5a Lauzerte (*E.v.*)	11	13.7	17	20
E. ravouxi				
Bavaria (D)	8	11.5	15	19
Nyons (F)	10	12.6	15	18
Corsica (F)	7	10.3	13	18
Swiss Valley (CH)	10	12.4	18	21

the cuspis usually overlaps or at least reaches the digitus, with very few exceptions.

The subgenital plates did not differ between populations or species.

Male wing venation

Wing venation in Epimyrma ♀♀ is quite variable (André 1896, Kutter 1973). In ♂ forewings the radial cell is short and open, the cubital cell long and usually closed, the discoidal cell may be closed, open, or nearly lacking, and the recurrens can be complete, incomplete, or absent. Reductions of wing venation need not be symmetrical in the two forewings of a specimen. We compared mainly the shape of the discoidal cells, which exhibits sizable differences between the species, but varies also within *E.k.* and *E.r.* considerably (Fig. 4).

Thus, table 4 shows the numbers of wings with open or closed discoidal cell. This character apparently is not appropriate for a differentiation of species or populations. A slightly better distinction is possible with the shape of the discoidal cell (table 4). In *E. ravouxi* this cell is near to quadratic, with a slightly shorter anterior border. This is also true for a good deal of the N'Italian and the Spanish populations of *E.k.*, but already in these populations, and more in the Calabrian (no 19, *E.f.*) and the Lauzerte (no 5, *E.v.*)

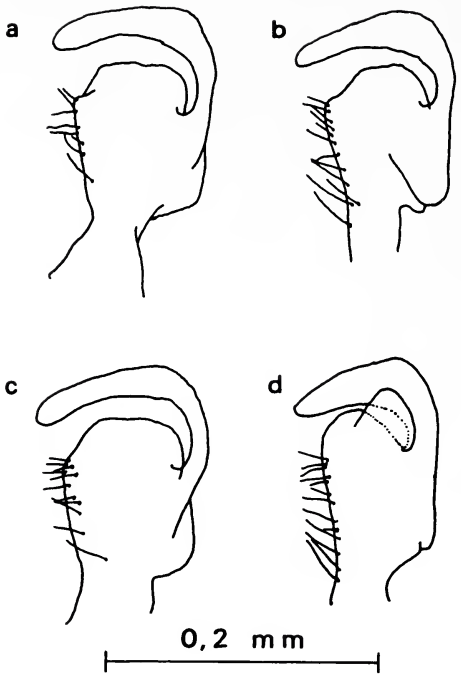


Fig. 3: Volsellae and laciniae of *Epimyrma* ♂♂. a: Population no. 14 (*E. kraussei*); b: Pop. no. 19 (*E. foreli*); c: Pop. no. 5a (*E. vandeli*); d: *E. ravouxi* from Corsica.

populations the anterior border becomes shorter until the discoidal cell is triangular.

Shape of the petioli in ♀♀ and ☿☿

In several publications (e.g. Menozzi 1931, Sadil 1953) the profiles of ♀ and ☿ petioli and postpetioli were used as the most important characters for the determination of *Epimyrma* species. Kutter (1973), however, clearly demonstrated with ♀♀ from a single *E. ravouxi* colony that these profiles may vary to such an extent that they are useless for species discrimination.

Nevertheless, we again studied this character, using a slightly modified method of Wehner (1983). The outlines of the petioli of 10 ♀♀ and 10 ☿☿ (exceptions: Population 12b: 5 ☿☿, and population 5a: 3☿☿) per population were drawn with the aid of a Wild M5

Table 3. Morphological comparison of the shape of volsella and lacinia in ♂♂ of *Epimyrma kraussei* Emery 1915 (= *E. vandeli* Santschi 1927, = *E. foreli* Menozzi 1921), and of *E. ravouxi* (André 1896) from different populations

species/population	*n volsellae and laciniae where* antrum open	cuspis reaches digitus	c. overlaps digitus	n ♂♂ checked
E. kraussei				
no 14 Tignale	16	2	–	10
no 12b Biolo	17	1	–	10
no 1 Calpe	19	–	–	10
no 19 Calabria (*E.f.*)	20	–	–	10
no 5a Lauzerte (*E.v.*)	21	1	–	11
E. ravouxi				
Bavaria (D)	–	–	20	11
Nyons (F)	1	3	12	9
Corsica (F)	2	4	12	10
Swiss Valley (CH)	1	3	17	11

dissecting microscope and a drawing tube at about × 88. The drawings then were superimposed in such a way that they all were of the same size and overlapped to a maximal degree (Fig. 5). However, sizes and profiles of the petioli are varying within each population so much that a clear distinction of populations by this character is impossible. Even between *E. kraussei* and *E. ravouxi* we could not find any reliable differences in the petiolar outlines. The character, therefore, is useless for taxonomical purposes in the *Epimyrma* species investigated, and it can neither support nor contradict a synonymization of *E.f.* and *E.v.* with *E. kraussei.*

Karyology

Karyotypes were studied using the air-drying technique of Imai et al. (1977). Usually we made preparations from testes of ♂ pupae, and a few from cerebral ganglia of prepupae. *E. kraussei* from several populations (pop. no. 1, 5b, 6, 7, 9, 12a) and *E. vandeli* (pop. no. 5a) were checked, whereas no preparations of *E. foreli* could be made.

A total of 215 metaphase cells of 16 *E. kraussei*-♂ pupae from 8 colonies of 6 different localities showed 10 chromosomes each (Fig. 6). 6 cells had 9 chromosomes, and 5 cells had the diploid number of

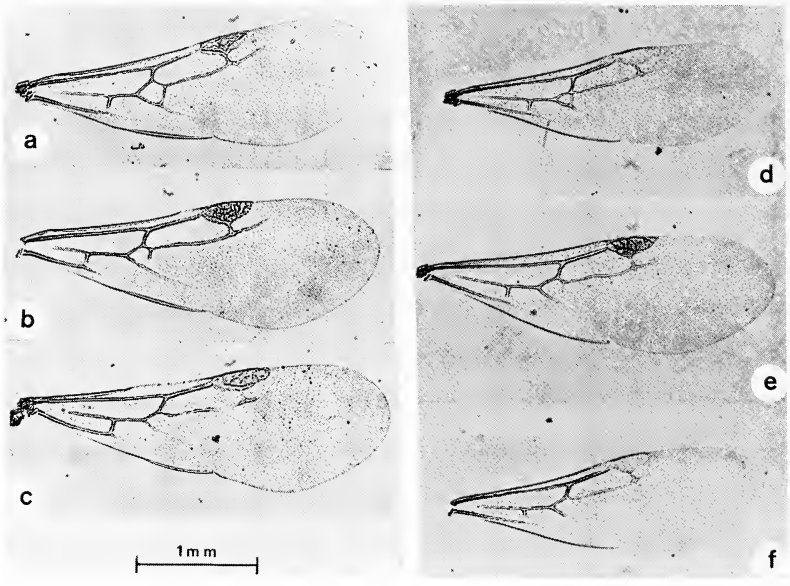


Fig. 4: Forewings of *Epimyrma* ♂♂. Left: Variation of wing venation of *E. ravouxi* from 3 populations; reduction of the subrectangular discoidal cell. a: Corsica, b: Swiss Valley, c: Taubertal, Bavaria. Right: Variation of wing venation within one *E. kraussei*-population (no. 1, Calpe, Spain). d,e,f: Reduction of the subtriangular discoidal cell.

2n = 20. 9 cells of 2 additional, apparently ♀, prepupae contained 20 chromosomes, 2 others had 17 and 15, respectively. Chromosome numbers of less than the haploid (n = 10) or diploid (2n = 20) number are probably due to loss of chromosomes during preparation. Single diploid cells in haploid ♂ ♂ were occasionally found in other species, too (e.g. Hauschteck 1962, 1965).

In 2 *E. vandeli* ♂ pupae from a colony from the type locality (pop. 5a), 26 and 15 cells, respectively, were checked. They all had 10 chromosomes each.

The karyotypes of *E. kraussei* and *E. vandeli* with n = 10 chromosomes are apparently identical. They consist of 6 small to medium-sized metacentrics, 3 medium-sized submetacentrics and 1 large subtelocentric. *E.k.* and *E.v.* share this karotype with all the species of this genus so far studied [*E. bernardi* Espadaler 1982, *E. corsica* (Emery 1895), *E. ravouxi* (André 1896) and *E. stumperi* (Kutter

Table 4. Wing venation in forewings of ♂♂ of *Epimyrma kraussei* Emery 1915 (= *E. vandeli* Santschi 1927, = *E. foreli* Menozzi 1921), and of *E. ravouxi* (André 1896) from different populations. Total numbers of wings checked for open or closed discoidal cell (left part of the table) and those checked for the shape of this cell (right part) differ because characters could not always be surely defined.

species/population	n wings with discoidal cell			shape of discoidal cell			
	open	closed	(total)	subrectangular	subtriangular	triangular	(total)
E. kraussei							
no 14 Tignale	9	9	(18)	8	9	–	(17)
no 12b Biolo	16	1	(17)	15	1	–	(16)
no 1 Calpe	8	10	(18)	6	8	6	(20)
no 19 Calabria (*E.f.*)	2	18	(20)	–	10	8	(18)
no 5a Lauzerte (*E.v.*)	8	14	(22)	–	12	9	(21)
E. ravouxi							
Bavaria (D)	24	–	(24)	22	–	–	(22)
Nyons (F)	6	12	(18)	7	2	–	(9)
Corsica (F)	12	3	(15)	17	–	–	(17)
Swiss Valley (CH)	22	–	(22)	20	–	–	(20)

1950)], and with *Myrmoxenus gordiagini* Ruszky 1902, a species very closely related to *Epimyrma* (Buschinger et al. 1983, Fischer unpubl.). No host species of *Epimyrma* and no other Leptothoracine species having this particular karyotype could yet be found. Thus, we may suppose that *E. foreli* as well has the karyotype of the genus, and no arguments for or against the synonymization of the 3 species in question can be derived from our karyological studies.

Biological data

Host specificity

The host species of *E. kraussei* in all populations investigated, including those ascribed to *E. vandeli* and *E. foreli,* is invariably *Leptothorax* (*Temnothorax*) *recedens* (Nylander 1856). All other *Epimyrma* species have different host species belonging to the subgenus *Myrafant* (Kutter 1973, Espadaler 1982, Buschinger & Winter 1985), and no other *Epimyrma* species has ever been found with *Temnothorax* hosts. In or close to the localities where we have collected *E. kraussei* (table 1) we usually found several other *Leptothorax* species, particularly often *L. (Myrafant) unifasciatus* (Latreille 1798), which then was parasitized by the slavemaking ants, *E. ravouxi* or *Chalepoxenus sp.,* but never by *E. kraussei.* Host specificity, is thus apparently a good character for species discrimination in the genus *Epimyrma,* and the joint use of *Temnothorax* by *E.v., E.f.,* and *E.k.* is an argument for their synonymization.

Population Data

Reproductive biology and colony foundation

Epimyrma species, as far as is known, may differ considerably with respect to their sex ratios. Thus, *E. ravouxi* has a sex ratio of about 1.5 (♂/♀); in *E. kraussei* from population no. 14 (Tignale) this ratio is about 0.3 in field colonies; and 0.2 in laboratory culture (Winter & Buschinger 1983), and in *E. corsica* it is 0.08 (Buschinger & Winter 1985). Sex ratios correspond well with the reproductive biology of the species concerned: *E. ravouxi* is characterized by extranidal mating, whereas *E. kraussei* (pop. no. 14 Tignale) and *E. corsica* mate inside the mother nests and thus continually inbreed. The inseminated, dealate ♀♀ of *E.k.* and *E.c.* remain in the mother

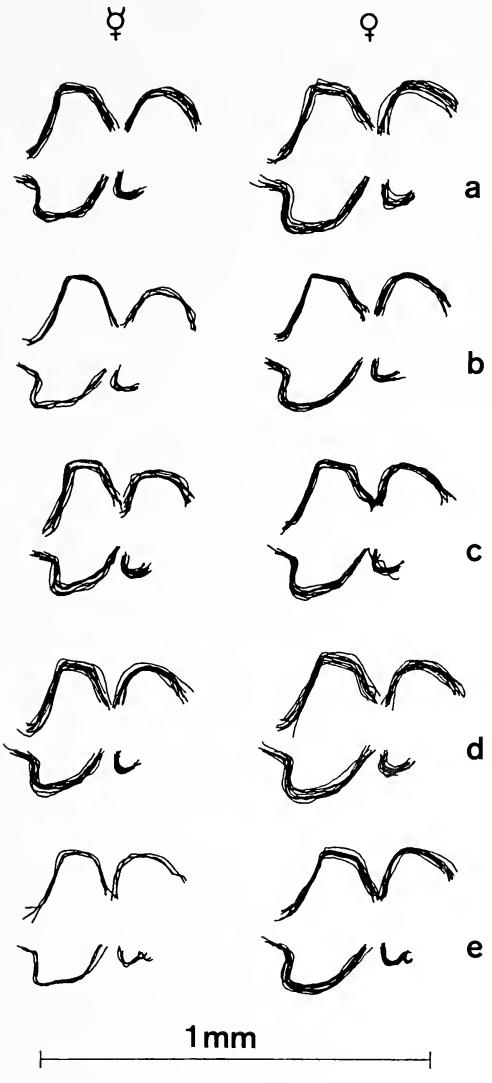


Fig. 5: Shape of petiolus and postpetiolus in *Epimyrma* ♀♀and ☿☿. a,b,c: *E. kraussei* from populations no. 1 (a), 12b (b), 14 (c); d: no. 19 (*E. foreli*); e: no. 5a (*E. vandeli*). Usually the drawings of 10 specimens (b☿: 5, e☿: 3) were superimposed following the method of Wehner 1983.

Table 5. Production of sexuals and sex ratios in populations of *Epimyrma kraussei* (= *E. foreli*, = *E. vandeli*). Mean values in ( ). (a, b): Sexuals found in field colonies in fall; (c, d, e): Sexuals produced in laboratory culture from colonies collected in spring. Colonies with relatively high numbers of host ♀♀ were selected from the field material for laboratory culture.

population	lab/field	n colonies	host ♀♀	production of ♂♂	production of ♀♀	sex ratio ♂/♀
(a) no 14 Tignale (*E.k.*)	field	19	371 (19.5)	71 (3.7)	224 (11.8)	0.32
(b) no 19 Calabria (*E.f.*)	field	22	505 (22.9)	24 (1.1)	221 (10)	0.11
(c) no 14 Tignale (*E.k.*)	lab	23	1082 (47)	113 (4.9)	537 (23.3)	0.21
(d) no 19 Calabria (*E.f.*)	lab	12	298 (24.8)	16 (1.3)	140 (11.7)	0.11
(e) no 5a Lauzerte (*E.v.*)	lab	5	86 (17.2)	8 (1.6)	54 (10.8)	0.148

nests over winter, and colony foundation through invading of a host colony occurs in spring. *E.r.* young queens, on the other hand, begin with colony foundation immediately after swarming, in late summer.

In most of the populations of *E.k., E.f.* and *E.v.,* we found evidence of a reproductive biology identical to that of *E.k.* pop. no 14 (Tignale), where we first have observed this kind of behavior (Winter & Buschinger 1983). 3 of the 11 colonies of *E.v.,* which were collected on 31 March and 1st April, contained young *Epimyrma*-♀♀ still engaged with throttling the host colony queens. The *E.f.*-population, on the other hand, was studied in fall, October 3–10, and most of the colonies contained dealate young ♀♀, a few alate ones, and some ♂♂. Reproductive behavior, thus, is identical in *E.k., E.v.* and *E.f.,* with intranidal mating and colony foundation in spring. So far as it could be checked, also the production of sexuals and the sex ratios are quite similar (table 5), the sex ratios indicating a generally high ♀-bias.

Epimyrma worker-numbers

Slave-making ant species are characterized by the presence of a comparatively high number of ☿☿ in their nests, apart from incipient colonies. In the genus *Epimyrma,* we found a considerable variation of ☿ numbers in different species, dependent upon their respective type of parasitism. Thus, *E. ravouxi,* an active slave-maker, has up to 77 *E.*-☿☿ (mean 24.9) in a nest, whereas the "degenerate slavemaker", *E. kraussei,* had an average of only 3.5 and a maximum of 10 *E.*-☿☿ (Buschinger & Winter 1983). *E. corsica* (Emery 1895) has lost the ☿-caste completely (Buschinger & Winter 1985). *E. vandeli* was originally said to be workerless, whereas ☿☿ had been described of *E. kraussei* and *E. foreli.* We therefore censused the *E.*-☿☿ in most of our field-collected colonies, and also the ☿-production of a representative number of colonies in laboratory culture.

In table 6 we compare the *Epimyrma* ☿-numbers of 4 larger populations including 2 ascribed to *E. kraussei* (no 14 and 2a), and the populations no 5a (*E.v.*) and no 19 (*E.f.*), and of 5 local populations of *E. kraussei* from the Spanish Pyrenees with nests always found in close vicinity.

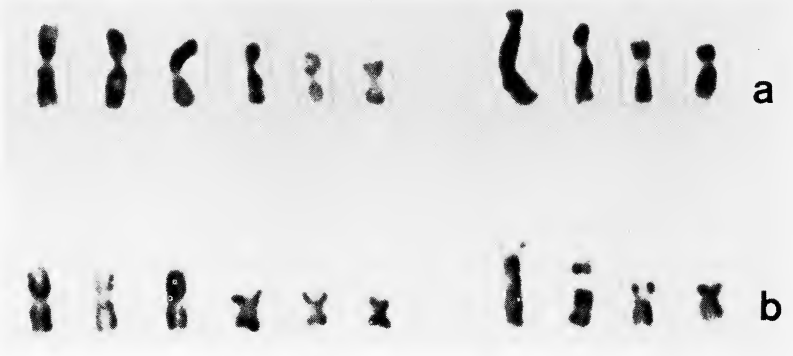


Fig. 6: Karyotypes of a: *Epimyrma kraussei* from pop. no. 5b (Aude, S'France) and b: *Epimyrma ravouxi* from pop. no. 12a (Lago di Como, N'Italy).

Most striking is the fact, that our 11 field colonies of *E. vandeli* did not contain any E.-♀♀. This corresponds to the original description of 6 colonies without ♀♀ (Vandel 1927). In laboratory culture, however, we obtained a few ♀♀ from colonies of this population (see below).

Workerlessness is also found in a certain amount of colonies in most populations of *E. kraussei.* In part, this is due to the fact the newly founded colonies do not yet contain *E.*-♀♀, and most of our collecting was done in spring during the time of colony foundation. Therefore, it is not surprising that the population of *E. foreli* is the only one where all colonies contained at least one *E.* ♀: The sample was entirely collected in the fall. On the contrary, our material from the type locality of *E. vandeli* was collected in spring, and in 3 of the 11 colonies the *E.*-♀ was still engaged in throttling the *Temnothorax* queen. A few more colonies may as well have been incipient ones, where the host queen had already been eliminated. Furthermore, 3 colonies in the laboratory produced unusually high amounts of *E.*-♂♂, and when dissected, the queens proved to be poorly inseminated, having very few sperm cells in their receptacula. The lack of *E.*-♀♀ in our sample is thus at least in part explained by these facts.

The highly variable average and median values of ♀-numbers as well as the maximum values in other populations are also very remarkable. In some populations, like that of *E. foreli,* but also at

Table 6. Numbers of *Epimyrma*-♀♀ in field populations of *E. kraussei* Emery 1915 (= *E. vandeli*, = *E. foreli*).

population	n colonies censused	n Epimyrma ♀♀/colony mean	median	range	% colonies lacking E.-♀♀	
no 14 Tignale (*E.k.*)	82	2.07	1.5	0–10	46.3	spring & fall
no 2a Banyuls (*E.k.*)	36	5.33	3.5	0–20	11.1	spring
no 19 Calabria (*E.f.*)	22	6.64	5	1–26	0.0	fall
no 5a Lauzerte (*E.v.*)	11	0	0	0	100.0	spring
no 3a Pont de Bar (*E.k.*)	7	1.0	0	0– 7	85.7	spring
no 2d Faro de Sarnella (*E.k.*)	16	2.31	1	0– 9	56.2	spring
no 2c Selva de Mar (*E.k.*)	5	6.8	5	0–15	20.0	spring
no 3d Broto (*E.k.*)	5	7	4	0–16	20.0	spring
no 3b Tremp/Tolva (*E.k.*)	6	10.5	10.5	0–24	16.6	spring

Banyuls (no 2a) and along the Spanish Pyrenees (no 2c, 3b, 3d), we found a few colonies with 15 to more than 20 *E.*-♀♀, which would be sufficient for an effective slave-raiding. As was suggested for *E. kraussei* from Tignale (Buschinger & Winter 1983), however, we believe that slave-raids do occur only exceptionally, if at all, in the other populations now studied: Most colonies comprise but very few *E.*-♀♀, and colonies with higher *E.*-♀-numbers on average do not contain more host species workers than those with few or no *E.*-♀♀. From table 6 we may conclude that *Epimyrma kraussei* has established numerous local populations in which the reduction of ♀-numbers has occurred to highly variable degrees. The population ascribed to *E. vandeli* then would be close to one end of the scale which is complete loss of the ♀-caste like in *E. corsica* (Buschinger & Winter 1985), and *E. foreli* is among the populations with highest *E.*-♀-numbers. It must be stated, however, that a geographical variation of ♀-numbers, e.g., in the sense of a cline, is lacking: Populations with low ♀-numbers have been found in S'France (no 5a, *E. vandeli*) and in N'Spain (no 3a), and high ♀-numbers occur close to the latter locality (no 3b) as well as in S'Italy (no 19, *E. foreli*).

In laboratory culture the ♀-production of *Epimyrma* colonies roughly corresponds to the field data. Table 7 provides a comparison of ♀-production in colonies from 3 populations. Most important is the fact that *E.*-♀♀ appeared in 2 of the 5 laboratory-kept colonies from population no 5a (Lauzerte, *E. vandeli*).

Worker numbers, thus, are not contradictory to a synonymization of *E.v.* and *E.f.* with *E. kraussei.*

Crossbreeding experiments

Intranidal mating is an excellent condition for experimental crossbreeding of sexuals from different populations and even species. Colonies are kept in nearly natural annual cycles with a long hibernation of about 6 months at 10°C a "spring" and "fall" phase in daily temperature rhythms of 10°C (12h, dark) and 20°C (12h, light) for 2 weeks each, and a summer phase of 15°C (10h, dark) and 25°C (14h, light) for 2 weeks, followed by 2 months of 17°C (10h, dark) and 28°C (14h, light), and again 2 weeks of 15°C/25°C when pupation decreases. For details of formicaries, feeding etc. see Buschinger (1974). All ♂ pupae from colonies of 2 populations or species are exchanged. Further ♂ pupae arising newly from the

Table 7. Worker-production in colonies of *Epimyrma kraussei* Emery 1915 from 3 populations, in the first summer after collecting (including the populations of *E. foreli* Menozzi 1921 and *E. vandeli* Santschi 1927).

		Epimyrma ♀♀ produced			
population	n colonies	total	mean	median	range
no 14 Tignale (*E.k.*)	23	12	0.52	0	0- 2
no 19 Calabria (*E.f.*)	12	24	2.0	1	0-10
no 5a Lauzerte (*E.v.*)	5	5	1.0	0	0- 4

remaining brood are either removed or exchanged. Usually the foreign pupae are easily accepted, and also the sexuals hatching from them. After dealation of the young ♀♀ a few of them are dissected for control of insemination. In the following spring the ♀♀ leave the nest chambers and can be placed with host colonies, where they found their own colonies. The first sexual offspring usually develops from rapid brood in the year of colony foundation (Winter & Buschinger 1983).

It must be said, however, that the rate of successful colony foundations is generally low, both with cross-mated ♀♀ and those having normally mated with brothers, Quite often this is due to insufficient insemination, and perhaps to not yet optimal laboratory conditions. We therefore present only a preliminary survey of successful crossbreedings (table 8) without giving data on numbers of replicates or numbers of offspring produced. These experiments are being continued.

Table 8 clearly reveals that crossbreeding between different *E.k.* populations, and also between *E.k.* and *E.v.* or *E.f.*, is possible. This result, however, can only weakly support our supposition of the synonymy of the 3 species, since we also succeeded in crossbreeding *E.k.* with *E. corsica,* and with *E. bernardi,* both of which are morphologically and biologically distinct good and species.

Discussion and Conclusion

The meaning of the morphological and biological characters studied in *E. kraussei, E. vandeli* and *E. foreli,* has been discussed with reference to the question of synonymy of the 3 species already in the respective sections. We found no morphological characters which would allow a clear distinction between them. The karyotype is apparently homologous in all *Epimyrma* species. The 3 species

investigated have a common host species, *Leptothorax* (*T.*) *recedens,* which is not parasitized by any other *Epimyrma* species. The numbers of *Epimyrma*-♀♀ are variable, but low in all the 3 species, which therefore should represent "degenerate slavemakers" as was already stated for *E. kraussei* (Buschinger & Winter 1983). Field data and laboratory breeding results indicate that the 3 species have a highly ♀-biased sexual production, intranidal mating and inbreeding, that the young ♀♀ overwinter in their mother nests and invade own host colonies in spring. Crossbreeding experiments reveal that a strict genetical isolation is lacking. The 3 original samples, comprising only few specimens, were apparently described as separate species mainly because they were found in quite distant localities, and because the variability of their slight morphological differences could not be evaluated then.

We therefore synonymize *E. vandeli* Santschi 1927 and *E. foreli* Menozzi 1921 with *E. kraussei* Emery 1915.

Population structure and reproductive biology in this species, however, are highly remarkable (Winter & Buschinger 1983). The inbreeding system with young queens spreading on foot, and thus over only short distances, must result in an extremely restricted gene flow, even if a rare mating of sexuals from neighboring colonies might occur. The populations from different continents (northern Africa, southern Europe) and islands (Sardegna, Corsica), but also from more neighboring localities (southern France, northern Spain), must have been isolated for a very long time. This isolation, in our opinion, is responsible for the differences in coloration, morphology of wings and genitalia, and worker numbers, which we observed in certain populations. The replacement of one of these characters by another one can only occur through interdemic selection, through supplantation of a local population by another one which is somewhat more effective. Since *E. kraussei,* however, does not inhabit large, continuous habitats, but instead forms numerous small, patchily distributed populations, this process must be slow and rare. The reduction of worker numbers in favor of a higher ♀ production should be highly adaptive in this species. Since, however, the genetical basis for this evolution cannot spread, e.g., through flying ♂♂, we may speculate that different demes just have reached different degrees of worker reduction. Crossbreeding experiments have been started in order to find out whether or not

Table 8. Successful crossbreeding experiments with *Epimyrma kraussei* from different populations, including *E. foreli* and *E. vandeli*. Numbers of colonies are given in which ♀ and/or ♀̆ offspring of crossmated ♀♀ was obtained. "Interspecific" crossbreedings underlined.

♂♂ from popul.	Calpe (*E.k.*)	Lauzerte (*E.v.*)	Nyons (*E.k.*)	Corsica (*E.k.*)	Tignale (*E.k.*)	Krk (*E.k.*)	Calabria (*E.f.*)
♀♀ from popul. no 1 Calpe (*E.k.*)		1		4	7		
5a Lauzerte (*E.v.*)					1		
7 Nyons (*E.k.*)					3		
9 Corsica (*E.k.*)	4						
14 Tignale (*E.k.*)		3	1	1		6	1
16 Krk (*E.k.*)	1						

worker number in *E. kraussei* populations is genetically determined. If so, we may predict that somewhere in the range of *E. kraussei,* populations will be found with high ♀-numbers, and still actively slave-raiding, and other perhaps truly workerless demes. The evolution from outbreeding and slave-raiding towards intranidal mating and reduction of worker numbers and slave-making behavior, is an apparently widespread trait in the genus *Epimyrma.* Intranidal mating has been found also in *E. bernardi* and in *E. corsica,* two species which are morphologically clearly separated from *E. kraussei.* Whereas *E. bernardi* "still" produces a considerable amount of ♀♀, *E. corsica* has lost this caste completely (Buschinger & Winter 1985). Future studies will be necessary to find out whether worker reduction in *Epimyrma* is developing in several species or species groups independently, in parallel evolution, or whether the species with different worker numbers form a series of descent. The present study of *E. kraussei* evidently favors the first alternative.

Summary

Epimyrma vandeli Santschi 1927 and *E. foreli* Menozzi 1921 are junior synonyms of *E. kraussei* Emery 1915. A comparison was made of the type specimens and of newly collected material from the type localities of *E.v.* and *E.f.,* and from numerous populations of *E.k.*. No reliable morphological differences could be found, despite a certain variation in ♂ genitalia, wing venation and body coloration of different populations. Karyotypes are homologous in all *Epimyrma* species and populations yet studied. The host species is *Leptothorax* (*Temnothorax*) *recedens* (Nylander 1856) in all *E.k.* populations including *E.v.* and *E.f.,* whereas all other *Epimyrma* species have different host species. *Epimyrma* ♀-numbers vary between populations, *E.v.* having a particularly low, and *E.f.* quite a high one, both, however, remaining within the range of the other *E.k.* populations. Sexual production is similar in all populations with a remarkably low ♂-production. In all populations studied, sexuals mate within the mother nests, and inseminated, dealate young ♀♀ remain there over winter until they leave for colony foundation in spring. *E.v.* and *E.f.* could be successfully crossbred with *E.k.,* and sexuals from several *E.k.* populations among each other. Differences between *E.k.* populations presumably are due to their

quasi-clonal structure with very restricted or lacking gene flow between colonies and demes.

Acknowledgements

This work was supported by grants of the Deutsche Forschungsgemeinschaft.

References

André, E. 1896: Description d'une nouvelle fourmi de France. - Bull. Soc. Ent France **2**: 367–368.

Bitsch, J. 1979: Morphologie abdominale des Insectes. In: Grassé, P.-P., Traité de Zoologie, t. VIII, fasc. II, 290–578; Masson, Paris.

Buschinger, A. 1974: Experimente und Beobachtungen zur Gründung und Entwicklung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* (Nyl.). - Ins. soc. **21**: 381–406.

Buschinger, A. 1982: *Epimyrma goesswaldi* Menozzi 1931 = *Epimyrma ravouxi* (André 1896) - Morphologischer und biologischer Nachweis der Synonymie (Hym., Formicidae). - Zool. Anz. **208**: 352–358.

Buschinger, A. & Winter, U. 1983: Population studies of the dulotic ant, *Epimyrma ravouxi,* and the degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). - Entomol. Gener. **8**: 251–266.

Buschinger, A. & Winter, U. 1985: Life history and male morphology of the workerless parasitic ant *Epimyrma corsica* (Hymenoptera: Formicidae). - Entomol. Gener. **10**: 65–75.

Buschinger, A., Winter, U. & Faber, W. 1983: The biology of *Myrmoxenus gordiagini* Ruzsky, a slave-making ant (Hymenoptera, Formicidae). - Psyche **90**: 335–342.

Cagniant, H. 1968: Du nouveau sur la répartition des *Epimyrma* d'Algérie (Hymenoptères - Formicidae - Myrmicinae). - Bull. Soc. Hist. Nat. Toulouse **104**: 427–429.

Emery, C. 1915: Contributo alla conoscenza delle formiche delle isole italiane. -Ann. Mus. Civ. Stor. Nat. Genova, Ser. 3a, **46**: 244–270.

Espadaler, X. 1983: *Epimyrma bernardi* n.sp., a new parasitic ant. - Spixiana **5**: 1–6.

Hauschteck, E. 1962: Die Chromosomen einiger in der Schweiz vorkommender Ameisenarten. - Vierteljahresschr. Naturf. Ges. Zürich **107**: 213–220.

Hauschteck, E. 1965: Halbe haploide Chromosomenzahl im Hoden von *Myrmica sulcinodis* Nyl. (Formicidae). - Experientia **21**: 323–325.

Imai, H. T., Crozier, R. H. & Taylor, R. W. 1977: Karyotype evolution in Australian ants. - Chromosoma **59**: 341–393.

Kutter, H. 1950. Über zwei neue Ameisen. - Mitt. Schweiz. Ent. Ges. **23**: 337–346.

Kutter, H. 1973: Beitrag zur Lösung taxonomischer Probleme in der Gattung *Epimyrma* (Hymenoptera Formicidae). Mitt. Schweiz. Ent. Ges. **46**: 281–289.

MENOZZI, C. 1921: Formiche dei dintorni di Sambiase di Calabria. - Boll. Lab. Zool. gener. Agr. Portici **15**: 24–32.

MENOZZI, C. 1931: Revisione del genere *Epimyrma* Em. (Hymen. Formicidae) e descrizione di una specie inedita di questo genere. - Mem. Soc. Ent. Ital. **10**: 36–53.

SADIL, J. 1953: *Epimyrma zaleskyi* nov. spec. (Hym., Formicoidea). - Casop. Cesk. Spol. ent. **50**: 188–196.

SANTSCHI, F. 1927: Notes myrmecologiques. I. Sur quelques nouvelles fourmis de France. - Bull. Soc. Ent. France **1927**: 126–127.

VANDEL, A. 1927: Observations sur les moeurs d'une Fourmi parasite: *Epimyrma vandeli* Santschi. - Bull. Soc. Ent. France **1927:** 289–295.

WEHNER, R. 1983: Taxonomie, Funktionsmorphologie und Zoogeographie der saharischen Wüstenameise *Cataglyphis fortis* (Forel 1902) stat. nov. (Insecta: Hymenoptera: Formicidae). - Senckenbergiana biol. **64**: 89–132.

WINTER, U. 1979: *Epimyrma goesswaldi* Menozzi, eine sklavenhaltende Ameise. -Naturwissenschaften **66**: 581.

WINTER, U. & BUSCHINGER, A. 1983: The reproductive biology of a slavemaker ant, *Epimyrma ravouxi,* and a degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). - Entomol. Gener. **9**: 1–15.

MALE BIOLOGY IN THE QUEENLESS PONERINE ANT *OPHTHALMOPONE BERTHOUDI* (HYMENOPTERA: FORMICIDAE)

By Christian Peeters* and Robin Crewe

Department of Zoology, University of the Witwatersrand, Johannesburg 2001, South Africa

Introduction

Various ponerine ants exhibit significant modifications in their pattern of male dispersal, and this is associated with changes in the queenright social structure. In some species the queen caste has become permanently wingless (= ergatoid queens), and in others it has been replaced by mated laying workers (= gamergates; Peeters and Crewe, 1984). Thus, male nuptial flights take on new characteristics since they have to locate flightless sexual partners. Data on male behavior are only available for a few of the ponerine species without a queen caste, but generally males disperse individually and orientate to foreign nests, around which mating then occurs. Brown (1953) observed low-flying males entering nests in two species of *Rhytidoponera.* Mating can occur outside the nest entrances (e.g. in *R. chalybaea*; Ward, 1981), or inside the nest (e.g. in *Diacamma rugosum*; Wheeler and Chapman, 1922).

Ophthalmopone berthoudi Forel is permanently queenless, and details of its reproductive system and polydomous organization appear elsewhere (Peeters and Crewe, 1985, MS). This paper deals with the pattern of male behavior in the field and the characteristics of male production in a breeding system made up exclusively of laying workers.

Methods

Colonies of *Ophthalmopone berthoudi* were studied in one locality in Mkuzi Game Reserve (north-eastern Natal, South Africa), during 1981–1983. Observations were made throughout the year,

*Present address: School of Zoology, University of New South Wales, P.O. Box 1, Kensington N.S.W., Australia 2033.

Manuscript received by the editor May 20, 1986.

but the ones specifically reported in this paper were made during the period of male activity (January–April). Male behavior was usually studied near colonies under intensive study (Peeters, 1984). In such colonies the location of all the nest entrances was known (colonies are polydomous), and all the workers active outside the nests had been color-marked with individual codes. In addition, a few males were marked on the thorax and then released. The presence of males was determined by observation of their activity outside nests and by examination of the contents of excavated nests.

Results

Dates of male activity

Normal winged males are produced in this species and were found inside most nests excavated during January–April (Table 1). This limited period of male production was confirmed by finding male pupae during January–April only. A subjective impression is that the number of males present above ground reached a peak in February. Excavations also revealed that males are present in every nest of a colony. However, nests collected in the same month could contain different numbers of males (Table 1). During January and February, a few males were seen to be carried between the nests of a colony. This carrying did not follow any organized pattern, and occurred together with the recruitment of workers and brood. Many of the cocoons that were transferred between nests during that period contained male pupae (A sample of cocoons then found in the nests yielded 70 male pupae and 248 worker pupae).

The investment in male production does not appear exceptional in this queenless species; a colony (464 workers) with five nests excavated in February 1982 yielded 60 males (Table 1), and this is in addition to those that had already departed as well as pupae.

Dispersal behavior

Every day during a three-week observation period in January–February 1982, a few males (1–8) left from each of six nests under intensive observation. Departing males left the nests, often climbed up low vegetation and flew off. Once on the wing, they could no longer be followed. The time of departure (9H00 to 12H00) often coincided with the period when workers were no longer active on the surface because of high soil temperatures. Male exit times appeared not to be affected by cloudy or cooler weather.

Table 1. Size of the male population in nests excavated during January–April. Males were not present at other times of the year.

Date of excavation	Number of nests excavated	Number of males found in each nest (together with number of adult workers)
January 1981	4 #	5(145), 0(84), 6(142), 10(227)
January 1982	1	17(>140)
January 1983	3 #	3(116), 9(222), 6(121)
February 1982	5 +	7(20), 9(80), 19(168), 13(72), 12(124)
March 1982	2 +	0(119), 0(77)
April 1981	3 +	0(318), 0(75), 1(445)
April 1983	2 +	0(106), 2(121)

from 2 colonies
+ from same colony

Evidence that males remain in their natal nests until they are physiologically ready to mate was adduced from the following observations. An adult male that was painted while being carried between two nests, remained inside the second nest for nine days before it left and flew off. Dissection of males collected during excavations revealed that there was little or no sperm in the vasa deferentia and ejaculatory ducts of many of them.

After the initial dispersal flight, males alighted on the ground and appeared to search for nests haphazardly. They walked quickly with frequent changes of direction, and investigated little holes and depressions in the soil. They regularly climbed up short grass stems or low vegetation from which they flew off, often for only a short distance. This behavior was interspersed with ground searches. On a number of occasions, males were observed either landing very close to nest entrances, or walking straight towards occupied nests shortly after landing. Five marked males were observed outside one nest on two successive days, indicating that after locating a foreign nest,

Behavior around the entrances of foreign nests

During the period of their activity, males were observed waiting immobile outside nest entrances, either on the ground or on top of short grass stems. The working assumption was that such males did not originate from these nests, because they always flew away from their natal nests. Some nests frequently had many males in their vicinity, while other nearby nests seldom had any around them.

Males usually investigated entrance holes with their antennae and hesitantly walked in; some ran out immediately afterwards. Individual males were repeatedly evicted from nests by workers (in nests

under intensive study, these were often marked workers, i.e. active on the surface). Males were held by their legs, wings or antennae, and resisted fiercely; some managed to struggle free. After releasing the males in the vicinity of the nests (30 cm –1 m away), the workers ran back into the entrance holes. The uninjured males cleaned their antennae and then immediately attempted to enter the nests again. On some occasions a number of workers cooperated in the eviction of foreign males, and some workers also chased males when they came across them outside the nests. Eviction did not always follow a male's entrance, and some marked males remained underground for at least 15 minutes.

Discussion

In *Ophthalmopone berthoudi* copulation was never observed above ground, and it is inferred that it occurs exclusively inside foreign conspecific nests. This is an unusual situation in ants, who usually mate some distance from the nests. However, copulation can take place in the immediate vicinity of nests in queenright and queenless ponerines, and in socially parasitic myrmicines (e.g. *Harpagoxenus*; Buschinger and Alloway, 1979). In *Rhytidoponera chalybaea,* in which colonies have either a queen or gamergates, large numbers of workers and males mill around nest entrances, and males make repeated attempts to mate with workers (Ward, 1981). However, males also enter nests and may mate with workers there. In the queenless *R. metallica,* workers attract males by the release of a pygidial gland pheromone; this distinct behavior ('sexual calling') occurs outside the nest entrances (Hölldobler and Haskins, 1977). The pygidial gland has been found in *O. berthoudi* (Villet et al., 1984), and we speculate that if young workers release this sex pheromone, they only do so inside the nests and hence encounter males underground. Sexual calling was never observed in the field or in the laboratory.

Direct data are not available on the activities of males inside foreign nests, and the occurrence of mating is inferred from the large proportion of inseminated workers in nests excavated after the period of male activity (Peeters and Crewe, 1985). The existence of many gamergates in some nests (up to 108) strongly suggests that males copulate more than once; otherwise, such nests would need to be visited by larger numbers of males than we observed entering any

nest. The substantial variations in the percentages of gamergates present in different nests at any one time of the year (Peeters and Crewe, 1985) suggest that the number of male visits to a particular nest is irregular. Some nests may be located more often than others, and consequently varying numbers of young workers become mated. In polydomous colonies such as these, gamergates can be transferred between nests and, hence, a colony should survive from year to year as long as one of its nests is visited by males.

The exit of males from their natal nests is not coordinated, and they disperse over a period of a few weeks. This is different to the situation in queenright species where the emergence of all the male and female reproductives is synchronized in time (e.g. in *Camponotus herculeanus,* through the release of a mandibular gland pheromone by the males; see Hölldobler and Bartz, 1985). Dispersal is then often associated with the initiation of new nests, which must occur during optimal environmental conditions (e.g. after rain). In contrast, copulation in *O. berthoudi* is not followed by independent colony foundation by the mated workers, because colonies reproduce by fission (Peeters, 1984). Thus it is no longer selectively advantageous for males to disperse simultaneously in response to a specific environmental cue. However, males continue to be produced only during a short period of the year. Unmated workers show no ovarian activity in *O. berthoudi,* and haploid eggs are laid exclusively by gamergates (Peeters and Crewe, 1985). Egg fertilization is thus a voluntary act by the mated workers, and males are produced following the first summer rains. Sperm exhaustion is unlikely since individual gamergates lay relatively few eggs during their lifetime. It is not known whether all the gamergates in a nest produce haploid eggs; the inter-nest transfer of male adults and pupae would make this hard to determine.

The importance of chemical attractants during nest location remains unclear. In *Leptogenys ocellifera,* a ponerine with ergatoid queens, dispersing males search for the chemical trails that lead from the nests into the surroundings (Maschwitz and Mühlenberg, 1975), and males of *Megaponera foetens* follow trails laid by workers during raids on termite nests (Longhurst and Howse, 1979). This is impossible in *O. berthoudi* because continuous trails are not laid. There is evidence that discrete scent marks are deposited on the substrate by inexperienced foragers (Peeters and Crewe, MS), but this may be of no use to males. It is conceivable that the pygidial

gland secretions also work as a long-distance attractant. In addition to signalling sexual receptiveness to the males inside the nests, these volatile secretions (which are produced by many workers) may diffuse out of the nests and be perceived by searching males.

Males of *O. berthoudi* need to enter foreign nests in order to find sexual partners. The colony units have distinct identities (Peeters, 1984), and alien males are recognized as different by workers, which then attempt to remove them from the nest; similar hostility is also displayed in *R. chalybaea* (Ward, 1981). This aggression contrasts with the acceptance of alien males by workers in ponerine species with ergatoid queens, e.g. males in *Leptogenys* and *Megaponera* were not attacked following their entry into foreign colonies (Wheeler, 1900; Longhurst and Howse, 1979). In the queenless *Dinoponera gigantea,* Overal (1980) observed a male being carried into a nest by a forager. Carrying of males in *O. berthoudi* was always between the nests of a single polydomous colony and is thus not equivalent to the observations made by Overal. Access by males to foreign nests may be facilitated by the fact that the older workers that perform activities on the surface and are responsible for the evictions, are usually not active during the daily peaks of male activity. The younger workers confined inside the nests are those likely to become mated (Peeters and Crewe, 1985), and these probably do not behave aggressively towards foreign males.

If the queenright ancestors of this species exhibited the typical formicid pattern of reproduction, then male and female reproductives would have been produced seasonally. With the change to worker reproduction, the sexually-attractive workers do not disperse from their nests prior to mating, and mating is no longer coupled with colony foundation, hence the times of male activity no longer need to be synchronized with female activity periods or with appropriate environmental conditions for colony foundation. This relaxation of the selective pressures on the timing of male dispersal has resulted in an extended mating period. Nonetheless, male activity remains seasonal. This has no adaptive significance in *O. berthoudi,* because young workers that can be mated occur throughout the year. However it has the effect of ensuring that an adequate number of infertile workers are present in the colonies.

Acknowledgments

We are grateful to R. H. Crozier for comments on the manuscript. We thank the Natal Parks Board for permission to work in Mkuzi Reserve, and Peter Goodman for his hospitality. This work was supported by grants from the University of the Witwatersrand and the Council for Scientific and Industrial Research.

References

Brown, W. L.
1953. Characters and synonymies among the genera of ants. Part I. Breviora, Mus. Comp. Zool., **11**: 1–13.

Buschinger, A. and T. M. Alloway
1979. Sexual behaviour in the slave-making ant, *Harpagoxenus canadensis* M. R. Smith, and sexual pheromone experiments with *H. canadensis, H. americanus* (Emery), and *H. sublaevis* (Nylander) (Hymenoptera; Formicidae). Z. Tierpsychol., **49**: 113–119.

Hölldobler, B. and C. P. Haskins
1977. Sexual calling behavior in primitive ants. Science, **195**: 793–794.

Hölldobler, B. and S. H. Bartz
1985. Sociobiology of reproduction in ants. *In:* Experimental Behavioral Ecology and Sociobiology (eds. B. Hölldobler, M. Lindauer) Gustav Fischer Verlag, Stuttgart pp. 237–257.

Longhurst, C. and P. Howse
1979. Some aspects of the biology of the males of *Megaponera foetens.* Insectes Soc., **26**: 85–91.

Maschwitz, U. and M. Mühlenberg
1975. Zur Jagdstrategie einiger orientalischer *Leptogenys*-Arten (Formicidae: Ponerinae). Oecol., 20, 65–83.

Overal, W. L.
1980. Observations on colony founding and migration of *Dinoponera gigantea.* J. Ga Entomol. Soc., **15**: 466–469.

Peeters, C. P.
1984. Social organization, breeding biology and the process of reproductive differentiation in *Ophthalmopone berthoudi* Forel, a ponerine ant. Unpublished Ph.D. Thesis, University of the Witwatersrand Johannesburg, South Africa.

Peeters, C. and R. Crewe
1984. Insemination controls the reproductive division of labour in a ponerine ant. Naturwiss., **71**: 50–51.
1985. Worker reproduction in the ponerine ant *Ophthalmopone berthoudi:* an alternative form of eusocial organization. Behav. Ecol. Sociobiol., **18**: 29–37.

MS. Foraging and recruitment in ponerine ants: solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). Submitted.

VILLET, M., C. PEETERS AND R. CREWE

1984. The occurrence of a pygidial gland in four genera of ponerine ants (Hymenoptera: Formicidae). J. Georgia Entomol. Soc., **19**: 413–416.

WARD, P. S.

1981. Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae) II. Colony origin, seasonal cycles, and reproduction. Psyche, **88**: 109–126.

WHEELER, W. M.

1900. A study of some Texan Ponerinae. Biol. Bull., **2**: 1–31.

WHEELER, W. AND J. CHAPMAN

1922. The mating of *Diacamma*. Psyche, **29**: 203–211.

NEARCTIC SPECIES OF THE NEW WOLF SPIDER GENUS *GLADICOSA* (ARANEAE: LYCOSIDAE)*

By Allen R. Brady

Department of Biology, Hope College
Holland, Michigan 49423

This is the second paper in a projected series of systematic studies of the Nearctic Lycosidae described primarily in the genus *Lycosa.* Over 50 species of medium to large size wolf spiders from the Nearctic Region have been placed in this genus. However, recent studies indicate that several distinct genera are included under *Lycosa.* Matters have been complicated at the generic level by C. F. Roewer (1954) who listed 44 new genera of Lycosinae in the Katalog der Araneae. They are *nomina nuda,* lacking descriptions. Later Roewer (1959, 1960) defined these 44 genera, thus validating the names, and added seven more new ones to the Lycosinae as well. These genera were established primarily on the basis of differences in the number of posterior cheliceral teeth and eye arrangement (particularly eyes of the anterior row). Investigations of North American Lycosidae (Brady 1962, 1972, 1979) indicate that the number of posterior cheliceral teeth is an unreliable character in delimiting genera. Recent studies indicate that color patterns on the dorsal surface of the carapace, length of legs relative to body size, and particularly the structure of the male and female genitalia are most reliable in determining generic relationships. Certain features of the eye arrangement, as well as information about habitat, behavior, and life history are also useful. In the final analysis, it is the unique combination of all these features that should be employed to distinguish genera.

Gladicosa gen. nov.

Lycosa (part) Walckenaer 1837: 338. Emerton 1885: 485. Marx 1890: 562; 1892: 160. Stone 1890: 423, 426. Montgomery 1902: 538, 546, 566; 1904: 277–280; 1905: 174; 1909: 514. Banks 1901: 184; 1910: 55, 57; 1911: 454. Chamberlin 1904: 147; 1908: 225, 226, 265; 1924: 28. Petrunkevitch 1911: 560. Comstock 1913: 631, 639;

*Manuscript received by the editor July 15, 1986

1940: 644, 650. Bishop and Crosby 1926: 207. Wood 1926: 174. Crosby and Bishop 1928: 1067. Elliott 1930: 5; 1932: 423. Worley and Pickwell 1931: 91, 93. Chickering 1932: 351. Gertsch 1934: 7, 8; 1949: 82. Gertsch and Wallace 1935: 20–22; 1937: 10. Kaston 1935: 191; 1936: 103, 114; 1938: 184; 1948: 322, 328; 1981: 322, 328. Allard 1936: 67. Jones 1936: 69. Chamberlin and Ivie 1944: 142, 144. Bonnet 1957: 2607, 2635, 2645. Fitch 1963: 108–109. Whitcomb, Exline, Hunter 1963: 656. Whitcomb and Bell 1964: 45. Dorris 1965: 408; 1968: 36. Drew 1967: 194. Harrison 1969: 14–16. Bultman, Uetz, Brady 1982: 26.

Leimonia (part) Simon 1864: 352.

Trochosa (part) Montgomery 1904: 301, 305. Chamberlin and Ivie 1942: 35.

Avicosa (part) Roewer 1954: 236.

Hogna (part) Roewer 1954: 258.

Scaptocosa (part) Roewer 1954: 293.

Varacosa (part) Roewer 1954: 306.

Alopecosa (part) Bonnet 1955: 248.

Type species. *Gladicosa gulosa* (Walckenaer)

Etymology. The generic name is a combination of *gladius* (Latin for sword) referring to the unique sword-shaped embolus of the male palpus, and *cosa* derived from the generic name *Lycosa.* It is considered feminine.

Diagnosis. *Gladicosa* may be distinguished from other lycosid genera by the following combination of characters: (1) the swordlike or bladelike form of the embolus (em) and its clockwise orientation in ventral view of the left palpus of the male (Fig. 33), (2) the modification of the terminal apophysis (ta), which is also broadly flattened and parallels (and partly supports) the embolus (Figs. 33, 34), (3) the rectangular or wedge shape of the transverse piece (tp) of the scape of the epigynum, together with its white pearlescent appearance, in whole or part (Fig. 10) and (4) the dorsal color pattern illustrated in Figures 1–5 and described below.

Description. Total length 7.8 to 18.8 mm. Carapace length 4.2 to 8.3 mm; width 3.1 to 6.4 mm. Carapace viewed dorsally, narrowing at level of PLE row, smoothly convex along lateral margins, with posterior margin concave; viewed laterally essentially the same height from eye region to posterior declivity (highest point is posterior cephalic region in front of dorsal groove with the carapace sloping very slightly anteriorly). Dorsal groove long and distinct. Dorsal color pattern with light uneven submarginal stripes and wide median light colored stripe, narrow between ALE, widening until just anterior to dorsal groove (where it is usually constricted), becoming wider again parallel to groove, and then narrowing as it

follows thoracic declivity to posterior edge of carapace. Black markings framing median stripe at posterior declivity. Dark areas of carapace brown to dark brown and black. Light stripes pale yellow to yellow-orange (Figs. 1–5).

Anterior median eyes (AME) slightly larger than anterior lateral eyes (ALE). Anterior eye row much narrower than posterior median eye row (PME), with dorsal tangent slightly procurved. Posterior lateral eye row (PLE) much the widest (see *Tables 1–6*).

Chelicerae dark reddish brown to black; anterior and posterior margin each with three teeth, the anterior triad crowded more closely together.

Legs when compared to body dimensions relatively longer than in *Trochosa;* without distinct annulations; yellow, yellow-orange to golden brown in color. Order of leg length IV-I-II-III. Tibial spination in female: leg I, 2-2-2 ventral, 1-0 or 1-1 prolateral; leg II 2-2-2 ventral, 1-1 prolateral; leg III 2-2-2 ventral, 1-1 prolateral, 1-1 retrolateral, 1-1 dorsal; leg IV 2-2-2 ventral, 1-1 prolateral, 1-1 retrolateral, 1-1 dorsal. Tibial spination in the male is the same with the addition on leg I of 1-1 retrolateral and leg II 1-1 retrolateral.

Dorsal abdominal pattern variable according to size and hirsuteness, but generally with anterio-lateral black markings aligned with those on carapace, cardiac area well marked, and often with pattern of chevrons as indicated in Figures 1–5. Dark colors on dorsum of abdomen brown to black, lighter colors cream to tan or beige. Venter of abdomen cream to light brown in *gulosa, huberti,* and *euepigynata;* dark brown to black in *pulchra* and *bellamyi.* Region anterior to epigastric furrow of contrasting darker or lighter color respectively.

Male palpus with stridulatory file situated retrolaterally at tip of tibia. Cymbium with cluster of macrosetae at tip, and with stridulatory scraper retrolaterally at base. Male palpal sclerites as seen in ventral view: Palea (pa) concave, largely hidden by embolus, visible along retrolateral margin. Embolus (em) blade-like, tapering to a point, with clockwise orientation (from left to right) in left palpus, which is opposite to that of most Lycosinae. Conductor (co) concave, with cuplike portion containing tips of the terminal apophysis (ta) and the embolus. Terminal apophysis large, flattened and paralleling embolus, with its tip serving partly as a conductor. Median apophysis (ma) with a flattened ridge extending retrolaterally and

coming to a point near margin of cymbium (cy); heavily sclerotized spur directed medially (Figs. 30, 33, 34).

Epigynum of female with scape shovel-shaped with elongate longitudinal piece (lp) (handle) and rectangular or trapezoidal transverse piece (tp) (blade). The transverse piece is unusual in being wholly or partly translucent white or pearlescent in appearance (Fig. 10). Spermathecae (s) smooth and round to ovoid (Fig. 7), rarely elongate ovoid (Fig. 15); usually their diameter apart.

Methods

The techniques and methods employed in the study of *Gladicosa* were essentially the same as for *Trochosa* (Brady 1979) and are described there. Color descriptions are based upon appearance of specimens in alcohol illuminated by microscope lamp. Measurements are listed in millimeters, but for *Gladicosa* the mean and standard error (SEM) are listed instead of the mean and range as in the previous paper. Methods and techniques of measurement are described in the paper on *Trochosa* (Brady 1979). Under *Records* specific localities are given for uncommon species and the peripheral range for common species, otherwise localities of specimens examined are indicated by counties.

Acknowledgments

This study was made possible by the loan of large numbers of specimens from the Museum of Comparative Zoology, Cambridge, Massachusetts, the American Museum of Natural History, New York City, and the Canadian National Collection, Ottawa, Canada. I wish to thank sincerely the curators of those collections, Dr. H. W. Levi, Dr. N. J. Platnick, and Dr. C. D. Dondale respectively for the use of these materials. The loan of type specimens from the Museum of Comparative Zoology, the American Museum and the Philadelphia Academy of Natural History is gratefully acknowledged. Thanks are offered to Mr. Donald Azum for loan of the latter.

I am indebted to the following individuals and institutions for making available regional collections that provided a much better picture of geographical distribution and clarified the relationships of certain populations: Dr. Richard Brown and Ms. Pat Miller of the Entomological Museum, Mississippi State University; Mr. Tim

Lockley, Deta State Research Center, USDA, Stoneville, Mississippi; Dr. G. B. Edwards and Dr. H. K. Wallace of the University of Florida, Gainesville; and Dr. Andrew Penniman, Defiance College, Defiance, Ohio.

Special thanks are extended to Dr. C. D. Dondale and Dr. H. W. Levi who consented to review the manuscript and offered constructive criticism and friendly advice. I am also grateful to Mr. F. R. Wanless for sending specimens of *Lycosa pulchra* Keyserling from the L. Koch collection maintained in the British Museum (Natural History). A note of special appreciation to Ms. Amy Youatt, who helped with general sorting, compilation of locality data, and preparation of distribution maps.

National Science Foundation grant DEB-7803561 assisted in defraying expenses of the investigation. A summer grant from the faculty development program at Hope College (1980) helped to initiate this project.

Key to Females

1a Transverse piece (tp) of scape of epigynum rectangular, about equal in length and width (Figs. 6–14) 2

1b Transverse piece (tp) of scape of epigynum irregular in shape (Figs. 15–17) or, if rectangular, much wider than long (Figs. 18–26) 3

2a Transverse piece entirely pearlescent in appearance. Longitudinal piece (lp) lacking indentations where it joins transverse piece (Figs. 6–9) ..... *gulosa*

2b Transverse piece only partly pearlescent white. Longitudinal piece (lp) with indentations at posterior end where it joins transverse piece (Figs. 10–14) ..... *pulchra*

3a Transverse piece irregular in shape and broadly joined by longitudinal piece (Figs. 15–17) ..... *euepigynata*

3b Transverse piece somewhat rectangular, much wider than long and narrowly joined by longitudinal piece 4

4a Width of transverse piece greater than length of longitudinal piece. Longitudinal piece about the same width throughout its length (Figs. 18–20) ..... *huberti*

4b Width of transverse piece equal to or less than length of transverse piece. Longitudinal piece wider anteriorly, narrowing posteriorly (Figs. 21–26) ..... *bellamyi*

Key to Males

1a Both embolus (em) and terminal apophysis (ta) bladelike, paralleling one another with each separate and drawn out to a point (Figs. 27, 28, 35–42) 3

1b Embolus bladelike, but terminal apophysis not resembling it; the two not as distinctly separated as above (Figs. 29–34, 43–46) 2

2a Relatively small species. Total length 7.8 to 11.0 mm (Figs. 29–34). Not reported from central Texas ..... *bellamyi*

2b Relatively large species. Total length 10.4 to 13.9 mm (Figs. 43–46). Distribution central Texas ..... *euepigynata*

3a Embolus with relatively short, pointed tip (Figs. 27, 28) ..... *huberti*

3b Embolus with longer drawn out tip that is curved at end 4

4a Tip of embolus pointed; median apophysis (ma) with large retrolateral spur (Figs. 35–36) ..... *gulosa*

4b Tip of embolus flattened; median apophysis (ma) with small retrolateral spur (Figs. 37–42) ..... *pulchra*

Gladicosa gulosa (Walckenaer), comb. nov.

Figures 5, 6–9, 35, 36. Map 1.

Lycosa gulosa Walckenaer, 1837: 338. Male holotype from North America, destroyed. Marx 1890: 562. Chamberlin 1908: 225, 226, 265, pl. 21, figs. 4, 7, ♂ ♀. Montgomery 1909: 514. Petrunkevitch 1911: 560. Comstock 1913: 631, 639, figs. 720 g–h, ♀ ♂; 1940: 644, 650, figs. 720 g–h, ♀ ♂. Bishop and Crosby 1926: 207. Wood 1926: 174. Crosby and Bishop 1928: 1067. Elliott 1930: 5; 1932: 423. Worley and Pickwell 1931: 91, 93. Chickering 1932: 351. Gertsch 1934: 7; 1949: 82. Gertsch and Wallace 1935: 20. Kaston 1935: 191; 1936: 103, 114; 1938: 184; 1948: 322, 328, pl. 57, figs. 1106–1109, ♀ ♂; 1981: 322, 328, figs. 1106–1109, ♀ ♂. Allard 1936: 67. Fitch 1963: 108–109, fig. 46. Whitcomb, Exline, Hunter 1963: 656. Whitcomb and Bell 1964: 45. Dorris 1965: 408; 1968: 36. Drew 1967: 194. Harrison 1969: 14–16. Bultman, Uetz, Brady 1982: 26.

Leimonia gulosa: Simon 1864: 352.

Lycosa kochi: Emerton 1885: 485, pl. 46, figs. 6–6c, ♀ ♂; 1902: 74, figs. 179, 180, ♀. Stone 1890: 423, 426, pl. 15, fig. 3. Marx 1892: 160. Gertsch and Wallace 1935: 21, figs. 39, 42, ♂ ♀. Not *Lycosa kochi* Keyserling.

Lycosa helluo: Banks 1901: 184 (part).

Lycosa nigraurata Montgomery, 1902: 538, 546, pl. 30, fig. 53, ♂. Male holotype from Medford, Burlington Co., New Jersey (N.J. Stone), examined. Synonymized with *Lycosa purcelli* Montgomery by Montgomery 1904: 305.

Lycosa purcelli Montgomery, 1902: 538, 566, pl. 30, figs. 30, 31, ♀ ♂. Female syntype from Philadelphia, Philadelphia Co., Pennsylvania, May, 1888, and

male syntype from Point Pleasant, Ocean Co., New Jersey, 30 April 1889 (N.J. Stone), examined. Synonymized with *Lycosa kochi:* Emerton by Gertsch and Wallace 1935: 21.

Trochosa purcelli, Montgomery, 1904: 301, 305.

Lycosa pulchra: Chamberlin 1904: 147 (part); Banks 1910: 57 (part).

Varacosa gulosa: Roewer 1954: 306.

Alopecosa gulosa: Bonnet 1955: 248.

Discussion. The nomenclatural history of *G. gulosa* is complex. Walckenaer's (1837) seven-line description without figures is not diagnostic for this species. The locality given is North America, and that doesn't help. To complicate matters, Emerton (1885) misidentified this species as *Tarentula kochi* Keyserling and transferred it to the genus *Lycosa.* Gertsch and Wallace (1935) discussed the systematic and nomenclatural problems associated with *G. gulosa* and suggested using the name *Lycosa kochi* Emerton for this species since Emerton (1885) had placed the species in a different genus. However, according to Article 49 of the International Code of Zoological Nomenclature (1985): "A previously established species-group name wrongly used to denote a species-group taxon because of misidentification cannot be used for that taxon even if it and the taxon to which the name correctly applies are in, or are later assigned to, different genera, except when a previous misidentifcation is deliberately used in fixing the type species of a new nominal genus." Bonnet (1955) points out that the name *nigraurata* or *purecelli* of Montgomery should have been used for the species. Montgomery (1904) himself synonymized *nigraurata* with *purcelli* and the name *purcelli* has been used only by Montgomery (1902, 1904). The name *gulosa,* on the other hand, has been employed numerous times since Gertsch and Wallace's (1935) invocation of *kochi,* and even by Gertsch (1949) in his book *American Spiders.* It therefore seems best to retain the name *gulosa* for this species to promote stability of nomenclature by preserving a long accepted name in its accustomed meaning.

Color. Females. Face yellow or yellow-orange, to pale golden brown. Eye region darker with nacelles black. Chelicerae yellowish brown to dark reddish brown, almost black at distal ends. Condyles yellow or orange, to golden brown.

Carapace light brown to brown, with broad yellow to yellow-orange median stripe. Narrow irregular submarginal yellow stripes suffused with brown. Posterior declivity with black patches as in Figure 3.

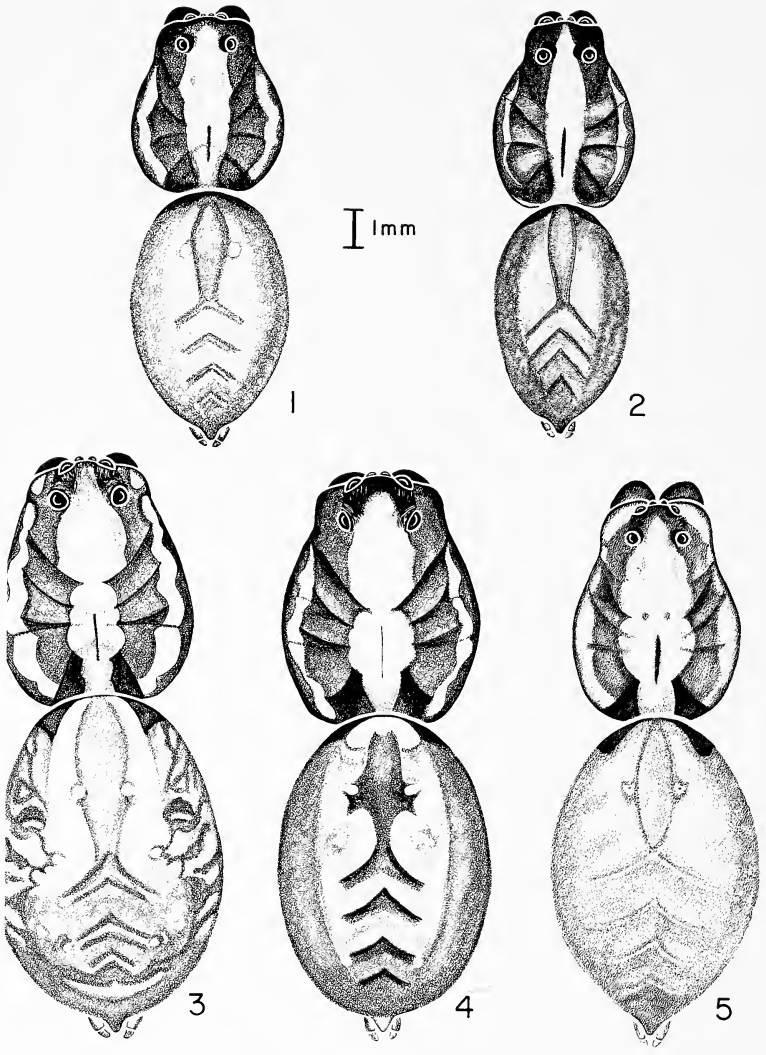


Fig. 1. *Gladicosa huberti* (Chamberlin), female from Bar M Ranch near Boston, Thomas Co., Georgia, 2 Mar. 1973. Fig. 2. *Gladicosa bellamyi* (Gertsch and Wallace), female from 2 mi. N of Stoneville, Washington Co., Mississippi, 9–11 May 1983. Fig. 3. *Gladicosa pulchra* (Keyserling), female from Gainesville, Alachua Co., Florida, 14 June 1935. Fig. 4. *Gladicosa gulosa* (Walckenaer), female from 4 mi. S of New Richmond, Allegan Co., Michigan, 16 Sept. 1974. Fig. 5. *Gladicosa euepigynata* (Montgomery), Camp Verde, Kerr Co., Texas, Dec. 1939.

Dorsum of abdomen light brown to brown with pair of black anterior-lateral patches as in Figure 5. Anterior cream to yellow spots mark depressions of internal muscle attachments. Cardiac area faintly indicated. Venter of abdomen cream or light beige to pale yellowish brown. Few scattered darker spots. Overlaid with fine coat of white hair.

Legs yellow or pale yellow-orange to yellowish brown, darker distally. Femora with dusky bands on dorsal and lateral surfaces. Ventral surface lighter yellow.

Labium and endites brownish orange to brown with distal ends yellow to cream. Sternum yellow to light golden brown.

Color. Males. Face yellow to yellow-orange, darker brownish in eye region. Chelicerae with basal areas yellow to orange-yellow, darker brown to reddish brown distally. Condyles orange-yellow to orange. Cymbia of palpi dark brown.

Carapace brown with a broad median yellow stripe and irregular yellowish submarginal stripes obscured by thicker clothing of white hair.

Dorsum of abdomen beige to light brown with black markings along sides beginning anteriorly and continuing posteriorly. Black markings often more prominent than in female. Posterior of dorsum without distinct chevrons as in other species. Venter of abdomen pale yellow to beige, clothed with white hair which is more abundant laterally.

Legs yellow to brownish yellow. Darker dorsally without dusky markings on femora as in female.

Labium and endites orange-yellow to orange-brown with distal ends lighter yellow to beige. Sternum orange to orange-brown.

Measurements. Ten females and ten males from Allegan Co., Michigan. See Table 1.

Diagnosis. *Gladicosa gulosa* is closest to *G. pulchra* in size and coloration. The markings of *pulchra* offer greater contrast, and chevrons are usually visible on the dorsum of the female abdomen (compare Fig. 5 with Fig. 4). The epigyna of the females and the palpi of the males also resemble one another in appearance, but are distinctly different when compared in detail. The epigynum of *gulosa* has the transverse piece entirely pearlescent white, whereas *pulchra* has some white, but nearly always shows darker brown sclerotized areas on the transverse piece (compare Figs. 6, 8, 9 with Figs. 10, 11, 13, 14). In *gulosa* the embolus is pointed at the end, whereas that of *pulchra* is somewhat spatulate in shape (compare Figs. 35, 36 with Figs. 37, 38).

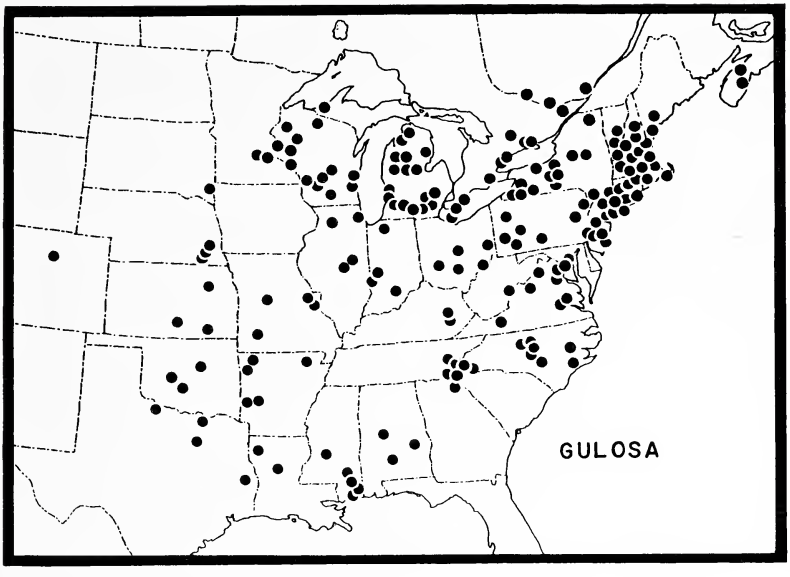
Table 1. Measurements of ten females and ten males of *Gladicosa gulosa* from Allegan Co., Michigan.

Females:	Mean SEM		Mean SEM
Ant. Eye Row	.985 ± .023	Femur I	4.26 ± .06
PME	1.218 ± .016	Pat.-Tibia I	5.50 ± .09
PLE	1.623 ± .020	Meta. I	3.13 ± .05
POQ	1.138 ± .015	Tarsus I	1.86 ± .03
Car. Width	4.36 ± .08	Total I	14.74 ± .22
Car. Length	5.88 ± .09	Femur IV	4.92 ± .08
Body Length	13.18 ± .49	Pat.-Tibia IV	5.77 ± .08
Pat.-Tibia II	4.96 ± .09	Meta. IV	5.40 ± .07
Pat.-Tibia III	4.37 ± .08	Tarsus IV	2.34 ± .02
		Total IV	18.44 ± .24

Males:	Mean SEM		Mean SEM
Ant. Eye Row	.900 ± .025	Femur I	4.13 ± .06
PME	1.141 ± .021	Pat.-Tibia	5.46 ± .09
PLE	1.503 ± .028	Meta. I	3.46 ± .06
POQ	1.049 ± .018	Tarsus I	1.89 ± .03
Car. Width	4.14 ± .06	Total I	14.93 ± .23
Car. Length	5.50 ± .12	Femur IV	4.63 ± .08
Body Length	11.46 ± .30	Pat.-Tibia IV	5.50 ± .10
Pat.-Tibia II	4.79 ± .08	Meta. IV	5.27 ± .08
Pat.-Tibia III	4.18 ± .07	Tarsus IV	2.33 ± .05
		Total IV	17.73 ± .30

Natural History. Kaston (1948) reports *gulosa* running over dead leaves on forest floors in Connecticut. I have found it in leaf litter of deciduous woods in Michigan. Here it is found in more open Oak woodlands as opposed to the shaded floor of Beech-Maple forests. In Michigan and New England *gulosa* usually matures late in the fall, overwinters as an adult, and mates in early spring. Kaston (1936) made the following observations of courtship behavior in the species:

> Immediately upon coming in contact with the female, or within 3 minutes thereof, the male begins to drum his palps rapidly against the floor of the cage. These drumming movements are made so rapidly that a distinct purring or humming sound can be heard. The palps are used alternately and are raised only a very short distance during the process. The body is held at an angle so that the posterior end of the abdomen almost touches the floor. As a consequence when the male begins to twitch his abdomen in a vertical plane the tip strikes



Map 1. Distribution of *G. gulosa.*

the floor. However, I could not detect any sounds made by this part of the body. It is highly probable that the vibrations set up in the substratum by the tapping movements of the palps and abdomen are perceived by the female. This may exert an exciting influence on her in a manner analogous to that which occurs in web-building species, where the male tweaks the threads of the female's snare.

The male now moves slowly toward the female without courting. When near her he reaches over to touch her. At first she may jump at him and chase him away. Later, if she is receptive she allows him to stroke her legs or abdomen. After this contact with the female the male resumes his courtship movements. Later on, if the male gets more excited he begins to raise his forelegs off the floor about 1 or 2 mm, and lower them quickly. During this process the legs quiver violently.

After 13 minutes of this courting one male began to mount the female, but before he could get into the final copulatory position, she ran away from him. Another male had courted only seven minutes when the female allowed him to mount. The position is the usual one for Lycosids, the male using his palps

alternately during the 10 minutes the act lasted. This duration time may not be the usual one for the species, however, for one pair were observed in the field, when collected, which were already *in copula* and remained so for about another half hour.

The sound produced during courtship was also reported by Allard (1936). Observations were made on a collecting trip in the Bull Run Mountains of Virginia during late April. He described the sound as a distinct purring produced by drumming rapidly upon dry leaf surfaces. He reports:

> The creatures were very wary, but with care I was able to examine their movements critically from a distance of only a few inches. When the spider moved and made its sounds, the fore part of the body quivered perceptibly and the palpi, too, executed gentle up and down movements. The quivering movements brought the chelicerae directly in contact with the dry leaf surface, and the latter alone appeared to be responsible for the rather loud sounds I had heard.

According to Allard these tapping sounds could be heard a distance of 10 feet or more.

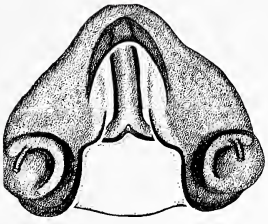
Rovner (1975) investigated sound production in three species of *Schizocosa* and six species of *Lycosa,* including *gulosa.* Previous investigators, as with *gulosa* above, had regarded such sounds as being solely percussive, generally produced by a tapping or scraping of the palps or the chelicerae against the substratum. High-speed

---

Figs. 6–9. *Gladicosa gulosa* (Walckenaer) 6–7. Female from 4 mi. S of New Richmond, Allegan Co., Michigan, 16 Sept. 1974. 6. Epigynum. 7. Internal genitalia. 8. Epigynum of female from Pepperell, Middlesex Co., Massachusetts, Apr. 1973. 9. Epigynum of female from Cove Creek Valley, 15 mi. S of Prairie Grove, Washington Co., Arkansas.

Figs. 10–14. *Gladicosa pulchra* (Keyserling). 10. Epigynum of female from Stone Co., Mississippi, 21 Dec. 1964. 11. Epigynum of syntype from North America. 12–13. Female from Gainesville, Alachua Co., Florida, 14 June 1935. 12. Internal genitalia. 13. Epigynum. 14. Epigynum of holotype of *Lycosa insopita* Montgomery [= *Gladicosa pulchra* (Keyserling)] from Austin, Travis Co., Texas.

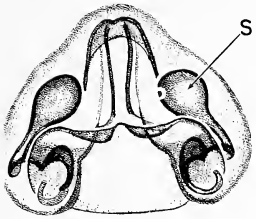
Figs. 15–17. *Gladicosa euepigynata* (Montgomery). 15–16. Female from Camp Verde, Kerr Co., Texas, Dec. 1939. 15. Internal genitalia. 16. Epigynum. 17. Epigynum of holotype of *Lycosa euepigynata* Montgomery [= *Gladicosa euepigynata* (Keyserling)] from Austin, Travis Co., Texas. lp, longitudinal piece of scape; s, seminal receptacle; tp, trnasverse piece of scape.



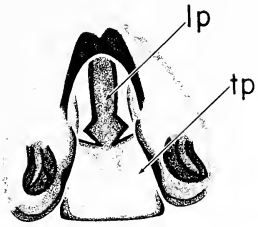
6

8

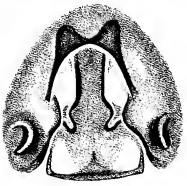
9



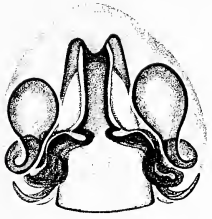
7



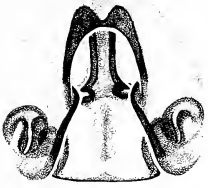
10



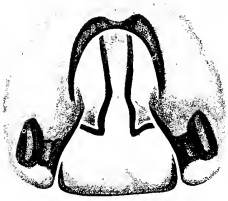
11



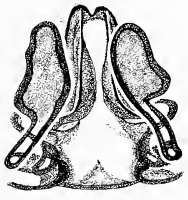
12



13

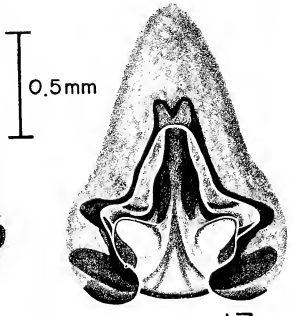


14



15

16



17

film analysis by Rovner (1975) revealed the prescence of a stridulatory organ at the tibio-tarsal joint. This apparatus consists of a file on the distal end of the tibia and a scraper at the base of the palpal cymbium. Further examination revealed a group of stout spines or macrosetae at the tip of the palpal tarsus. These spines apparently aid in coupling the tarsus to the substratum. Thus, the sound produced by *gulosa* ©and other lycosids is not generated simply by drumming, but involves a rapid oscillation at the tibio-tarsal joint facilitated by macrosetae that anchor the palpus to the substratum.

Kaston (1948) reports seeing mature females of *gulosa* from September, through winter, to June suggesting that some may live for two years. Egg sacs appear in early April and are produced until late May. Egg sacs vary from 6–10 mm in diameter and egg counts range from 118–274, each egg about 1 mm in diameter.

Distribution. From southern Canada in the northeast to eastern Texas in the southwest. Not recorded from Florida and a single specimen from Colorado (Map 1).

Records. CANADA. *Nova Scotia.* Bridgewater; Kentville. *Quebec.* Ft. Coulonge; King Mtn., Gatineau National Park; Ste. Rose. *Ontario.* Arnprior; Belleville; Chatterton; Haliburton; Marmora; Mazinaw Lake; Ottawa; Pelee Island; Port Credit; Rondeau Provincial Park; Simcoe; Toronto.

UNITED STATES. *Maine.* Androscoggin Co.: Poland Spring, 15 June 1904, ♀ (J. H. Emerton); York Co.: Wells, 12 Aug. 1933 (W. Ivie). *New Hampshire.* Belknap; Carroll; Cheshire; Hillsboro; Sullivan. *Vermont.* Caledonia; Windham; Windsor. *Massachusetts.* Barnstable; Berkshire; Essex; Franklin; Hampden; Middlesex; Norfolk; Worcester. *Connecticut.* Providence; Fairfield; Litchfield; Middlesex; New Haven; Windham. *New York.* Allegany; Cattaraugus; Courtland; Essex; Fulton; Monroe; Nassau; Oneida; Onondaga; Queens; Richmond; Rockland; Steuben; Suffolk; Sullivan; Tompkins; Westchester; Wyoming. *New Jersey.* Bergen; Burlington; Camden; Mercer; Ocean; Union. *Pennsylvania.* Butler; Cambria; Carbon; Mifflin; Philadelphia; Pike; Venango; Westmoreland. *Ohio.* Champaign; Columbiana; Hocking; Knox; Ottawa; Washington. *Maryland.* Anne Arundel; Baltimore City; Montgomery. *District of Columbia.* Washington. *West Virginia.* Pocahontas. *Virginia.* Fairfax; Falls Church (Indep. City); King William;

Montgomery; Prince Edward; Richmond (Indep. City); Rockingham; Shenandoah. *Kentucky.* Breathitt; Wolfe. *Tennessee.* Sevier. *North Carolina.* Beaufort; Buncombe; Chatham; Cherokee; Durham; Hartnett; Haywood; Henderson; Jones; Lee; Macon; Onslow; Orange; Swain; Transylvania; Wake. *Georgia.* Rabun. *Alabama.* Bibb; Butler; Lee. *Mississippi.* Forrest; George; Hinds; Jackson; Perry. *Louisiana.* Caddo; Grant. *Michigan.* Allegan; Barry; Calhoun; Charlevoix; Cheboygan; Clare; Iosco; Jackson; Lake; Livingston; Midland; Oakland; Ontonagon; Osceola; Ottawa; Roscommon; Washtenaw; Wexford. *Indiana.* Jackson; LaPorte; Parke; Vermillion. *Wisconsin.* Adams; Buffalo; Chippewa; Dane; Ozaukee; Polk; Rusk; Sauk; Sheboygan; Vernon; Velas; Washburn; Waushara. *Illinois.* Champaign; Cook; Ogle; Piatt; Shaunee. *Minnesota.* Hennepin; Ramsey. *Missouri.* Boone; Greene; St. Charles; St. Louis City. *Arkansas.* Carroll; Lawrence; Montgomery; Polk; Washington. *South Dakota.* Lincoln Co.: Newton Hills St. Pk., 6 mi. SSE of Canton, 9 June 1957, ♀ (T. J. Cohn). *Nebraska.* Jefferson Co.: Fairbury, 1 May 1957, ♀ (W. F. Rapp, Jr.); Lancaster Co.: Lincoln, 1941, ♂♂♀ (M. J. Harbaugh); Saline Co.: Crete, 12 Sept. 1948, ♀ (J. & W. Rapp). *Kansas.* Cowley Co.: Winfield, ♀♀; Kingman Co.: Kingman Co. St. Pk. near Calista, 13 Oct. 1963, ♂:3♀♀ (J. & W. Ivie); Riley Co.: Manhattan, ♂♂♀ (N. Banks), Apr. 1903, ♀ (T. H. Sheffer). *Oklahoma.* Canadian Co.: Yukon, 10 Sept., 3♂♂:♀♀ (N. M. Newport); Cleveland Co.: Norman, ♂♂♀ (J. H. Emerton); Creek Co.: Drumright, 26 Feb. 1927, ♀ (Byers). *Texas.* Dallas Co.: Dallas, 28 Jan. 1954, ♂ (E. E. Gilbert), White Rock Creek, 13 Dec. 1934, ♀ (N. E. Vickery & S. Jones); Grayson Co.: 6 mi. N of Denison, 20 Oct. 1963, ♀ (K. W. Haller); Jasper Co.: Jasper, 26 Jan. 1962, ♂♂ (High School Sci. Club); Wichita Co.: Burkburnett, 12 Oct. 1964, ♂:4♀♀ (K. W. Haller). *Colorado.* Bluebell Canvon near Boulder, 23 Oct. 1944, ♀ (R. E. Gregg).

Gladicosa pulchra (Keyserling), comb. nov.
Figures 4, 10–14, 37–42. Map 2.

Tarentula pulchra Keyserling, 1877: 628, pl. 7, figs. 13, 14, ♂♀. Syntypes (♂♀) from "North America," L. Koch collection, deposited in the British Museum (Natural History), examined. Banks 1893: 124.

Lycosa pulchra: Montgomery 1904: 277. Banks 1910: 57; 1911: 454. Banks, Newport, and Bird 1932: 31. Gertsch 1934: 8. Gertsch and Wallace 1935: 21, figs. 38, 41, ♂♀. Jones 1936: 69.

Lycosa gulosa: Chamberlin 1908: 265 (part).

Lycosa insopita Montgomery, 1904: 278, 280, figs. 3, 4, ♂♀. Syntypes (♂♀) from Austin, Travis Co., Texas, deposited in the American Museum of Natural History, examined; 1905: 174; 1909: 514. Petrunkevitch 1911: 560. First synonymy with *Lycosa pulchra* by Gertsch 1934.

Scaptocosa pulchra: Roewer 1954: 293.

Alopecosa pulchra: Bonnet 1955: 256.

Discussion. Montgomery (1904) described this species under *Lycosa insopita.* He apparently did not have the Keyserling syntypes for comparison. Gertsch (1934) was the first to recognize the synonymy.

Color. The range of color in *G. pulchra* is greater than that of *G. gulosa.* I have noted light forms and dark forms of *pulchra.* These do not represent a genetic polymorphism but are the extremes in a color continuum. There is no discernible correlation between geographic locality and color pattern among the specimens examined. The darker forms are much more numerous than the light colored ones. The range of color is indicated in the following descriptions.

Color. Female. Face orange-brown to dark reddish brown. Chelicerae dark reddish brown to black with condyles lighter orange-brown.

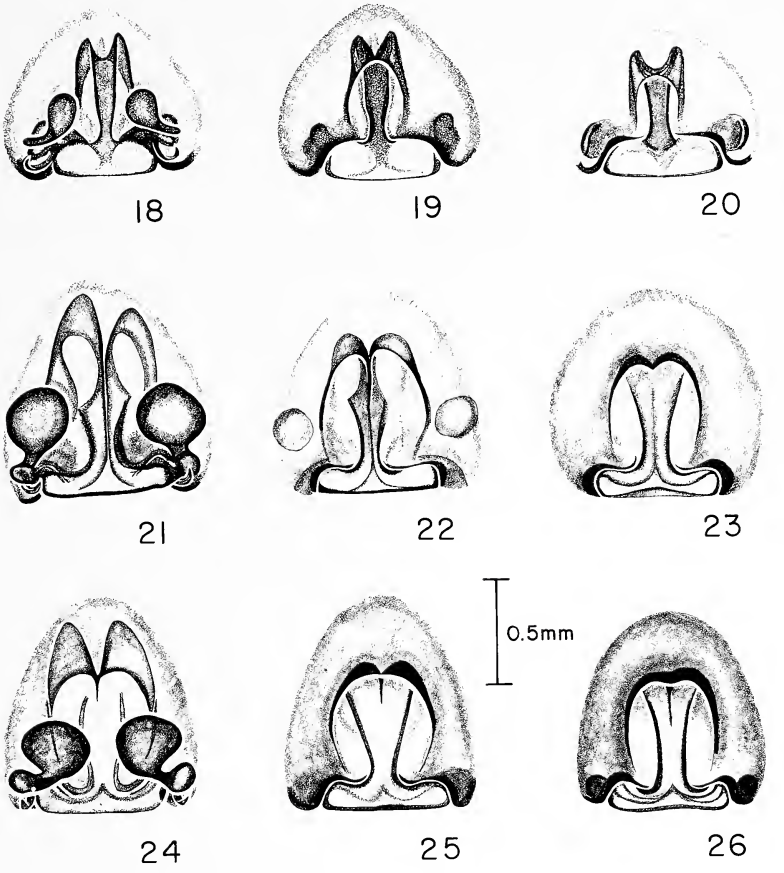
Carapace dark brown to a dark reddish brown with a broad median yellow stripe suffused with white hair. Irregular lighter submarginal yellow stripes similarly clothed with white hair. Pattern as in Figure 4.

Dorsum of abdomen brown to brown mottled with black. Anterio-lateral areas black, blending with similar black areas on cephalothorax. Five pairs of white spots (in well-marked specimens) beginning in cardiac area and continuing posteriad. White spots connected by dark brown chevrons as in Figure 4. Cardiac area darker brown, outlined by lighter brown or yellowish.

Venter of abdomen dark brown to almost black posterior to epigastric furrow. Yellowish anterior to furrow.

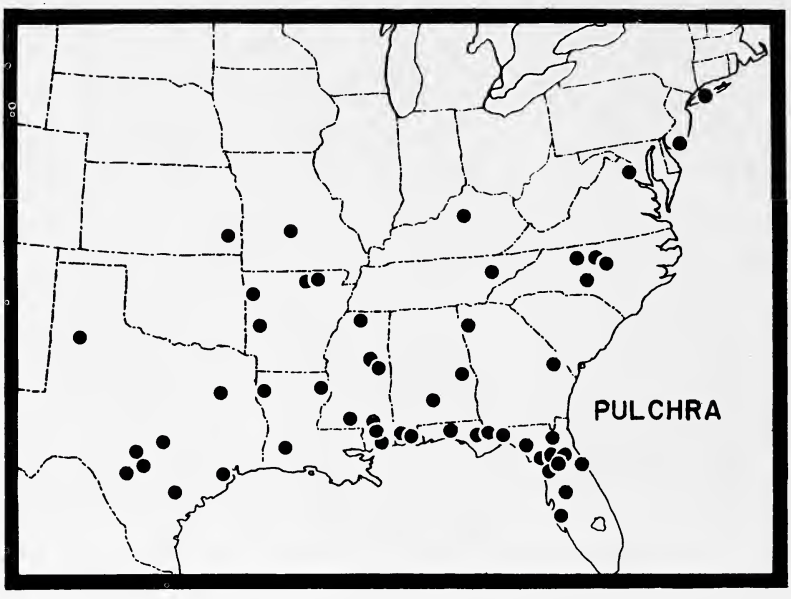
Legs light brown with darker black annulations on femora to dark reddish brown without distinct annulations.

Labium and endites light brown to black with pale yellowish distal ends. Sternum yellow brown (golden), dark reddish brown to black.



Figs. 18–20. *Gladicosa huberti* (Chamberlin). 18–19. Female from Bar M Ranch near Boston, Thomas Co., Georgia, 2 Mar. 1973. 18. Internal genitalia. 19. Epigynum. 20. Epigynum of female from Welaka Reserve, Putnam Co., Florida, 11 Nov. 1972.,

Figs. 21–26. *Gladicosa bellamyi* (Gertsch and Wallace). 21–22. Holotype female from Liberty Co., Florida, 12 Apr. 1935. 21. Internal genitalia. 22. Epigynum. 23. Epigynum of holotype of *Trochosa cherokee* Chamberlin and Ivie, [= *Gladicosa bellamyi* (Gertsch and Wallace)]. Ft. Gibson, Muskogee Co., Oklahoma, 21 July 1937. 24–26. Females from 2 mi. N of Stoneville, Washington Co., Mississippi. Internal genitalia. 25. Epigynum. 26. Epigynum.



Map 2. Distribution of *G. pulchra.*

Color. Male. Face yellow-orange to orange-brown. Dark in ocular area. Chelicerae brownish orange to dark reddish brown. Cymbia of palpi yellow-orange to dark reddish brown.

Carapace orange-brown to dark orange-brown with broad yellow to pale orange median stripe overlaid with white hair. Irregular submarginal stripes of same color, sometimes indistinct.

Dorsum of abdomen with median area light to medium brown, bordered by black. Five pairs of white spots beginning in cardiac area and continuing posteriad. Spots joined by black chevrons. Cardiac area brown, enclosed by lighter pale brown to yellow-brown. Pattern similar to female. Venter of abdomen brown to black posterior to epigastric furrow. Light brown to pale yellow or cream anterior to furrow.

Labium and endites yellow-orange to orange with distal ends cream. Sternum yellow-orange to orange.

Measurements. Ten females and ten males from Florida. See Table 2.

Diagnosis. Gladicosa pulchra is closest to *G. gulosa* in size, coloration, and genitalic structure. *Gladicosa pulchra* is a larger species

than *gulosa* (compare Table 1 with Table 2) and is usually darker in color with a more distinct pattern (compare Fig. 4 with Fig. 3). In most specimens of *pulchra* the venter of the abdomen is dark brown to black behind the epigastric furrow, while that of *gulosa* is yellowish to light brown. Differences between female and male genitalia of these two species are noted under *gulosa* and in the keys.

Natural History. Little is known of the habitat or behavior of *pulchra.* I've collected this species in Florida from the trunks of deciduous trees where their color blends well with the bark substrate. G. B. Edwards (personal communication) has collected specimens from similar microhabitats in Florida. Pat Miller (personal communication) reported collecting both male and female *pulchra* from the trunks of pine trees at night in Perry, Florida, on December 5, 1982. Montgomery (1904) reported finding *pulchra* near Austin, Texas, in drier habitats than *gulosa* and less abundantly. He noted that the females live under stones where they make a shallow horizontal burrow lined with silk. Whether this behavior is consistent throughout the life cycle or represents a temporary adjustment to molting or egg laying is a question to be answered. *Gladicosa pulchra* is not the abundant inhabitant of deciduous leaf litter, as are *gulosa* and *huberti.* Of the species investigated *pulchra* is the most variable in coloration of the body and structure of the epigynum. It is possible that more than one species is represented in this complex.

Roble (1986) reported rearing *Mantispa viridis* from a *Gladicosa pulchra* egg sac. It is the first record of a lycosid spider serving as a host of *M. viridis.* When the spider died, its egg sac was opened and a mantispid cocoon and 95 surviving spiderlings were found. This corroborates an earlier observation of high spiderling survival within a mantispid-infested egg sac of *Lycosa rabida.*

Distribution. From Long Island, New York, along the East Coast to Texas in the southwest. Limited in its northern range inland to the southern parts of Kansas and Missouri and northern Kentucky. More abundant in the southeastern United States (Map 2).

Records. UNITED STATES. *New York.* Suffolk Co.: Coram, Long Island, 19 Oct. 1934, ♂ (E. L. Bell). *New Jersey.* Cape May Co.: Cape May, 29 Sept. 1945, ♂ (C. & M. Goodnight). *Virginia.* Alexandria (Indep. City); Falls Church (Indep. City); Fairfax. *Kentucky.* Woodford Co.: Kentucky River, 16 Sept. 1920, ♂. *Tennessee.*

Table 2. Measurements of ten females and ten males of *Gladicosa pulchra* from Florida.

Females:	Mean SEM		Mean SEM
Ant. Eye Row	1.304 ± .028	Femur I	5.46 ± .12
PME	1.734 ± .040	Pat.-Tibia I	7.23 ± .16
PLE	2.284 ± .052	Meta. I	4.23 ± .10
POQ	1.622 ± .036	Tarsus I	2.18 ± .05
Car. Width	5.50 ± .16	Total I	19.09 ± .43
Car. Length	7.23 ± .19	Femur IV	5.93 ± .14
Body Length	15.89 ± .56	Pat.-Tibia IV	7.36 ± .18
Pat.-Tibia II	6.75 ± .16	Meta. IV	6.75 ± .19
Pat.-Tibia III	5.88 ± .14	Tarsus IV	2.70 ± .07
		Total IV	22.73 ± .51

Males:	Mean SEM		Mean SEM
Ant. Eye Row	1.176 ± .022	Femur I	5.79 ± .11
PME	1.604 ± .032	Pat.-Tibia I	7.88 ± .19
PLE	2.044 ± .050	Meta. I	5.46 ± .15
POQ	1.514 ± .032	Tarsus I	2.47 ± .06
Car. Width	4.94 ± .14	Total I	21.59 ± .50
Car. Length	6.54 ± .18	Femur IV	6.19 ± .11
Body Length	12.35 ± .33	Pat.-Tibia IV	7.71 ± .16
Pat.-Tibia II	12.02 ± .17	Meta. IV	7.83 ± .18
Pat.-Tibia III	6.09 ± .16	Tarsus IV	2.95 ± .09
		Total IV	24.69 ± .51

Knox Co.: Knoxville, 8 Oct., ♀ (W. B. Cartwright). *North Carolina.* Alamance; Durham; Moore; Wake. *Georgia.* Floyd; Screven. *Florida.* Alachua; Baker; Citrus; Gadsden; Lake; Leon; Levy; Liberty; Marion; Oklaloosa; Putnam; Polk; Sarasota; Taylor, Volusia. *Alabama.* Baldwin; Butler; Lee; Mobile. *Mississippi.* Forrest; Jackson; Marshall; Noxubee; Oktibbeha; Pike; Stone. *Louisiana.* Caddo; Evangeline; Madison. *Missouri.* Pulaski Co.: Richland, 20 Apr. 1962, ♀ (W. Ivie). *Arkansas.* Lawrence; Montgomery; Sharp; Washington. *Kansas.* Bourbon Co.: Redfield, 14 Oct. 1963, ♀ (J. & W. Ivie). *Texas.* Bandera Co.: Dec. 1939, 3♀♀ (D. & S. Mulaik); Comal Co.: Hancock, 27 May 1948, ♀ with egg case (I. J. Anderson); DeWitt Co.: 16.4 mi. SE of Cuero, 23 Dec. 1955 (W. McAlister); Hale Co.: Wimberley, 1948, ♀ (Exline coll.); Harris Co.: Clear Lake near Seabrook, Sept. 1959, ♀ (J. C. Bequaert); Kerr Co.: Raven Ranch, Dec. 1939, ♂♂ : 10♀♀ (D. & S. Mulaik); Smith Co.: Tyler St. Pk., 12 Mar. 1982, ♀ (S. M. Roble); Travis Co.: Austin, ♂♀♀ (T. H. Montgomery).

Gladicosa huberti, comb. nov.
Figures 1, 18–20, 27, 28. Map 3.

Lycosa huberti Chamberlin, 1924: 28, pl. 6, fig. 44, ♀. Female holotype from Talisheek, St. Tammany Par., Louisiana, 4 March 1920 (H. E. Hubert), deposited in the Museum of Comparative Zoology, examined. Gertsch and Wallace 1935: 22, figs. 40, 43, ♂♀. Chamberlin and Ivie 1944: 144. Bonnet 1957: 2645.
Scaptocosa huberti: Roewer 1954: 293.

Discussion. *Gladicosa huberti* together with *G. pulchra* were placed in the genus *Scaptocosa* by Roewer (1954) with *Lycosa missouriensis* (Banks) [= *Geolycosa*] as the type species. Five other North American species now considered to be in *Geolycosa* and one species of *Schizocosa* were included in *Scaptocosa* as well. It is not clear what distinguishes this odd assemblage.

Color. Females. Face orange-brown to reddish brown with eye nacelles black. Chelicerae dark reddish brown (mahogany) to black. Condyles orange-brown.

Carapace orange-brown to reddish brown with broad median pale orange stripe from PME to posterior edge. Lighter irregular submarginal stripes less distinct than median. Pattern as in Figure 1.

Dorsum of abdomen brown to dark brown with cardiac area outlined in black. Chevrons faintly indicated along posterior half with white spots marking their lateral edges. Anterior lateral edges of dorsum darker as in Figure 1. Venter pale yellow-orange to darker brown. Lateral areas darker in pale-colored individuals, concolorous brown in others.

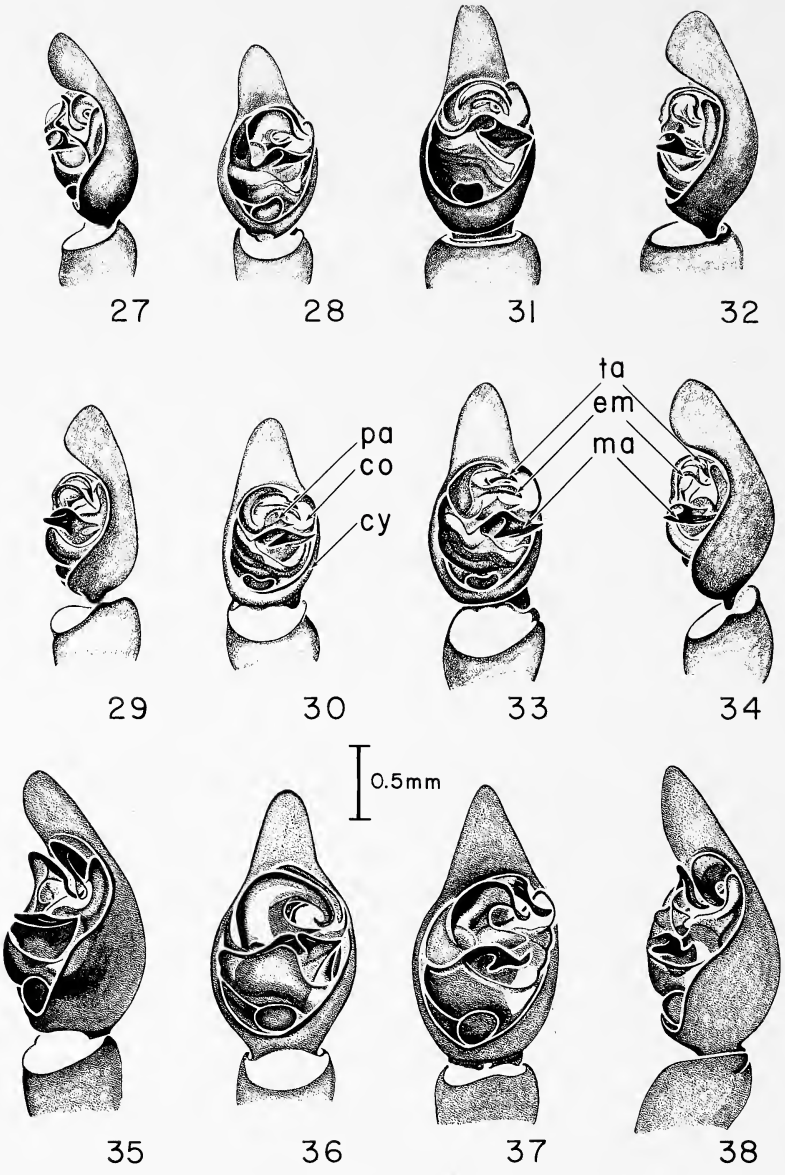
Legs yellow-orange to orange-brown, without darker annulations.

Labium and endites orange-brown to dark reddish brown, with distal ends yellowish to cream. Sternum yellow-orange to light orange-brown.

Color. Males. Face dark orange-brown to very dark reddish brown, eye region black. Chelicerae dark reddish brown to black. Condyles lighter. Cymbia of palpi dark red-brown.

Carapace orange-brown to darker reddish brown with light orange broad median stripe from eye region to posterior edge. Lighter, irregular submarginal stripes, not so distinct as median one.

Dorsum of abdomen medium to dark brown with cardiac area lighter, outlined by black line which is enclosed in turn with lighter color extending laterally. Anterior lateral areas marked by black color, which extends more posteriad than in female. Venter of


27
28
31
32
pa
co
cy
29
30
ta
em
ma
33
34
0.5mm
35
36
37
38

abdomen orange-brown to dark brown. Central area somewhat lighter.

Legs yellow-orange to orange-brown, somewhat lighter ventrally, without darker bands.

Labium and endites yellow-orange to dark reddish brown, with distal ends pale yellow to cream. Sternum yellow to reddish orange-brown.

Measurements. Ten females and ten males from Georgia and Florida.

Diagnosis. *Gladicosa huberti* is closest to *G. bellamyi* in body size and shape of the epigynum, but resembles *G. gulosa* in coloration and structure of the male palpus. *Gladicosa huberti* is lighter in color than *bellamyi* and smaller in size than *gulosa.* It may be distinguished from either of these species by comparing the epigynum (Figs. 19, 20) to *bellamyi* (Figs. 22, 23, 25, 26) or *gulosa* (Figs. 6, 8, 9) and the palpus (Figs. 27, 28) to *bellamyi* (Figs. 29–34) or *gulosa* (Figs. 35, 36).

Natural History. Nothing concerning the natural history of this species is reported in the literature. I have collected it in leaf litter near the edge of woods in Georgia and in a marshy area near the edge of a pond beneath a pine tree canopy in Florida. The great majority of the adult specimens were collected from February through April (see *Records* below).

Distribution. Southeastern United States (Map 3).

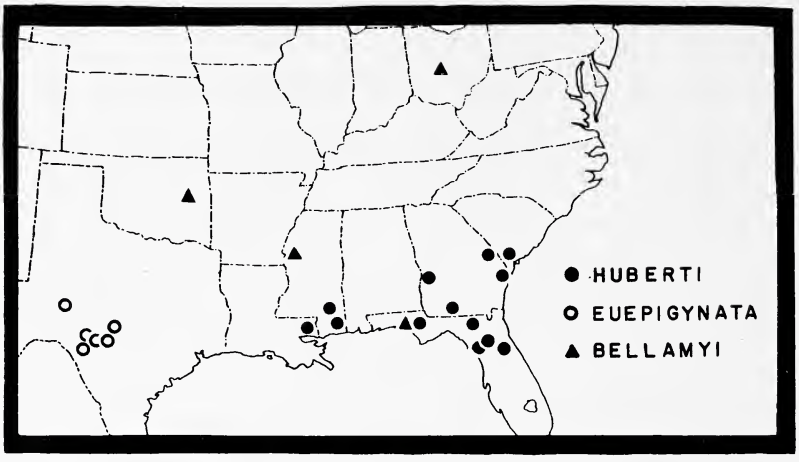
Records. *South Carolina.* Jasper Co.: Ridgeland, 28 Mar.–6 Apr. 1975, ♀ with egg case (D. Brody). *Georgia.* Chatham Co.: 8 mi.

Figs. 27–28. *Gladicosa huberti* (Chamberlin), left palpus of male from Bar M Ranch near Boston, Thomas Co., Georgia, 2 Mar. 1973. 27. Retrolateral view. 28. Ventral view.

Figs. 29–34. *Gladicosa bellamyi* (Gertsch and Wallace). 29–30. Male from Sharon Woods Metropolitan Park, Columbus, Franklin Co., Ohio 1–8 May 1973. 29. Left palpus, retrolateral view. 30. Left palpus, ventral view. 31–34. Males from 2 mi. N of Stoneville, Washington Co., Mississippi 9–31 May 1983. 31. Ventral view. 32. Retrolateral view. 33. Ventral view. 34. Retrolateral view.

Figs. 35–36. *Gladicosa gulosa* (Walckenaer), left palpus of male from 4 mi. S of New Richmond, Allegan Co., Michigan, 16 Sept. 1974. 35. Retrolateral view. 36. Ventral view.

Figs. 37–38. *Gladicosa pulchra* (Keyserling), left palpus of male syntype of *Lycosa pulchra* Keyserling from North America. 37. Ventral view. 38. Retrolateral view. co, conductor; cy, cymbium; em, embolus; ma, median apophysis; pa, palea; ta, terminal apophysis.



Map 3. Distribution of *G. huberti, euepigynata,* and *Bellamyi.*

W of Savannah, 5 Apr. 1943, ♀, 3 mi. SE of Savannah, 8 Apr. 1943, ♀ (W. Ivie); Chattahoochee Co.: Fort Benning, 31 Oct. 1943, ♀ (D. C. Beck); Screven Co.: 1 mi. N of Sylvania, 9 Apr. 1943, ♂, 2 mi. N of Sylvania, 11 Apr. 1943, ♀♀, 7 mi. N of Sylvania, ♀ (W. Ivie); Thomas Co.: Bar M Lodge near Boston, 2 Mar. 1973, ♂♂♀♀oo (A. R. Brady).

Florida. Alachua Co.: 6 Apr. 1935, ♀ with egg case, 26 Nov. 1936, ♂♀, 2–3 Feb. 1937, 4♂♂:4♀♀:o, 18 Feb. 1937, ♂♀♀, 6 Mar. 1937, ♀, 23–27 Apr. 1937, 7♀♀, 12 June 1937, 3♀♀, 20 Nov. 1938, ♀ (H. K. Wallace); Calhoun Co.: Blountstown, 28 Apr. 1935, ♀ (H. K. Wallace); Columbia Co.: 27 Apr. 1935, ♂:4♀♀ (H. K. Wallace), 3 Feb. 1938, ♀ (Beck); Levy Co.: 20 Apr. 1935, ♀ (H. K. Wallace); Putnam Co.: Welaka Reserve, 11 Nov. 1972, 3♂♂:♀♀ (A. R. Brady).

Mississippi. Forrest Co.: Camp Shelby near Hattiesburg, Oct.–Nov. 1943, ♀ (C. D. Michener); George Co.: Lucedale, Mar. 1930, ♀♀ (Dietrich).

Gladicosa bellamyi (Gertsch and Wallace) comb. nov.
Figures 2, 21–26, 29–34. Map 3.

Lycosa bellamyi Gertsch and Wallace, 1937: 10, fig. 14, ♀. Female holotype from Liberty Co., Florida, 12 April 1935 (H. K. Wallace) deposited in the American Museum of Natural History, examined. Chamberlin and Ivie 1944: 142. Bonnet 1957: 2635.

Trochosa cherokee Chamberlin and Ivie, 1942: 35, fig. 76, ♀. Female holotype from Fort Gibson, Muskogee Co., Oklahoma, 21 July 1937 (Standish-Kaiser) deposited in the American Museum of Natural History, examined. NEW SYNONYM.
Avicosa bellamyi: Roewer 1954: 236.

Discussion. *Gladicosa bellamyi* was placed in the new genus *Avicosa* by Roewer (1954) with *Avicosa avida* (Walckenaer) [= *Schizocosa*] as the type species. Two other North American species now placed in *Schizocosa* (*minnesotensis* and *wasatchensis* = *mccooki*) as well as *Lycosa ceratiola* and *Tarentula pictilis* (now *Alopecosa pictilis*) were also included in this new genus. *Avicosa* is certainly an artificial conglomeration without systematic foundation.

Table 3. Measurements of ten females and ten males of *Gladicosa huberti* from Georgia and Florida.

Females:	Mean SEM		Mean SEM
Ant. Eye Row	.959 ± .013	Femur I	3.63 ± .09
PME	1.138 ± .018	Pat.-Tibia I	4.68 ± .11
PLE	1.478 ± .025	Meta. I	2.56 ± .09
POQ	1.048 ± .019	Tarsus I	1.57 ± .03
Car. Width	3.84 ± .12	Total I	12.48 ± .32
Car. Length	5.09 ± .11	Femur IV	4.12 ± .09
Body Length	11.18 ± .46	Pat.-Tibia IV	5.03 ± .10
Pat.-Tibia II	4.27 ± .11	Meta. IV	4.53 ± .09
Pat.-Tibia III	3.68 ± .08	Tarsus IV	2.03 ± .03
		Total IV	15.70 ± .31

Males:	Mean SEM		Mean SEM
Ant. Eye Row	.861 ± .006	Femur I	3.62 ± .05
PME	1.061 ± .009	Pat.-Tibia	4.85 ± .06
PLE	1.364 ± .011	Meta. I	3.11 ± .04
POQ	.966 ± .010	Tarsus I	1.71 ± .03
Car. Width	3.60 ± .04	Total I	13.30 ± .17
Car. Length	4.81 ± .07	Femur IV	4.14 ± .06
Body Length	8.98 ± .17	Pat.-Tibia IV	4.96 ± .07
Pat.-Tibia II	4.32 ± .06	Meta. IV	4.61 ± .07
Pat.-Tibia III	3.67 ± .05	Tarsus IV	2.03 ± .03
		Total IV	15.73 ± .22

Color. Females. Face orange-brown to dark reddish brown. Chelicerae dark reddish brown to black. Condyles lighter yellowish.

Carapace dark brown to dark reddish brown with broad median yellow-orange to pale brownish orange stripe from PME to posterior declivity as in Figure 2. Indistinct submarginal stripes of same color.

Dorsum of abdomen pale yellow-brown to medium brown, often with darker brown cardiac mark and darker chevrons posteriorly as in Figure 2. Slight indication of black counter-shading anterio-laterally. Venter of abdomen dark brown posterior to epigastric furrow; median area sometimes mottled with light orange-brown. Lighter yellowish anterior to furrow.

Legs brown to dark brown dorsally. Pale yellowish brown to golden brown ventrally. Legs without distinct bands.

Labium and endites dark reddish brown to orange-brown with distal ends lighter golden to yellow.

Color. Males. Face dark red-brown. Eye region black. Chelicerae dark brown to black with inner distal margins lighter orange-brown. Condyles lighter orange to yellow. Cymbia of palpi brown to dark brown.

Carapace dark reddish brown overlaid with fine black hair. Broad median pale yellow-orange to orange-brown stripe from PME to posterior edge.

Dorsum of abdomen beige to light brown. Black countershading in anterio-lateral areas, extending posteriorly farther than in female. Indistinct chevrons posteriorly. In some specimens the median longitudinal area of the dorsum is pale yellow to cream with darker brown at edges and along sides. Venter of abdomen dark brown to black posterior to epigastric furrow, lighter yellowish brown anteriorly. Lateral areas often somewhat lighter in color.

Legs orange-brown to dark brown dorsally, paler golden to yellowish brown ventrally. Without darker bands. Tibia and metatarsus I black, tarsus yellow.

Table 4. Measurements of ten females and ten males of *Gladicosa bellamyi* from Ohio.

Females:	Mean SEM		Mean SEM
Ant. Eye Row	.891 ± .016	Femur I	3.39 ± .08
PME	1.135 ± .018	Pat.-Tibia I	4.46 ± .11
PLE	1.478 ± .024	Meta. I	2.47 ± .05
POQ	1.065 ± .015	Tarsus I	1.53 ± .03
Car. Width	3.66 ± .08	Total I	11.85 ± .26
Car. Length	4.86 ± .09	Femur IV	3.95 ± .09
Body Length	10.43 ± .27	Pat.-Tibia IV	4.86 ± .11
Pat.-Tibia II	4.05 ± .09	Meta. IV	4.51 ± .10
Pat.-Tibia III	3.49 ± .08	Tarsus IV	1.96 ± .04
		Total IV	15.28 ± .33

Males:	Mean SEM		Mean SEM
Ant. Eye Row	.839 ± .014	Femur I	3.31 ± .06
PME	1.071 ± .013	Pat.-Tibia I	4.59 ± .06
PLE	1.369 ± .019	Meta. I	2.79 ± .04
POQ	.993 ± .014	Tarsus I	1.62 ± .03
Car. Width	3.34 ± .05	Total I	12.30 ± .15
Car. Length	4.40 ± .06	Femur IV	3.73 ± .06
Body Length	8.56 ± .14	Pat.-Tibia IV	4.59 ± .06
Pat.-Tibia II	3.97 ± .05	Meta. IV	4.38 ± .07
Pat.-Tibia III	3.40 ± .04	Tarsus IV	1.98 ± .04
		Total IV	14.68 ± .17

Labium and endites orange-brown to dark brown with distal ends lighter yellow to golden. Sternum light orange-brown to darker reddish brown.

Measurements. Ten females and ten males from Ohio, and ten females from Mississippi. See Tables 4 and 5.

Table 5. Measurements of ten females of *Gladicosa bellamyi* from Mississippi.

	Mean SEM		Mean SEM
Ant. Eye Row	.925 ± .013	Femur I	4.23 ± .07
PME	1.216 ± .011	Pat.-Tibia I	5.73 ± .10
PLE	1.553 ± .021	Meta. I	3.54 ± .09
POQ	1.121 ± .009	Tarsus I	1.95 ± .03
Car. Width	4.15 ± .08	Total I	15.44 ± .26
Car. Length	5.32 ± .09	Femur IV	4.82 ± .08
Body Length	9.94 ± .19	Pat.-Tibia IV	5.91 ± .11
Pat.-Tibia II	5.04 ± .07	Meta. IV	5.61 ± .10
Pat.-Tibia III	4.33 ± .07	Tarsus IV	2.43 ± .04
		Total IV	18.75 ± .31

Diagnosis. *Gladicosa bellamyi* is closest to *G. huberti* in body size and in shape of the epigynum (compare Figs. 22, 23, 25, 26 with Figs. 19, 20). It is more darkly colored than *huberti* and the light submarginal stripes on the carapace are narrower. *Gladicosa bellamyi* can be easily distinguished from *huberti* by the structure of the male palpi (compare Figs. 29–34 with Figs. 27, 28). Other than the type specimens of *Lycosa bellamyi* and *Trochosa cherokee,* this species is represented by specimens taken in pitfall traps near Stoneville, Mississippi and Columbus, Ohio. The males from Mississippi, which

are the predominant sex in these collections, are distinctly larger than the Ohio males as indicated by the *Measurements,* but the similarity of coloration, genitalic structure, and anatomical proportions led me to think that only one species is represented. The southern populations are simply larger in size.

Natural History. Andrew Penniman (personal communication) collected this species in some abundance by using pitfall traps in a wooded area in central Ohio. The collecting period extended from 24 April to 28 August 1973 and the relative abundance of the sexes taken in these traps is indicated in the records below. Four females with egg cases were collected from 29 May–12 June. The egg cases contained 53, 56, 91, and 106 eggs. Tim Lockley (personal communication) also captured this species in pitfall traps placed at the edge of a deciduous woods in Mississippi. Most of these specimens were males as indicated in the records below. A single female with egg case was collected between 3–6 June 1983.

Distribution. Ohio southeastward to western Florida and southwestward to Oklahoma (Map 3).

Records. Ohio. Franklin Co.: Sharon Woods Metropolitan Park, Columbus, 24 April–1 May, 19♂♂:♀; 1–8 May, 28♂♂:3♀♀; 8–15 May, 23♂♂:10♀♀; 15–22 May, 8♀♀; 22–29 May, ♀♀; 29 May–5 June, ♂♂:7♀♀; 5–12 June, ♂♂:3♀♀; 19–26 June, ♀; 26 June–3 July, 3♀♀; 10–17 July, ♀; 21–28 Aug. 1973, ♂ (A. J. Penniman). *Florida.* Liberty Co.: 12 April 1935, ♀ (H. K. Wallace). *Mississippi.* Washington Co.: 2 mi. N of Stoneville, 21–25 April, ♂; 27–29 April, ♂; 29 April–2 May, 9♂♂; 2–4 May, 3♂♂; 4–6 May, 4♂♂; 6–9 May, 4♂♂; 9–11 May, ♂♂♀; 13–16 May, 5♂♂; 16–18 May, ♂♂; 23–25 May, ♂; 25–31 May, ♂♂; 3–6 June, ♂♀; 1–6 July 1983, ♀ (T. C. Lockley). *Oklahoma.* Muskogee Co.: Fort Gibson, 21 July 1937, ♀ (Standish-Kaiser).

Gladicosa euepigynata (Montgomery) comb. nov.
Figures 3, 15–17, 43–46. Map 3.

Lycosa euepigynata Montgomery, 1904: 277, 279, pl. 28, figs. 1, 2, ♂♀. Holotype female from Austin, Travis Co., Texas (T. H. Montgomery) deposited in the American Museum of Natural History, examined. Montgomery 1909: 514. Banks 1910: 55. Gertsch 1934: 8. Gertsch and Wallace 1935: 22, figs. 44, 45, ♀♂. Bonnet 1957: 2607.

Lycosa gulosa: Chamberlin 1908: 265 (in part). Petrunkevitch 1911: 560 (in part). Not *Lycosa gulosa* (Walckenaer).
Hogna euepigynata: Roewer 1954: 258.

Discussion. Chamberlin (1908) synonymized *G. euepigynata* with *G. gulosa* commenting upon the variation in size and color of *gulosa.* Montgomery (1909) rightfully defended his designation of *euepigynata* as a distinct species.

Color. Females. Face with sides orange-yellow, eye region brown. Chelicerae dark reddish brown, darker distally.

Carapace brown with broad, irregular median stripe of orange-yellow to yellow. Irregular submarginal stripes of orange-yellow, intersected by black lines radiating from thoracic area. Pattern illustrated in Figure 3.

Dorsum of abdomen mottled with beige, spots of white, and dark brown along the edges. Faint indications of chevron markings posteriorly as in Figure 3. A series of five white spots marking edges of chevrons. Venter of abdomen pale cream to yellow.

Legs yellow-gold to brownish orange. Pale ventrally with dorsal surfaces of femora marked by three irregular dark brown bands.

Labium reddish brown with distal end yellow. Endites orange-brown to reddish brown with distal ends yellow. Sternum orange-brown to reddish brown.

Color. Males. Face yellow to brownish yellow, eye region brown. Cymbia of palpi brown.

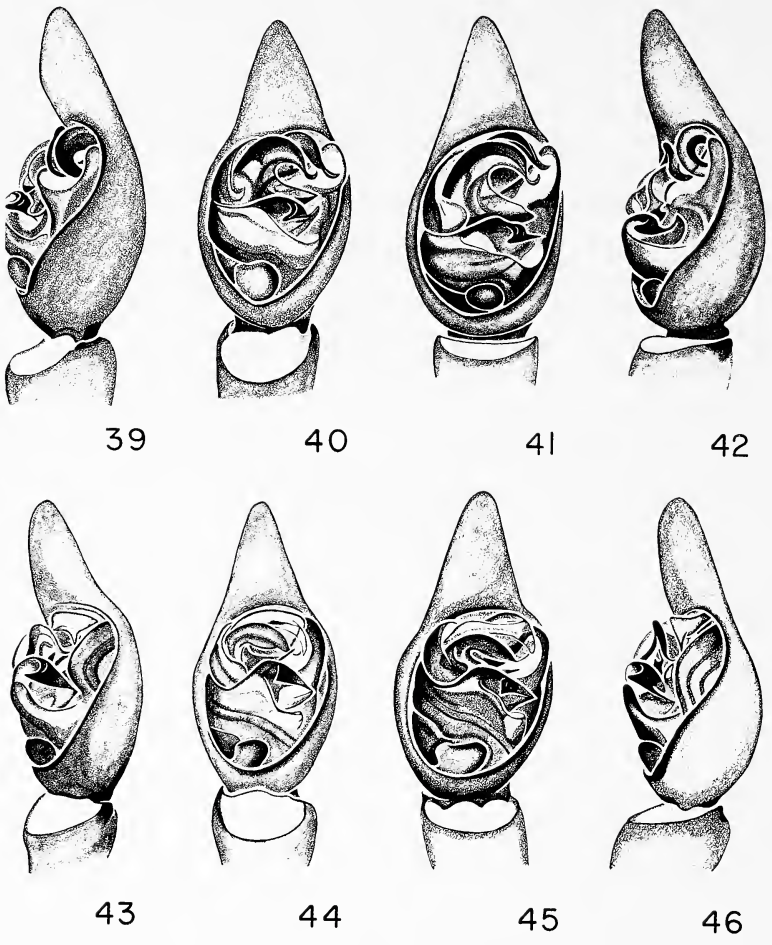
Carapace brown with broad median yellow stripe and irregular submarginal stripes of same color, producing a pattern very similar to that of female (Fig. 3).

Dorsum of abdomen with mottled pattern of light and dark brown overlaid with white hair. White hairs forming five paired spots beginning in cardiac area and continuing posteriad. Cardiac area outlined with dark brown. Overall pattern as in female (Fig. 3). Venter of abdomen cream to pale brown or beige.

Legs yellow to golden brown, darker on dorsal surface. Each femur with three dark brown irregular bands that are more distinct on dorsal surfaces.

Labium yellow to gold. Endites brown, with distal ends yellow. Sternum golden yellow.

Measurements. Ten females and ten males from Texas. See Table 6.



Figs. 39–42. *Gladicosa pulchra* (Keyserling). Left palpus of male syntype of *Lycosa insopita* Montgomery [= *Gladicosa pulchra* (Keyserling)] from Austin, Travis Co., Texas. 39. Retrolateral view. 40. Ventral view. 41–42. Left palpus of male from Gainesville, Florida, 14 June 1935. 41. Ventral view. 42. Retrolateral view.

Figs. 43–46. *Gladicosa euepigynata* (Montgomery). 43–44. Left palpus of male syntype of *Lycosa euepigynata* Montgomery from Austin, Travis Co., Texas. 43. Retrolateral view. 44. Ventral view. 45–46. Left palpus of male from Camp Verde, Kerr Co., Texas, Dec. 1939. 45. Ventral view. 46. Retrolateral view.

Table 6. Measurements of ten females and ten males of *Gladicosa euepigynata* from Texas.

Females:	Mean SEM		Mean SEM
Ant. Eye Row	1.268 ± .016	Femur I	5.39 ± .06
PME	1.692 ± .016	Pat.-Tibia I	7.06 ± .10
PLE	2.124 ± .024	Meta. I	4.15 ± .05
POQ	1.610 ± .014	Tarsus I	2.40 ± .02
Car. Width	5.32 ± .08	Total I	19.05 ± .21
Car. Length	7.21 ± .12	Femur IV	6.19 ± .08
Body Length	16.88 ± .35	Pat.-Tibia IV	7.51 ± .08
Pat.-Tibia II	6.54 ± .09	Meta. IV	6.86 ± .07
Pat.-Tibia III	5.76 ± .07	Tarsus IV	2.93 ± .02
		Total IV	23.48 ± .22

Males:	Mean SEM		Mean SEM
Ant. Eye Row	1.152 ± .018	Femur I	5.19 ± .10
PME	1.580 ± .018	Pat.-Tibia	6.87 ± .07
PLE	1.964 ± .028	Meta. I	4.54 ± .07
POQ	1.466 ± .016	Tarsus I	2.44 ± .04
Car. Width	4.84 ± .11	Total I	18.97 ± .25
Car. Length	6.60 ± .17	Femur IV	5.91 ± .09
Body Length	11.91 ± .28	Pat.-Tibia IV	7.20 ± .10
Pat.-Tibia II	6.24 ± .08	Meta. IV	6.82 ± .07
Pat.-Tibia III	5.59 ± .08	Tarsus IV	2.84 ± .05
		Total IV	22.76 ± .29

Diagnosis. *Gladicosa euepigynata* is closest to *G. pulchra* in size and coloration (compare Fig. 3 with Fig. 4). The epigynum of *euepigynata* (Figs. 15–17) and the palpus (Figs. 43–46) distinguish it from *pulchra* and all other species of *Gladicosa.*

Natural History. Montgomery (1904) reported this species as being abundant near Austin, Texas. There he found it under stones near water. Males were most numerous in January.

Distribution. South central Texas (Map 3).

Records. *Texas.* Bandera Co.: 2 mi. N of Medina, Dec. 1939, ♂♀ (S. & D. Mulaik); Hays Co.: 15 Apr. 1939, 3♀♀ (D. & S. Mulaik); Kerr Co.: Camp Verde, Dec. 1939, ♂:3♀♀, Raven Ranch, Dec. 1939, ♀♀, Turtle Creek, Dec. 1939, ♂♀ (D. & S. Mulaik); Kendall Co.: Dec. 1939, ♀ (D. & S. Mulaik); Tom Green Co.: San Angelo, Dec. 1939, ♀ (S. Mulaik); Travis Co.: Austin, 13♂♂:23♀♀ (R. V. Chamberlin).

References Cited

Allard, H. A.
1936. The drumming spider (*Lycosa gulosa* Walckenaer). *Proc. Biol. Soc. Washington,* **49**: 67–68.

Banks, N.
1893. Notes on spiders. *Jour. N.Y. Ent. Soc.,* **1**: 123–134.
1901. Notes on some spiders of Walckenaer, Koch and others. *Jour. N.Y. Ent. Soc.,* **9**: 182–189.
1910. Catalogue of Nearctic spiders. *Bull. U.S. Nat. Mus.,* **72:** 1–80.
1911. Some Arachnida from North Carolina. *Proc. Acad. Nat. Sci. Phila.,* **65:** 676–687.

Banks, N., N. M. Newport and R. D. Bird.
1932. Oklahoma spiders. *Publ. Univ. Okla., Biol. Surv.,* **4**(1): 7–49.

Bishop, S. C. and C. R. Crosby
1926. Notes on the spiders of the southeastern United States with descriptions of new species. *Jour. El. Mitch. Sci. Soc.,* **41**(3–4): 163–212.

Bonnet, P.
1955. Bibliographia Araneorum. *Toulouse,* **2**(1): 1–918.
1957. Bibliographia Araneorum. *Toulouse,* **2**(3): 1927–3026.

Brady, A. R.
1962. The spider genus *Sosippus* in North America, Mexico, and Central America (Araneae, Lycosidae). *Psyche,* **69**(3): 129–164.
1972. Geographic variation and speciation in the *Sosippus floridanus* species group (Araneae: Lycosidae). *Psyche,* **79**(1–2): 27–48.
1979. Nearctic species of the wolf spider genus *Trochosa* (Araneae: Lycosidae). *Psyche,* **86**(2–3): 167–212.

Bultman, T. L., G. W. Uetz and A. R. Brady
1982. A comparison of cursorial spider communities along a successional gradient. *Jl. Arachn.,* 10: 23–33.

Chamberlin, R. V.
1904. Notes on generic characters in the Lycosidae. *Canad. Ent.,* **36**: 145–148, 173–178.
1908. Revision of North American spiders of the family Lycosidae. *Proc. Acad. Nat. Sci. Philad.,* **60**: 158–318.
1924. Descriptions of new American and Chinese spiders, with notes on other Chinese species. *Proc. U.S. Nat. Mus.,* **63**(13): 1–38.

Chamberlin, R. V. and W. Ivie
1942. A hundred new species of American spiders. *Bull. Univ. Utah.,* **32**(13): 1–117.
1944. Spiders of the Georgia region of North America. *Bull. Univ. Utah,* **35**(9): 1–267.

Chickering, A. M.
1932. Notes and studies on Arachnida. II. Araneae from the Douglas Lake Region, Michigan I. *Pap. Mich. Acad. Sci.,* **15**: 349–355.

Comstock, J. H.
1913. The spider book. Doubleday & Page, *Garden City, New York,* 721 pp.

1940. The spider book. Rev. and ed. by W. J. Gertsch. Comstock, *Ithaca,* 729 pp.

Crosby, C. R. and S. C. Bishop

1928. Araneae *in* a list of the insects of New York. *Cornell Univ. Agr. Exper. Sta. Mem.,* **101:** 1034–1074.

Dorris, P. R.

1965. A list of spiders collected in northern Mississippi. *Trans. Amer. Micros. Soc.,* **84**(3): 407–408.

1968. A preliminary study of the spiders of Clark County, Arkansas compared with a five year study of Missisippi spiders. *Ark. Acad. Sci. Proc.,* **22**: 33–37.

Drew, L. C.

1967. Spiders of Beaver Island, Michigan. *Publ. Mus. Mich. St. Univ., Biol. Ser.,* **3**(3): 153–208.

Elliott, F. R.

1930. An ecological study of spiders of the Beech-Maple forest. *Ohio Jour. Sci.,* **30**(1): 1–22.

1932. Revision of and additions to the list of Araneae (spiders) of Indiana. *Proc. Indiana Acad. Sci.,* **41**: 419–430.

Emerton, J. H.

1885. New England Lycosidae. *Trans. Conn. Acad. Arts Sci.,* **6**: 481–505.

1902. The common spiders of the United States. *Boston,* 225 pp.

Fitch, H. S.

1963. Spiders of the University of Kansas Natural History Reservation and Rockefeller Experimental Tract. *Univ. Kan. Mus. Nat. Hist., Misc. Pub.,* **33**: 1–202.

Gertsch, W. J.

1934. Notes on American Lycosidae. *Amer. Mus. Nov.,* **693**: 1–25.

1949. American spiders. D. Van Nostrand Co., Inc., *Princeton, New Jersey,* 285 pp.

Gertsch, W. J. and H. K. Wallace

1935. Further notes on American Lycosidae. *Amer. Mus. Nov.,* **794**: 1–22.

1937. New American Lycosidae with notes on other species. *Amer. Mus. Nov.,* **919:** 1–22.

Harrison, J. B.

1969. Acoustic behavior of the wolf spider *Lycosa gulosa. Animal Behavior,* **17**: 14–16.

Jones, S. E.

1936. The Araneida of Dallas County: Preliminary note. *Field Lab.,* **4**(2): 68–70.

Kaston, B. J.

1935. The slit sense organs of spiders. *Jour. Morph.,* **58**: 189–207.

1936. The senses involved in the courtship of some vagabond spiders. *Ent. Amer.,* **16**(2): 97–167.

1938. New spiders from New England with notes on other species. *Bull. Brooklyn Ent. Soc.,* **33**(4): 173–191.

1948. Spiders of Connecticut. *Bull. Conn. St. Geol. Nat. Hist. Surv.,* **70**: 1–874.

1981. Spiders of Connecticut. Rev. ed. *Bull. Conn. St. Geol. Nat. Hist. Surv.*, **70**: 1–1020.

KEYSERLING, E. G.

1877. Ueber amerikanische Spinnenarten der Unterordnung Citigradae. *Verh. Zool.-Bot. Ges. Wien*, **26**: 609–708.

MARX, G.

1890. Catalogue of the described Araneae of temperate North America. *Proc. U.S. Nat. Mus.*, **12**: 497–594.

1892. A list of the Araneae of the District of Columbia. *Proc. Ent. Soc. Wash.*, **2**(2): 148–161.

MONTGOMERY, T. H.

1902. Descriptions of Lycosidae and Oxyopidae of Philadelphia and its vicinity. *Proc. Acad. Nat. Sci. Phila.*, **54**: 535–592.

1904. Descriptions of North American Araneae of the families Lycosidae and Pisauridae. *Proc. Acad. Nat. Sci. Phila.*, **56**: 261–323.

1905. The spermatogenesis of *Syrbula* and *Lycosa*, with general considerations upon chromosome reduction and the heterochromosomes. *Proc. Acad. Nat. Sci. Phila.*, **57**: 162–205.

1909. Remarks on Prof. Chamberlin's revision of North American Lycosidae. *Proc. Acad. Nat. Sci. Philad.*, **60**: 513–515.

PETRUNKEVITCH, A.

1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. *Bull. Amer. Mus. Nat. Hist.*, **29**: 1–791.

ROBLE, S. M.

1986. A new spider host association for *Mantispa viridis* (Neuroptera, Mantispidae). *Jl. Arach.*, **14**: 135–136.

ROEWER, C. F.

1954. Katalog der Araneae. Band 2, Institut Royal des Sciences Naturelles de Belgique, *Bruxelles*, **1**: 1–923.

1959, 1960. Exploration du Parc National de l'Upemba. Araneae, Lycosiformia II (Lycosidae). Institut des Parcs Nationaux du Congo Belge, *Bruxelles*. 1–518 (1958), 519–1040 (1959).

ROVNER, J. S.

1975. Sound production by wolf spiders: a substratum-coupled stridulatory mechanism. *Science*, **190**: 1309–1310.

SIMON, E.

1864. Histoire naturelle des Araignées (Aranéides). *Paris*. 540 pp.

STONE, W.

1890. Pennsylvanian and New Jersey spiders of the family Lycosidae. *Proc. Acad. Nat. Sci. Phila.* **1890**(3): 420–434.

WALCKENAER, C. A.

1837. Histoire naturelle des insectes: aptères. Tome I. Paris, 549 pp.

WHITCOMB, W. H.

1967. Wolf and lynx spider life histories. Univ. Arkansas Div. Agr., Dept. Ent., Term Rept. *NSF Grants*, 141 pp.

WHITCOMB, W. H. AND K. BELL
1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. *Agr. Exp. Sta., Univ. Ark. Bull.*, **690**: 3–84.
WHITCOMB, W. H., H. EXLINE AND R. C. HUNTER
1963. Spiders of the Arkansas cotton field. *Ann. Ent. Soc. Amer.*, **56**: 653–660.
WOOD, F. D.
1926. Autotomy in Arachnida. *Jour. Morph.* **42**: 143–195.
WORLEY, L. G. AND G. B. PICKWELL
1931. The spiders of Nebraska. *Univ. Stud. Nebraska*, **27**(1–4): 1–129.

NESTING ASSOCIATIONS OF WASPS AND ANTS ON LOWLAND PERUVIAN ANT-PLANTS

By Edward Allen Herre,[1,2] Donald M. Windsor,[1] and Robin B. Foster[1]

Introduction

Neotropical vespid wasps are known to form nesting associations with other species of wasps and ants. For instance, *Mischocyttarus immarginatus* nests primarily in association with the larger and more aggressive colonies of certain polybiine wasps in the savannas of northwestern Costa Rica (Windsor 1972, 1973). Examples of wasp species which form interspecific nesting associations with ants include *Polybia rejecta* and *Synoeca chalybea,* whose nests are usually associated with carton building *Azteca spp.* ant colonies throughout the neotropics (Vesey-Fitzgerald 1938, Richards 1945, DMW, RBF, EAH personal observations).

Often the ants with which wasps nest are involved in more or less specific associations with host ant-plants. In addition to *Azteca spp., Polybia rejecta* nests can be found in ant acacias which support healthy colonies of *Pseudomyrmex ferruginea* (DMW, RBF personal observations). Zikan (1949) has reported that several *Mischocyttarus* species nest on the ant plant *Cordia nodosa* (Boraginaceae) inhabited by *Azteca spp.* and an unidentified species of myrmecaceous Melastomataceae. Richards (1945) reported collecting at least one nest of *M. metoecus* and *M. decimus* from *C. nodosa* in Guyana.

Why do these nesting associations exist? Windsor (1972, 1973) demonstrated that *Mischocyttarus immarginatus* nests associated with nests of other, more aggressive wasps species survive longer and produce more brood. It appears that such nests suffer less damage from birds which destroy nests and rob brood. Richards (1951) suggested that nesting with ants such as *Azteca* may be one of relatively few possible defenses available to tropical wasps against

[1]Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama
[2]Department of Biology, University of Iowa, Iowa City, Iowa 52242, U.S.A.
Manuscript received by the editor March 20, 1986

the organized raids of army ants (Ecitonini). Below we describe numerous species of vespid wasps which form nesting associations with *Allomerus octoarticulatus* ants inhabiting the plant *Tococa guianensis* Aublet (Melastomataceae) and with *Pheidole spp.* ants inhabiting *Maieta poeppigii* Mart. ex Triana (Melastomataceae) and show that by nesting on these plants the wasps escape army ant raids.

Study Area

The study site is in Loreto, Peru, at Estacion Biologica Callicebus which is located 3–5 km. south of the village of Mishana on the Rio Nanay in Loreto, Peru. The village is approximately 30 km. east of the confluence of the Nanay with the Amazon River near Iquitos. The Estacion consists of a forest camp and an extensive trail network through the apparently uncut and non-indundated forest. The forest grows on low hills composed of a mosaic of white sand and dark brown sand and is drained by tea-colored streams. These sediments are derived from the ancient Guiana and Brazilian Shields and have been eroded and redeposited following the Andean uplift. White sand areas, though common in the Rio Negro drainage, are infrequent in the Western Amazon (see Kinsey & Gentry, 1979). The brown sand soils support a flora typical of much of the non-indundated Peruvian Amazon. The white sand soils have a distinctive flora which shows strong affinities to the flora of the Guiana Highlands. The latter areas also have a shorter forest canopy (20 m. vs. 30–35 m.); fewer lianas, straighter, thinner, and less-branched understory trees and shrubs; and a thick mat of roots over the white sand. The observations presented below were collected during 8 short visits (4 by EAH in August 1978, October 1978, in December 1979, and in June 1983; 1 by DMW in November 1978; and 3 by RBF in August 1974, 1978, and 1980).

Observations and Results

Understory ant-plants are common at Mishana, especially on the brown sand soils, and are represented by a diversity of families: (Melastomataceae) *Tococa* (3 spp.), *Maieta* (2 spp.); (Chrysobalanaceae) *Hirtella* (2 spp.); (Boraginaceae) *Cordia nodosa*; (Rubiaceae) *Duroia hirsuta.* Of these, only *Tococa guianensis* is abundant on the white sand areas. This 2–4 m. treelet is most common on

upper slopes and hilltops, primarily in gaps formed by treefalls. The population is polymorphic for a bright red-purple color on the undersides of the leaves. The petioles have a large, bilobed, hollow expansion (formicarium) with a pair of openings onto the undersides of the leaf blade (see figure 1). *Maieta poeppigii,* in contrast, is an arching shrub less than 1 m. tall most common on brown sand soils, primarily on lower slopes and streambanks. The formicarium of *Maieta* consists of a pair of raised, hollow chambers on either side of the midrib at the base of the leafblade.

Although we found colonies of at least eight different species of ants inhabiting different *Tococa guianensis* individuals (eg. *Azteca spp., Dolichoderus spp., Pseudomyrmex spp., Crematogaster spp.,* and *Gnamtogenys spp.*), the majority of the plants we encountered were occupied by colonies of the ant *Allomerus octoarticulatus (Allomerus)* (18 of 34 plants in one census). *Allomerus* builds a characteristic carton tunnel of cemented debris with small holes regularly spaced over the surface (see figure 1). These structures envelope most of the stems, connect the formicaria, and extend down the main stem to within 20 cm. of the ground. Most ant activity is confined to the formicaria and these tunnels. Unlike other species of ants which we observed on these plants, we did not observe *Allomerus* foraging off the host plant either on any casually observed plants or on focal plants watched at hourly intervals between 5 am. and 1 am. In addition, the presence of coccids and structures which may have been food bodies or feeding glands for the ants (see Roth, 1970) led us to believe that *Allomerus* derives all its nutrition either directly or indirectly from the host *T. guianensis,* much as *Pseudomyrmex satanica* is supported by farming coccids within the hollow outer twigs of *Triplaris cumminghami* (DMW, personal observation in Costa Rica). *Allomerus* aggressively recruits onto leaf surfaces when a plant is disturbed. However, the ants do not harm wasp broods although they will swarm all over the wasp nest.

Maieta poeppigii plants were overwhelmingly occupied by *Pheidole spp.* ants (94 of 101 plants). Unlike *Allomerus,* the *Pheidole spp.* do not build tunnels, although they do characteristically store debris in one of the two paired chambers at the base of each leaf. The *Pheidole spp.* ants are not particularly aggressive. Occasional minor workers can be found outside the formicaria. Major workers and minor workers emerge from the formicaria in large numbers

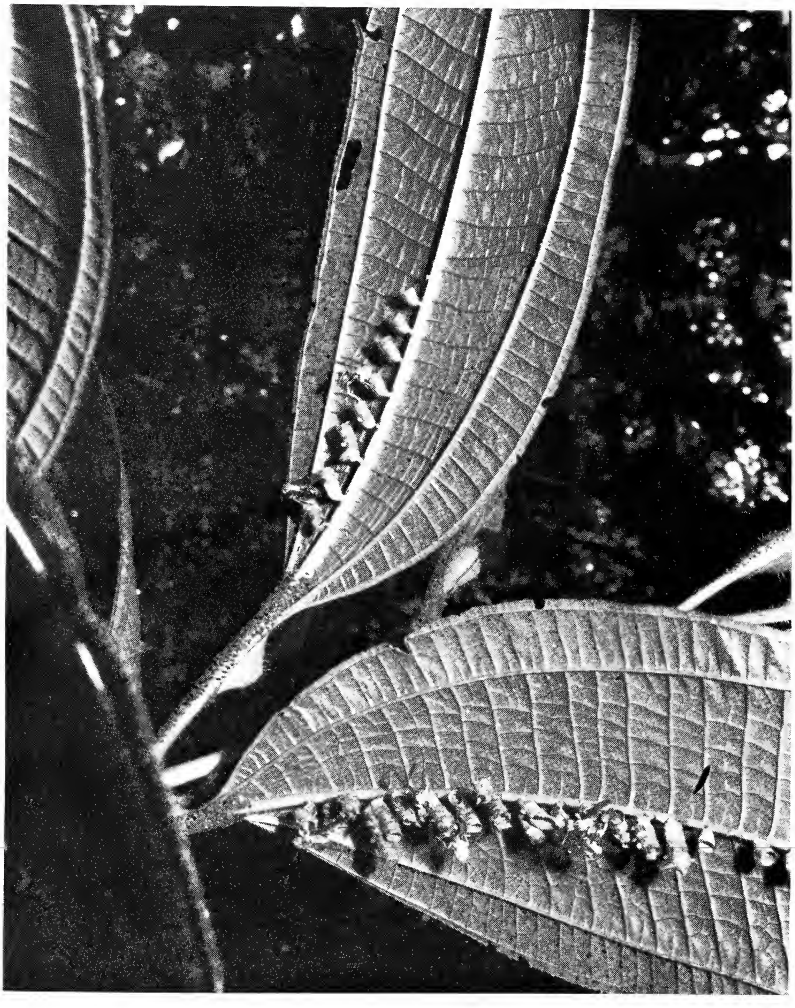


Figure 1. Nests and adults of the wasp *Mischocyttarus insolitis* shown beneath the leaves of *Tococa guianensis* plants inhabited by *Allomerus octoarticulatus* ants. Notice the separation of the cells on the multiple pedicels. Also notice the characteristic carton tunneling and formicaria used by the *Allomerus* ants

only if the leaves are violently shaken or if the formicaria are directly disturbed. The *Pheidole* ants were not observed on the wasp nests.

Of those wasps which construct small open nests, we found ten *Mischocyttarus* species and one *Polistes* species in the forest understory. All but two of thirty-one active colonies encountered occurred on the undersides of *Tococa guianensis* or *Maieta poeppigii* leaves and only when the plants were occupied by *Allomerus* and *Pheidole* ants, respectively (see table 1). Two of the *Mischocyttarus* wasp species, *M. latissimus* and *M. insolitis,* build multi-pediceled nests arranged in rows along the midrib of the leaf. The cells are fused in the nests of *M. latissimus* while the nests of *M. insolitus* consist of separate clusters of one to four brood cells with each cluster supported by its own pedicle (see photograph 1). The net result is the subdivision and separation of the broodcells which comprise the nests of *M. insolitus.* The other species of *Mischocyttarus* build nests more typical of the genus; a cluster containing all cells supported by a single pedicel. All of the *Mischocyttarus.* species are extremely timid, flying away from their nests at the slightest disturbance and making no attempt at brood defense. In addition, two colonies (one each of *Polybia signata* and *Polybia spp.*) out of six total colonies of socially complex, aggressively swarming Polybiinae wasps were found attached to limbs of *T. guianensis.*

A small number of *Tococa* plants supported a disproportionate number of wasp colonies and this was most obvious with the nests of *Mischocyttarus insolitis.* In a census of 43 *T. guianensis* plants with *Allomerus* ants, five plants were the host for single *Mischocyttarus* nests while seven plants had two or more colonies. In a survey of 116 *Maieta poeppigii* plants with *Pheidole spp.* ants, one plant had three nests and two plans each had one.

Several observations and manipulations we performed indicate that by nesting on these myrmecacious melastomes the wasps avoid nest plundering by army ants. While following the raiding swarms of *Eciton burchelli* and *Eciton rapax* we noticed that these ants never ran on to either *Tococa guianensis* or *Maieta poeppigii* plants. The avoidance of these two plants contrasted sharply with the army ants' rapid climbing and investigating most other plants in their path.

Table 1. A list of wasp species collected at Mishana, 1–5 November 1978. The number of nests found on each type of host plant (*Maieta, Tococa,* or other) is indicated. *Brachygastra melania* was previously only known from Bolivia.

Species with open nests:	Nest Found	*Maieta*	*Tococa*	other
Mischocyttarus synoecus Rich.	Yes	1		
M. lecointei Ducke	Y	4	2	1
M. pallidus Zikan	Y	2		
M. insolitus Zikan	Y		21	
M. latissimus Rich.	Y		2	
M. decimus Rich.	Y		1	
M. sp. near mirificus Zikan	Y			1
M. carbonarius Sauss.	Y		1	
M. silvicola Zikan	Y		1	
M. sp. near interruptus Rich.	Y		1	
Polistes rufiventris Ducke	Y		1	
P. pacificus	Y	(found in clearing near river)		
Species with closed nests:				
Angiopolybia pallens Lep.	Y			1
A. paraensis Spirola morph *ruficornis* Ducke	No			
Apoica thoracica R. du Buyss.	N			
Brachygastra bilineolata Spinola	N			
B. buyssoni Ducke	N			
B. melania Richards	N			
B. moebiana Sauss.	N			
B. myersi Bequaert	N			
Polybia signata Ducke	Y		1	
P. sp. near fastidiosuscula Sauss	Y			1
P. sp.	Y		1	1
P. rejecta F.	N			
P. liliaceae F.	N			
Protopolybia acutiscutis Cameron	N			
Pseudopolybia vespiceps Sauss.	Y			1
Stelopolybia angulicollis Spinola	N			
Synoeca surinama Lep.	N			
S. virginea F.	N			

The perceived avoidance was substantiated when we moved a twig that the *Eciton* ants were using as a bridge against a stem of *M. poeppigii.* The army ants stopped when they came in contact with the stem and although ants from the rear continued moving forward until there was a great tangled mass of ants at the front, no ants crawled onto the stem. Next, we placed stems of *Tococa guianensis* and *Maieta poeppigii* with intact leaves and formicaria across active *Eciton* trails and found that the trails were quickly rerouted around the plants. Similar responses were not obtained when we placed other plant species or *Tococa guianensis* without *Allomerus* inhabitants across the path of the army ants. Further, in three instances, we observed army ants passing by *T. guianensis* plants with *Allomerus* ants and active wasps nests. We removed two *T. guianensis* leaves minus formicaria with attached wasp nests, placed them on twigs at the same height off the ground as they had been on the plants, and put the twigs in front of the *Eciton* raiding swarms. In both instances the army ants swiftly scaled the twigs and seized the wasp brood.

Discussion

Predatory ants pose a particularly important threat to the nests and broods of tropical wasps (Jeanne 1972, Litte 1977). In discussing this problem in his revision of the genus *Mischocyttarus,* Richards (1945) states, "A number of species have entered into some sort of association with ants and have thereby found safety by firmly grasping the nettle.". Clearly the wasps nesting on these plants benefit by having a neutral border maintained for them. With access to the sole connection to the terrestrial world guarded by *Allomerus* or *Pheidole* ants, there is little or no risk that hostile army ant species will come plundering down the pedicel. In this light the unusual (for *Mischocyttarus* wasps) nest architecture of *M. insolitis* becomes more comprehensible.

As Jeanne (1979) demonstrated, building a highly subdivided nest composed of multiple combs uses materials for nest construction very inefficiently and requires a much higher expenditure of time and energy per cell than does the nest architecture more characteristic of polistine wasps. However, a highly subdivided nest no longer provides as concentrated a target for a bird which plunders by knocking down whole nests and then leisurely eating the brood (eg.

Windsor 1972). More passes are needed and the return in food per time and effort is less. Further, a subdivided nest is less vulnerable to being entirely wiped out by nest parasites which can move from cell to cell (eg. tineid moth larvae described by Jeanne 1979).

There appears to be no obvious benefit that the ants derive from the presence of the timid *Mischocyttarus* wasps. Why do the ants tolerate the presence of these wasps? A review of the ant species with which various vespid wasps are reported to form nesting associations shows that with the exception of some *Azteca* species, the ants all appear to be nutritionally supported by their host plants. Apparently the ants either cannot eat the wasp brood or do not recognize the wasp brood as a potential meal. Further, in the case of some ant-wasp associations such as that between *Azteca spp.* and *Polybia rejecta,* the wasps have been reported to benefit the associated ant colony by discouraging anteaters (R. Silberglied, personal communication). The *Tococa guianensis* plants on which the aggressive *Polybia* and *Polistes* wasps nested were difficult to approach without being stung. It is likely that the presence of these wasps reduces damage to the host plant and, consequently, the ant colony caused by mammals. Therefore, the *Mischocyttarus* wasps, while not being a detriment to the ants, may simply be taking good advantage of a tolerance that the ants have developed to more beneficial species of symbiotic wasps.

Acknowledgments

We wish to thank Don Francisco Pizarro for generous hospitality and essential logistic help during our various visits to Casaria Mishana, Dr. William Brown for kindly indentifying all ant species mentioned, Dr. J. J. Wurdack for identifying the *Tococa* and *Maieta* species, and, especially, the late O. W. Richards for identifying the wasp species and encouraging this work with his enthusiasm and expertise. D. E. Wheeler, D. M. Feener, L. Johnson and the Iowa Writing Seminar Group provided helpful comments on the manuscript. This work was supported by The Smithsonian Tropical Research Institute (DMW, EAH), The Harris Foundation (EAH), and The University of Iowa's Teaching and Research Fellowship Program (EAH).

Summary

Twelve species of vespid wasps were found nesting on two species of melastomataceous ant plants in a mixed lowland forest near Iquitos, Peru. Although eight different species of ants inhabited different individual plants of *Tococa guianensis* (Melastomataceae), wasps only nested on those plants inhabited by the ant *Allomerus octoarticulatus*. Nests were also found on *Maieta poeppigii* (Melastomaceae) inhabited by *Pheidole spp.* Several *Mischocyttarus* species exhibited nest architectures atypical of the group. Observations and manipulations indicate that by nesting on these ant plants inhabited by those particular ants the wasps avoid nest plundering by army ants.

References

Jeanne, R. L.

1972. Social Biology of the Neotropical Wasp *Mischocyttarus drewsenii*. Bull. Mus. Comp. Zool., Harvard Univ. **144**: 63–150.

1979. Construction and Utilization of Multiple Combs in *Polistes canadensis* in Relation to the Biology of a Predaceous Moth. Behav. Ecol. Sociobiol. **4**, 293–310.

Kinsey, W. G. and A. H. Gentry

1979. Habitat utilization in two species of *Callicebus*. in *Primate Ecology: Problem Oriented Field Studies*. R. W. Sussman ed. Wiley and Sons. New York.

Litte, M.

1977. Behavioral ecology of the Social Wasp *Mischocyttarus mexicanus*. Behav. Ecol. Sociobiol. **2:** 229–246.

Richards, O. W.

1945. A Review of the Genus *Mischocyttarus de Saussure*. Trans. Roy. Entomol. Soc. London. **95**: 295–462.

Richards, O. W. and M. J. Richards.

1951. Observations on the Social Wasps of South America (Hymenoptera, Vespidae). Trans. Roy. Entomol. Soc. London. **102**: 1–170.

Roth, I.

1976. Estructura Interna de los Domacios Foliares en *Tococa* (Melastomeae). Acta Biol. Venez., **9**(2): 221–258.

Vesey-Fitzgerald, D.

1938. Social Wasps (Hym. Vespidae) from Trinidad, with a note on the genus *Trypoxylon Latreille*. Trans. Roy. Entomol. Soc. London. **87**: 181–191.

Windsor, D. M.

1972. Nesting Association between two Neotropical Polybiine Wasps (Hymenoptera, Vespidae). Biotropica **4**: 1–3.

1973. Birds as Predators on the Brood of *Polybia* Wasps (Hymenoptera: Vespidae: Polistinae) in a Costa Rican Deciduous Forest. Briotropica **8**(2): 111–116.

ZIKAN, J. F.

1949. O Genero *Mischocyttarus Saussure* (Hymenoptera, Vespidae), com a decriciao de 82 especies novas. VBoln. Parq. nac. Itatiaia **1**: 1–251.

WINTER PREY COLLECTION AT A PERENNIAL COLONY OF *PARAVESPULA VULGARIS* (L.) (HYMENOPTERA: VESPIDAE)

By Parker Gambino
Department of Entomological Sciences
University of California
Berkeley, California, U.S.A. 94720

Introduction

Diet is a fundamental aspect of an organism's biology. In eusocial vespid wasps the food intake of a mature colony, including nutrition of immatures, is determined by the foraging behavior of workers. Yellowjackets of the genus *Paravespula* Blüthgen meet the protein requirements of the colony by capturing live arthropods and collecting flesh from dead animals. By enabling these species to utilize a broader resource base, scavenging likely contributed to the evolution in this genus of a colony cycle characterized by higher worker populations and greater longevity than in *Vespula* Thompson, a closely related genus in which only live prey is taken (MacDonald *et al.,* 1976).

Prey collection by freely foraging *Paravespula* colonies has been described in detail by Kleinhout (1958), Kemper and Dohring (1962), Broekhuizen and Hordijk (1968), and Archer (1977). Numerous shorter lists of prey are available, (cf. Spradbery (1973) for a literature review). Broekhuizen and Hordijk (1968) investigated the response of *P. vulgaris* (L.) to artificial manipulations of prey densities in trees, while MacDonald *et al.* (1974) offered various prey items in screen-enclosed foraging areas. Heinrich (1984) gave a good account of general foraging behavior of individual workers and Free (1970) investigated handling of honeybee prey by workers.

Paravespula species undergo an annual monogynous cycle over most of their range, but in mild-weathered areas, perennial polygynous colonies sometimes develop (Spradbery, 1973). These colonies, characterized by enormous populations of workers, occur especially

*Revised manuscript received by the editor July 7, 1986.

in areas recently invaded by *Paravespula.* Although perennation and polygyny represent significant deviations from the typical *Paravespula* pattern, the sporadic appearance of such colonies has hindered study. Published prey studies have addressed only annual colonies, thus the discovery of a perennial *Paravespula* colony at the University of California provided an opportunity to study its winter diet.

Materials and Methods

I first noticed the colony of *Paravespula vulgaris* (L.) on October 10, 1984. Typical annual colonies of this native species initiated in April or May usually begin to decline in the fall. The high level of activity (about 300 worker sorties per minute) indicated that this colony had been functional since at least spring 1984, and suggested that it might persist for another year. In fact, the colony remained vigorous through a second summer, with a final observation of external worker activity on February 6, 1986.

The colony was located about 25 m north of Callaghan Hall ticket kiosk on the Berkeley campus of the University of California, at elevation 75 m. The immediate surrounding area is a mixed stand of Monterey pine (*Pinus radiata* D. Don) and coast live oak (*Quercus agrifolia* Neé) over a grass ground cover dominated by *Ehrharta erecta* Lam. Strawberry Creek, flowing basically east to west, passes within 40 meters.

The subterranean nest was under a fallen log about 1 meter in diameter, which supported a lush growth of ivy (*Hedera helix* L.). Active entrance holes were at ground level on both sides of the log. The log was well shaded, although the west entrance received some direct afternoon sun.

To facilitate sampling, I constructed devices to restrict yellowjacket access to the nest at each entrance. To sample from the east entrance, I sealed it and netted the returning foragers as they hovered near it. After separating prey from the workers by shaking the net, I either allowed workers to fly from the net or anaesthetized them with carbon dioxide and removed them. A typical 40 minute net-sampling session involved approximately 40 sweeps of the net.

Beginning April 5, 1985, I used a modified funnel trap to collect from the west entrance. This passive method was more efficient at collecting foragers returning with prey. The trap was left in place

approximately 15 minutes per sampling session. Captured workers were anaesthetized and shaken from the trap. Anaesthetized workers were returned to the vicinity of the nest entrance for which they had been bound. Items separated from the workers were immediately transferred to 70% EtOH.

I identified sorted samples to lowest feasible taxonomic levels with the assistance of workers at the Essig Museum, University of California, Berkeley. An item which was recognizable as a single prey load was counted even if it was only a fragment of an organism. For example, a honeybee abdomen counted as one record of *Apis mellifera* L.

I visited the colony to observe wasp behavior daily from January 5 to May 10, 1985, and sampled approximately weekly. Time of day and environmental conditions during sampling varied somewhat, but most sessions were during the early to mid afternoon of bright sunny days.

Results

I analyzed a total of 1306 items, many of which were only fragments and/or badly mauled. Precision of identification was variable . Thus, while some relatively intact prey items could be identified to species, other more macerated fragments of arthropods could not be identified below phylum. Because there is no way to know which items were captured live (predation *sens. str.*) and which were scavenged, I classified all food items as prey. No items of food made or prepared by humans were identified.

The 914 prey items that could be identified at least to order are summarized in Table 1 according to taxa and collection dates.[1] Temporal variation of selected prey items in the colony's diet, illustrated in Figure 1, reflects the sequential availability of potential prey species, based on their life history patterns.

I began the study during the flight period of the sawfly, *Xyela radiatae* Burdick, when adults were so abundant that they actually crawled into my net during several collection sessions. Accordingly, *X. radiatae* was the dominant prey item in January (79% of determined specimens). Yellowjackets commonly hunted in the short

[1]A more detailed list of prey is available from the author on request.

Table 1. Prey items taken from *Paravespula vulgaris* foragers. Totals are inclusive; each higher category includes numbers of identified prey in lower categories within the hierarchy, if any.

	DATE																					
	January						February				March					April				May	
Prey Item	1	5	10	16	22	29	4	8	15	22	1	7	15	22	29	5	12	20	26	3	10
N	12	28	79	78	61	82	18	46	21	64	20	46	31	83	83	49	11	32	19	27	24
Annelida																					
Oligochaeta (Earthworm)	–	–	1	–	–	1	–	3	1	1	–	1	–	1	1	–	–	–	–	–	–
Arthropoda																					
Araneae (Spider)	–	1	–	2	–	6	–	11	2	4	2	8	2	2	4	–	1	1	–	–	2
Theridiidae	–	–	–	1	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Salticidae	–	–	–	1	–	–	–	1	1	1	–	2	–	1	1	–	–	–	–	–	1
Clubionidae	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anyphaenidae	–	1	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Thomisidae	–	–	–	–	–	–	–	–	–	1	1	1	–	–	1	–	–	–	–	–	–
Linyphiidae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Oxyopidae	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Pseudoscorpiones	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Insecta																					
Odonata: Zygoptera	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	–
Psocoptera	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemiptera (s.l.)	–	1	2	3	3	12	5	8	1	4	1	5	8	4	1	5	–	8	9	18	11
Reduviidae	–	–	1	2	1	1	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–
Cicadellidae	–	–	–	1	–	3	6	–	2	–	1	5	–	–	–	–	–	–	–	–	2
Membracidae	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	8	5	15	6

Table 1. (con'td)

Prey Item	DATE January 1	5	10	16	22	29	February 4	8	15	22	March 1	7	15	22	April 29	5	12	20	May 26	3	10
Neuroptera (larva)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1
Coleoptera	1	–	–	–	3	6	1	3	10	22	1	12	2	10	3	–	–	2	–	2	–
Byturidae: Byturellus grisescens	–	–	–	–	2	6	1	2	10	12	1	4	2	2	–	–	–	–	–	–	–
Malachiidae: Microlipus laticeps	–	–	–	–	–	–	–	–	–	–	–	–	–	7	3	–	1	–	–	1	–
Coccinellidae (larva)	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Chrysomelidae	1	–	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	–	–	–	–
Lepidoptera (larva)	–	1	–	2	1	8	1	5	6	18	13	7	13	52	72	43	10	19	10	2	2
Geometridae	–	–	–	1	–	1	–	1	–	2	–	3	7	24	18	2	–	–	3	–	–
Noctuidae	–	–	–	–	–	1	–	–	–	2	–	1	1	5	–	–	–	1	–	–	–
Tortricidae	–	–	–	–	–	–	–	–	–	–	–	–	8	3	13	–	–	6	–	–	–
Gelechiidae	–	–	–	–	–	–	–	–	–	1	–	–	–	1	3	–	–	2	–	–	–
Plutellidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	4	–	–	–
Hymenoptera	11	20	73	69	54	39	10	9	1	14	2	6	1	6	–	1	–	1	–	2	3
Symphyta	11	20	71	68	51	27	9	7	–	4	2	1	–	5	–	–	–	–	–	1	1
Xyelidae: Xyela radiatae	11	20	71	68	51	26	9	7	–	–	–	–	–	–	–	–	–	–	–	–	–
Tenthredinidae: Periclista	–	–	–	–	–	1	–	–	–	4	2	–	–	2	–	–	–	–	–	–	–
Apocrita	–	–	2	–	3	7	1	2	1	9	–	3	1	1	–	–	–	–	–	–	1
Ichneumonidae	–	–	–	–	2	4	–	–	–	1	–	1	1	–	–	–	–	–	–	–	1
Cynipidae	–	–	1	–	–	–	–	–	1	4	–	1	–	1	–	–	–	–	–	–	–
Chalcidoidea	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Formicidae	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–

Table 1. (con'td)

Prey Item	DATE																					
	January						February				March					April				May	
	1	5	10	16	22	29	4	8	15	22	1	7	15	22	29	5	12	20	26	3	10
Vespidae: Paravespula	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Apidae: Apis mellifera	–	–	1	–	1	3	1	2	–	1	–	–	–	–	–	–	–	–	–	–	–
Diptera	–	5	–	1	–	10	1	7	–	1	1	6	3	9	2	–	–	–	–	3	5
Nematocera	–	5	–	–	–	5	–	2	–	–	–	2	–	1	–	–	–	–	–	–	–
Brachycera	–	–	–	1	–	5	1	5	–	1	1	3	3	4	2	–	–	–	–	1	5
Orthorrhapha	–	–	–	–	–	2	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–
Syrphidae	–	–	–	–	–	1	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–
Dolichopodidae	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyclorrhapha	–	–	–	1	–	3	1	5	–	–	1	2	2	2	1	–	–	–	–	–	5
Acalypteratae	–	–	–	–	–	1	–	2	–	–	–	–	1	–	–	–	–	–	–	–	–
Calypteratae	–	–	–	1	–	2	1	2	–	–	1	1	1	2	1	–	–	–	–	–	–

grass near the colony, especially beneath *Pinus radiata,* the xyelid's host plant (Burdick, 1961). Workers flying close to the ground thoroughly scanned plant surfaces, paying special attention to areas of contrasting colors and textures to locate and capture surface-inhabiting arthropods, which comprised the vast majority of the colony's prey. I observed attempted and successful captures of *X. radiatae* adults on grass blades. These sawflies, presumably newly emerged from underground pupae, seemed especially vulnerable to *Paravespula* predation.

In late February, the beetle, *Byturellus grisescens* (Jayne), reached its greatest abundance in the prey samples. Although I was unable to capture any of these beetles myself, they oviposit on oak catkins (J. Doyen, pers. comm.). This was the first good suggestion of the importance of oak insects in the diet of the colony. Of the many tree species occurring on the University campus, *Q. agrifolia,* a native, is one of the most common.

As the season progressed, hunting at ground level became less frequent, and foragers shifted their attention to tree foliage, particularly *Q. agrifolia.* Local population explosions of caterpillars (Lepidoptera) in late March and April, and the treehopper, *Cyrtolobus vanduzeei* Goding, in May were also tracked by this colony (Fig. 1). Again, most of the identifiable Lepidoptera and Membracidae were of taxa known to be associated with *Q. agrifolia.*

Discussion

The wide taxonomic array of arthropod prey and focus on abundant prey species shown by the observation colony are consistent with known habits of the genus *Paravespula.* Scavenging, a characteristic of the genus, is suspected in the collection of pieces of earthworm and *Apis mellifera,* as well as some other items which were tangled in silk strands and may have been taken from spider webs. Collection of proteinaceous food prepared for human consumption, a habit accounting for the pest status of *P. vulgaris* in many areas (MacDonald *et al.,* 1976) was not detected. Although such food was certainly within the flight range of foraging workers, it was not common in the immediate vicinity of the colony, and foragers may have become conditioned to locate arthropod prey. In general, the data from the observation colony indicate that the flesh

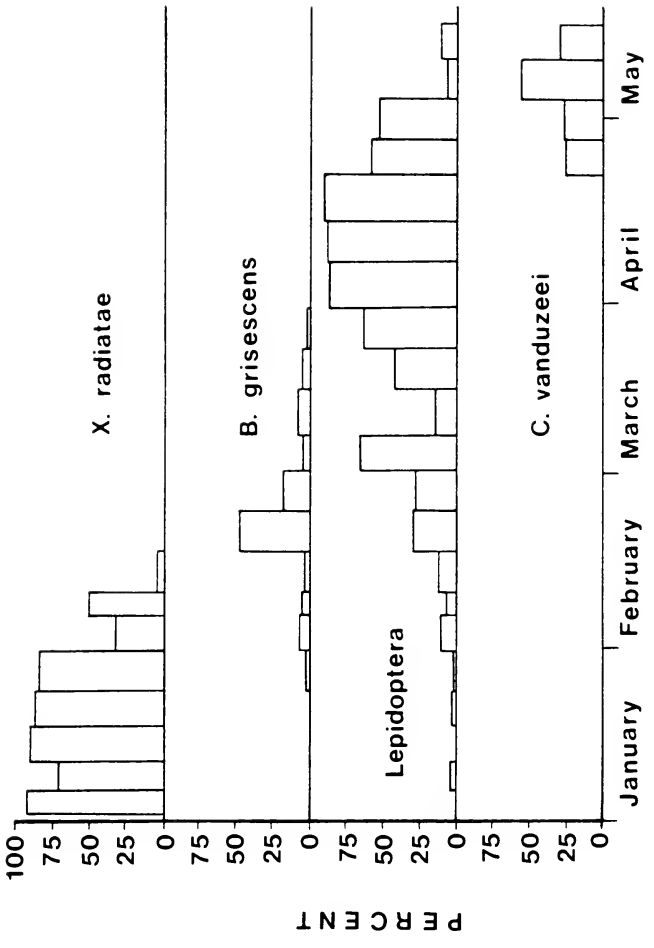


Figure 1. Temporal variation in prey composition. Percentages of identified items comprised of *Xyela radiatae* Burdick, *Byturellus grisescens* (Jayne), Lepidoptera larvae, and *Cyrtolobus vanduzeei* Goding.

collection behavior of perennial colonies probably does not differ substantially from that of annual colonies.

Summary

This study suggests that in coastal California natural food resources are sufficient to sustain healthy overwintering *Paravespula* colonies. The *P. vulgaris* colony under study took a wide assortment of prey, and adjusted its diet according to local abundances of prey species. *Q. agrifolia,* a native tree common in the vicinity of the colony, was the source of many of the insects comprising its diet.

Acknowledgments

The success of this study resulted from the contributions of many co-workers in the Department of Entomological Sciences, University of California, Berkeley. Vernard Lewis discovered the colony, and Tina Sterret provided technical assistance. Howell Daly, John Doyen, Jerry Powell, Evert Schlinger, Stuart McKamey, Woodrow Middlekauff, and Jim Whitfield assisted in identifying prey. Howell Daly, John De Benedictis and Woodrow Middlekauff reviewed the manuscript and offered suggestions for its improvement. Financial support was furnished in part by the Northern California chapter of the ARCS Foundation.

Literature Cited

Archer, M. E.
1977. The weights of forager loads of *Paravespula vulgaris* (Linn.) (Hymenoptera: Vespidae) and the relationship of load weight to forager size. Ins. Soc. **24**(1): 95–102.

Broekhuizen, V. S., and C. Hordijk
1968. Untersuchungen über die Beute von *Paravespula vulgaris* L. (Hym., Vespidae) und ihre Abhängigkeit von der Beutetierdichte. Z. Ang. Entomol. 62: 68–77.

Burdick, D. J.
1961. A taxonomic and biological study of the genus *Xyela* Dalman in North America. Univ. Calif. Publ. Entomol. **17**(3): 285–356.

Free, J. B.
1970. The behavior of wasps (*Vespula germanica* L. and *V. vulgaris* L.) when foraging. Ins. Soc. **17**(1): 11–20.

HEINRICH, B.
1984. Strategies of thermoregulation and foraging in two vespid wasps, *Dolichovespula maculata* and *Vespula vulgaris*. J. Comp. Physiol. B **154**: 175–180.

KEMPER, V. H., AND E. DOHRING
1962. Untersuchungen über die Ernährung sozialer Faltenwespen Deutschlands, inbesondere von *P. germanica* und *P. vulgaris*. Z. Ang. Zoologie **49**(2): 227–280.

KLEINHOUT, J.
1958. Het verzmelen van prooien van sociale wespen. De Levende Natuur **61**: 179–182.

MACDONALD, J. F., R. D. AKRE, AND W. B. HILL
1974. Comparative biology and behavior of *Vespula atropilosa* and *V. pensylvanica* (Hymenoptera: Vespidae). Melanderia **18**: 1–65.

MACDONALD, J. F., R. D. AKRE, AND R. W. MATTHEWS.
1976. Evaluation of yellowjacket abatement in the United States. Bull. Entomol. Soc. Amer. **22**(4): 397–401.

SPRADBERY, J. P.
1973. Wasps. University of Washington Press, Seattle. xvi + 408 pp.

YOUNG LARVAE OF *ECITON* (HYMENOPTERA: FORMICIDAE: DORYLINAE)[1]

By George C. Wheeler and Jeanette Wheeler
3358 NE 58th Avenue,
Silver Springs, Florida 32688

I. Instars

In our previous studies of ant larvae we have been concerned primarily with generic characterizations and differences based on mature larvae. We described immature stages when available, which wasn't often. And even when we did, we didn't know the instars. Never have we had a complete larval series from egg to semipupa. Yet many authors have stated quite glibly the number of larval instars. At least it seems glib to us, for we consider it hard work to establish the number of instars. To do this we require that following specimens: a first-instar larva inside an egg ready to hatch; a second instar larva inside a first ready to moult; a third-instar inside a second-instar ready to moult; etc.; and finally a mature larva. How can we prove maturity? By comparison with a semipupa, which will reveal all characters of a mature larvae except shape. For further confirmation one should have a worker pupa or a worker to verify size. The identification of sexual larvae presents a further complication. If the larva is larger than a worker semipupa it is probably a sexual or at least a queen. In most species we have not been able to recognize younger sexual larvae.

In polymorphic species (e.g., *Eciton, Atta, Acromyrmex, Camponotus*) such procedures are even more difficult. How can one tell whether a small larva is a young major or a mature minum or whether a large larva is a half-grown major or a mature intermediate?

Two interesting papers afford a partial solution to this problem: Tafuri (1955) on *Eciton hamatum* and Lappano (1958) on *E. burchelli*

Eciton is an ideal genus for such a study: there can be no mixing of broods; except for one all-sexual brood per year, all larvae will

[1]*Manuscript received by the editor June 30, 1986.*

become workers. All one needs to determine, then, is whether the larvae in such a brood foreshadow adult polymorphism, and if so, how? The solution depends upon the fact that at the middle of the statary phase the queen lays during one week a single batch of 60,000 to 130,000 eggs and then no more until the next statary phase.

"In *E. hamatum* the adult polymorphic workers form a continuous series from the smallest worker minor to the largest soldier form.... Besides differences in size there are apparent qualitative differences in this series marked primarily by the exceptional hooked manidbles and head pattern of the major workers." (Tafuri 1955: 32.) In the larvae, however, such differences "are not noticeably apparent." Any distinction of growth stages (i.e. nomadic days) is impossible on the basis of body size alone, because of overlapping. The larvae likewise form a smooth series from the smallest to the largest forms. The author therefore based his determination of larval age (in nomadic days) on the allelomorphic growth of the imaginal leg discs.

"[It] is highly probable that the largest larvae of any stage have developed from the eggs first to be laid and first to hatch and represent the potential major workers of the mature brood. Similarly, the smallests [larvae] presumably develop from the eggs last to be laid and last to hatch and represent the potential workers minima of the mature brood." (Lappano 1958: 49).

From these two articles we get the impression that larval development in *Eciton* is a smooth process from hatching to pupation without any such interruptions as molts. The word "instar" is not found in either of these articles.

So we re-examined our supply of doryline larvae and found graded series of larvae of *Eciton hamatum* sent to us by the late Dr. T. C. Schneirla (including some of the sample studied by Lappano) from Barro Colorado Island (Panama) and a similar supply of *E. burchelli* larvae collected in Trinidad by Dr. N. A. Weber.

The great advantage of the Tafuri/Lappano method is that it requires no technique and can be applied to either living or preserved material. However, after applying our tedious technique (Wheeler and Wheeler 1960) of cleaning, staining and mounting in balsam, we found that we had the prerequisite for identifying all instars, except the mature larva, which we had already studied (Wheeler and Wheeler 1984). We should warn, however, that the

preparation of these immature was the most difficult we have ever experienced.

II. Interspecific Differences

Whenever we have had two or more species in the same genus, we have either given a complete description of each or at least mentioned differences. We have not been willing to go beyond that, because we did not know the extent of intranidal or internidal or intraspecific differences. Here at last, we have series of *Eciton burchelli* and *E. hamatum* which embolden us to make a tentative comparison. Table 1 gives a few characters which can be measured for each instar in each species. The "spiracle diameter" which we have not mentioned previously, is the diameter of the atrium and not of the opening into it.

Eciton burchelli Westwood
Figure 1

Egg. About 0.3 × 0.54 mm.

First Instar Larva. Length 0.59–0.9 mm long (average 0.73 mm). Head greater in diameter than body which tapers to the posterior end. Anus subterminal. Segmentation distinct. Spiracles about 0.001 mm in diameter. Entire integument sparsely spinulose, the spinules minute and isolated. Body hairs lacking. Cranium subcircular. Antennae minute, just above midlength of cranium. Head hairs lacking. Labrum arcuate, about 1/4 width of cranium; with a few spinules and sensilla on and near ventral surface. Mandible with straight apical tooth which is feebly sclerotized, remainder not sclerotized. Maxilla broadly paraboloidal and appearing adnate; palp represented by 7 sensilla in a loose cluster; galea represented by 2 sensilla. Labial palp represented by 3 sensilla; opening of sericteries a short transverse slit.

Second Instar Larva. Length (through spiracles) 0.9–1.5 mm (average 1.2 mm). Head same diameter as T1 and AV, the widest parts of the body. Spiracles about 0.003 mm in diameter. Entire integument spinulose, the spinules moderately abundant and isolated. Body hairs 0.006–0.012 mm long; few, most on T1, fewer on T2 and T3. Cranium subhexagonal; integument with a few spinules. Antennae just above midlength of cranium. About 30 head hairs;

Table 1. Comparison of some characters in each instar of *Eciton burchelli* and *E. hamatum*.

	Instar I		Instar 2		Instar 3		Instar 4		Instar 5	
Character	*E. b.*	*E. h.*	*E. b.*	*E. h.*	*E. b.*	*E. h.*	*E. b.*	*E. h.*	*E. b.*	*E. h.*
Body length	0.59–0.9	0.5–0.9	0.9–1.5	1.3–1.8	1.5–2.9	2.5–3.5	3.2–7	3.5–4	5–9.2	4.4–12
Spiracle diameter	0.001	0.01	0.003	0.006	0.013	0.011	0.019	0.013	0.03	0.025
Body hairs length			0.006–0.012	0.006	0.037–0.075	0.013–0.037	0.025–0.15	0.025–0.05	0.1–0.2	0.075–0.2
number	none	none	few on T1–T3	ca 20 on T1	most on T1–T3	sparse, fewer post.	most on T1–T3 + A8–A10	most on T1+ A9–A10	uniform moder. abundt.	uniform moder. abundt.
Head width	0.15–0.19	0.2–0.33	0.22–0.25	0.23	0.29–0.37	0.33	0.4–0.49	0.36–0.48	0.66	0.57–0.63
Head hairs length			0.006–0.019	0.006	0.03–0.075	0.013–0.037	0.025 0.1	0.025–0.05	0.033–0.1	0.03–0.165
number	none	none	ca 30	ca 12	ca 60	ca 50	ca 100	ca 80	ca 125	ca 120

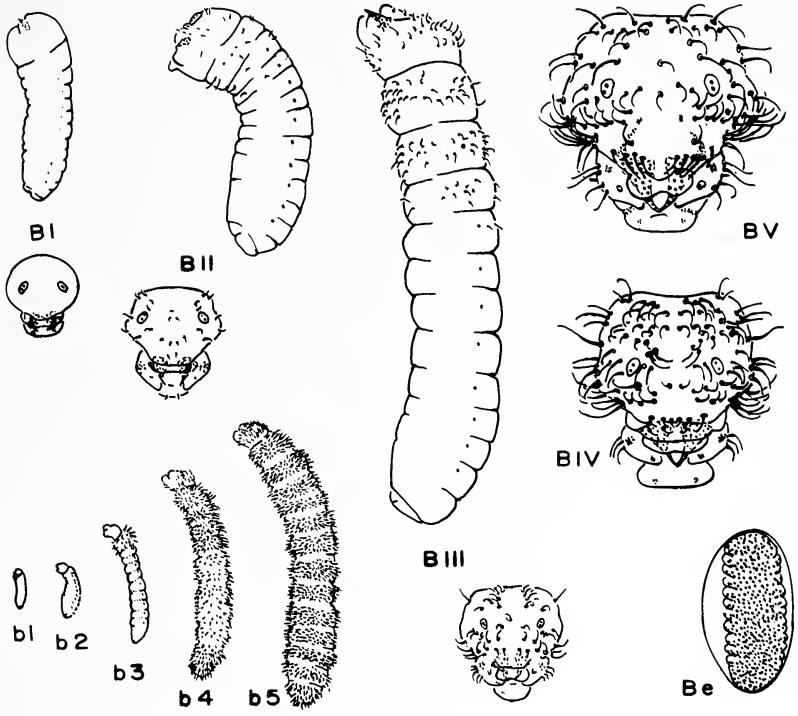


Figure 1. *Eciton burchelli.* BI, first instar larva; BII, second instar larva; BIII, third instar larva; BIV, head of fourth instar larva; BV, head of fifth instar (= mature) larva. Side views, × 38; head in anterior view, × 50. Be, egg nearly ready to hatch, × 38. b1–b5, larvae of the five instars in side view to show relative sizes, × 9.

0.006–0.019 mm long; simple. Labrum feebly bilobed. Otherwise similar to first instar larva.

Third Instar Larva. Length (through spiracles) 1.5–2.9 mm. Spiracles about 0.013 mm in diameter. Integumentary spinules more conspicuous and in rows. Body hairs 0.037–0.075 mm long; more numerous but largely confined to thorax. Cranium subhexagonal and with bulging genae. Head hairs 0.036–0.075 mm long, slender and flexuous; some dorsal hairs curved downward and a few ventral upward; about 60 present. Labrum with transverse rows of spinules on anterior and posterior surfaces on and adjacent to ventral surface; median sulcus with about 10 sensilla on and near ventral surface. Mandible with apical tooth slightly curved medially and with

medial border erose. Maxilla with apex narrowly paraboloidal and bearing rather long spinules in short transverse rows; palp represented by a cluster of 8 sensilla; galea a slight elevation with 2 sensilla. Anterior surface of labium with minute spinules in short transverse rows. Otherwise similar to second instar larva.

Fourth Instar Larva. Length (through spiracles) 3.2–7 mm. Diameter uniform. Spiracles about 0.019 mm in diameter. Integument with minute spinules in transverse rows. Body hairs 0.025–0.15 mm long; on all somites but most numerous on T1–T3 and AVIII-AX. Head hairs 0.025–0.1 mm long; about 100; several ventral hairs curved upward. Labrum with lateral borders sinuate. Maxillary palp represented by a cluster of 9 sensilla; galea a short sclerotized frustum with 2 apical sensilla. Labium with anterior surface bearing numerous short transverse rows of spinules; opening of sericteries a transverse slit in the bottom of a depression. Otherwise similar to third instar larva.

Mature larva. Length (through spiracles) 5–9.2 mm. Compared to *E. hamatum* in our 1984: 270.

Material studied: numerous larvae from Trinidad, courtesy of Dr. N. A. Weber.

Eciton hamatum (Fabricius)
Fig. 2

Egg. About 0.25 × 0.5 mm.

First Instar Larva. Length 0.5–0.9 mm. Head of same diameter as T1; body straight, diameter decreasing posteriorly. Spiracles about 0.001 mm in diameter. Entire integument spinulose, the spinules minute and isolated. No body hairs. Cranium transversely subelliptical. Antennae above midlength of cranium. No head hairs. Labrum cresentic. Mandibles subtriangular, with straight apical tooth, feebly sclerotized. Maxilla with broadly paraboloidal apex, appearing adnate; palp represented by a cluster of 6–8 sensilla; galea represented by 2 sensilla. Labial palp represented by 3 sensilla; opening of sericteries very short.

Second Instar Larva. Length (through spiracles) 1.3–1.8 mm. Body of nearly uniform diameter. Spiracles 0.006 mm in diameter. Integument coarsely spinulose, the spinules isolated. Body hairs 0.006 mm long, simple, few, mostly on venter of T1. Cranium transversely subelliptical. Head hairs about 0.006 mm long, simple, about

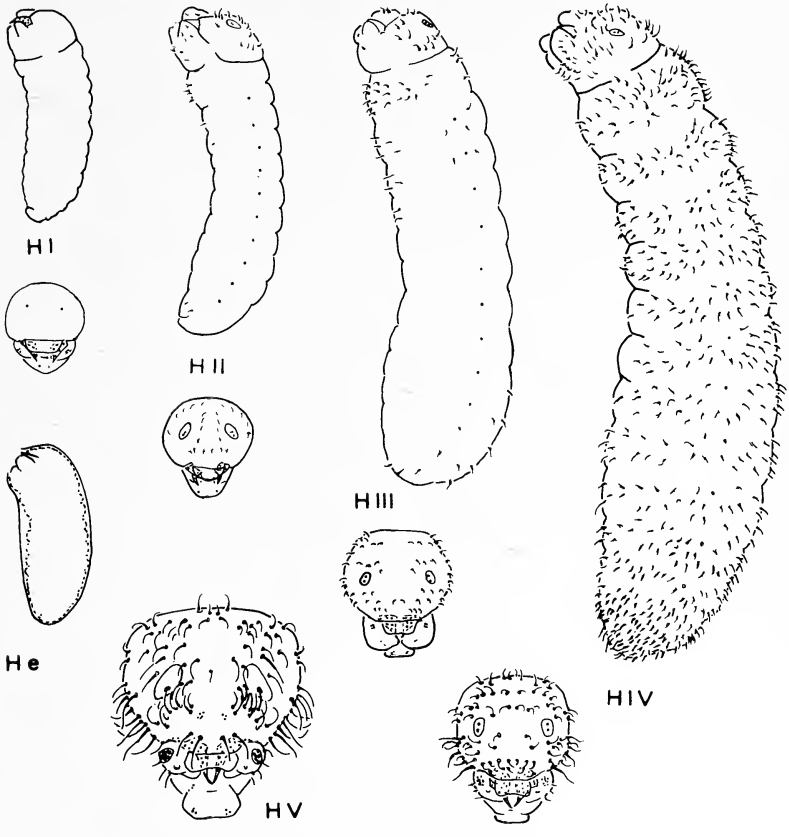


Figure 2. *Eciton hamatum.* HI, first instar larva; HII, second instar larva; HIII, third instar larva; HIV, fourth instar larva; HV, head of fifth instar (= mature) larva. Side views, × 38; heads in anterior view, × 50. He, larva inside egg with mouth parts breaking shell, × 38.

12. Maxillary palp represented by a cluster of 10 sensilla. Otherwise similar to first instar larva.

Third Instar Larva. Length (through spiracles) 2.5–3.5 mm. Widest at AVII. Spiracles about 0.01 mm in diameter. Body hairs 0.013–0.037 mm long, most on thorax and AI and a few of AVI-AX. Cranium slightly broader than long. Head hairs 0.013–0.037 mm long, about 50. Labrum feebly bilobed. Mandible with apical half more narrowly tapered to a sharp point, apex straight. Maxillary

palp a cluster of 8 sensilla. Labium with a few minute spinules medially. Otherwise similar to second instar larva.

Fourth Instar Larva. Length (through spiracles) 3.5–4 mm. Spiracle diameter about 0.013 mm. Body hairs 0.025–0.05 mm long, sparse, most numerous on T1 and AIX-AX. Head hairs 0.025–0.05 mm long; some dorsal hairs curved downward, few ventral upward; about 100. Labrum bilobed and with sinuate lateral borders; with a few spinules medioventrally. Mandible with apical half tapering to a narrow sharp point and slightly curved medially. Maxillary palp a cluster of 7 sensilla. Otherwise similar to third instar larva.

Fifth Instar Larva = Mature Larva. Length (through spiracles) 4.4–12.1 mm. Spiracles about 0.025 mm in diameter. Entire integument densely and coarsely spinulose, the spinules rather long and the rows so close together that the spinules overlap. Body hairs moderately numerous; 0.075–0.2 mm long, longest around anus. Cranium with entire integument spinulose, the spinules isolated or in rows. Head hairs 0.033–0.165 mm long; about 120; some ventral hairs curved strongly upward. Labrum with a few sensilla ventromedially; spinulose, the spinules minute and isolated or in short rows, on all surfaces. Mandible with 3–4 small denticles on apical half. Maxilla broadly paraboloidal and appearing adnate, entire surface spinulose, the spinules isolated or in short rows; palp a slightly elevated sclerotized cluster of 8 sensilla; galea a small sclerotized cone with 2 apical sensilla. Labium with entire surface spinulose, the spinules isolated or in short rows. Otherwise as in the fourth instar larva. See our 1984: Fig. 9 on p. 271.

Material studied: numerous larvae from Barro Colorado Island, Panama, courtesy of the late Dr. T. C. Schneirla.

Our tentative conclusions are:

1. In each species instars may be distinguished by spiracle diameter; body hair length and distribution; head hair length and number.

2. The two species are indistinguishable in the first and fifth instars. In the second instar they may be separated by a spiracle diameter; uniformity in length and distribution of body hairs; length and number of head hairs. In instar three: length and distribution of body hairs; length and number of head hairs. In the fourth instar: spiracle diameter; distribution and uniformity of length of body hairs.

Literature Cited

Lappano, Eleanor R.

1958. A morphological study of larval development in polymorphic all-worker broods of the army ant *Eciton burchelli*. Insectes Sociaux 5: 31–66.

Tafuri, J. F.

1955. Growth and polymorphism in the larva of the army ant (*Eciton (E.) hamatum* Fabricius). Jour. New York Entomol. Soc. **63**: 21–41.

Wheeler, G. C. and Jeanette Wheeler.

1960. Techniques for the study of ant larvae. Psyche **67**: 87–94.

1984. The larvae of the army ants: a revision. J. Kansas Entomol. Soc. **57**: 263–275.

SPATIAL DISTRIBUTION OF CASTES WITHIN COLONIES OF THE TERMITE *INCISITERMES SCHWARZI*[1]

By Peter Luykx, Jack Michel, Jeannette K. Luykx[2]

Introduction

In order to describe the social organization of termites with any precision, it is essential to have quantitative information on the spatial distribution of castes within the colony. Such information is important not only for descriptive purposes, but also because it can give clues to the interactions that take place within and among the different castes.

Precise information on caste distribution within colonies is ordinarily not easy to obtain, because colonies are usually completely disrupted in opening them up, and because in any case the description of spatial organization in large three-dimensional or dispersed colonies in quantitative terms is difficult. But in some locations, colonies of certain kalotermitid species offer a unique opportunity to obtain just such data. In the Oleta River Mangrove Preserve just north of Miami, Florida, large numbers of *Incisitermes schwarzi* are found in slender, dead mangrove tree-trunks, where they form nearly one-dimensional colonies. Because the colonies are relatively small and are entirely above ground, and because the termites do not forage outside the wood, whole colonies can be collected in segments and analyzed. The results of such an analysis are the subject of this paper.

While some of the findings of this study—the association of larvae with the royal pair, the aggregation of nymphs and alates—have been noted before in a casual way in the general descriptions of many other students of the Isoptera (e.g., Imms, 1919; Grassé, 1949), this is the first *quantitative* description of the spatial distribution of castes in a termite, and is worth putting on record for that reason.

---

[1]This is contribution no. 245 from the Program in Tropical Biology, Ecology, and Behavior, Dept. of Biology, Univ. of Miami.

[2]Department of Biology, University of Miami, Coral Gables, FL 33124, U.S.A.

Manuscript received by the editor June 7, 1986

Materials and Methods

Colonies of *Incisitermes schwarzi* Banks (Kalotermitidae) were collected from the Oleta River Mangrove Preserve, North Miami Beach, Florida, on four collecting trips carried out between the hours of 9 a.m. and 12 noon, at low tide, during the months of March, April and May, 1985. (In this species, the annual reproductive cycles of different colonies are not synchronized, so that different reproductive stages may be found at any time of the year (Luykx, 1986).) Colonies of *I. schwarzi* were found only in standing trunks, not in fallen dead wood. Small, dead mangrove trees *(Laguncularia racemosa)* 3–4 cm in diameter and 1–3 m tall were selected and quickly cut into 10–12 cm segments with a chain saw. To minimize the possibility of redistribution of the termites during the sectioning, the tree was not touched before the first cut was made; the first cut was made at ground level, and all subsequent cuts were made with the tree held horizontally (to prevent the vibration of the saw from shaking termites from one segment to a lower segment). Complete sectioning of each tree was accomplished with 60–90 seconds of the first cut. We estimate we might have killed about 5% of the termites in each colony with the saw.

If a dead tree had termites (about half the ones chosen did), the segments were put into numbered plastic bags and taken back to the laboratory for opening and analysis. Determination of the sex and caste of each individual in each segment was usually carried out within one day of collection. We obtained useful data on a total of 9 complete colonies.

For the purpose of this analysis, seven castes were distinguished: larvae (the first three instars), workers (or pseudergates: later instars, with wing buds not readily seen with the naked eye), early- and late-stage nymphs (the last two pre-imaginal molts, with elongated wing pads easily seen with the naked eye), alates (imagos), soldiers (small and large), and reproductives (king and queen). In the Kalotermitidae, the larvae, workers, nymphs, and alates represent a developmental series; the only truly sterile castes are the soldiers.

Males and females occur in all castes, with typically a slight excess of males among the soldiers and among the nymphs (Luykx, 1987). Except for a slight statistical tendency for soldiers of one sex to be associated with non-soldiers of the opposite sex, the sexes within the

colonies were distributed essentially at random (Luykx *et al.,* 1987), and will not be further considered here.

Results and Conclusions

The distribution of the castes in nine pieces of wood is represented in Fig. 1. In eight of the nine pieces a single colony was found. In one piece two colonies were found: PL487, and a small incipient colony consisting only of the royal pair, one soldier, one larva, and five workers. This small colony, PL488, contained entirely within a single short segment, does not, of course, give any information on caste distribution, and will not be considered further.

The major portion of most of the colonies (with the exception of PL476 and PL486) was found toward the bottom, where the wood was less deteriorated and less fragile. (The topmost portions of the dead trunks are often thoroughly tunneled and in a highly deteriorated condition, and rarely contain any termites.) In most colonies, the king and queen were found together in the lower part of the colony (Fig. 2). It seems likely that the royal pair might initiate the colony at any level in suitable dead wood, but then move down into sounder wood as the colony grows.

Larvae (the first two or three instars) were found preferentially in the same segments as the royal pairs. As illustrated in Fig. 2, among the segments with reproductives, 7 out of 9 had more larvae than expected for those segments. Twelve of the 14 segments with more larvae than expected also had a reproductive or was adjacent to one that did. That this is a real association, and not just a common tendency for both larvae and reproductives to be located in the lower parts of the colony, is suggested by colony PL476, the one colony in which the reproductives were found in a segment in the *upper* part of the colony: in this colony the larvae also were concentrated in this same segment (Fig. 2).

The members of the different castes representing successive stages of development—workers, early-stage nymphs, late-stage nymphs and alates—showed successively greater degrees of aggregation. For example, when the cumulative proportions of workers, early-stage nymphs, and late-stage nymphs in colony PL482 are plotted separately as a function of the segment number in which they were found, it is apparent that the workers were distributed over a wider number of segments than the early-stage nymphs, and the early-stage

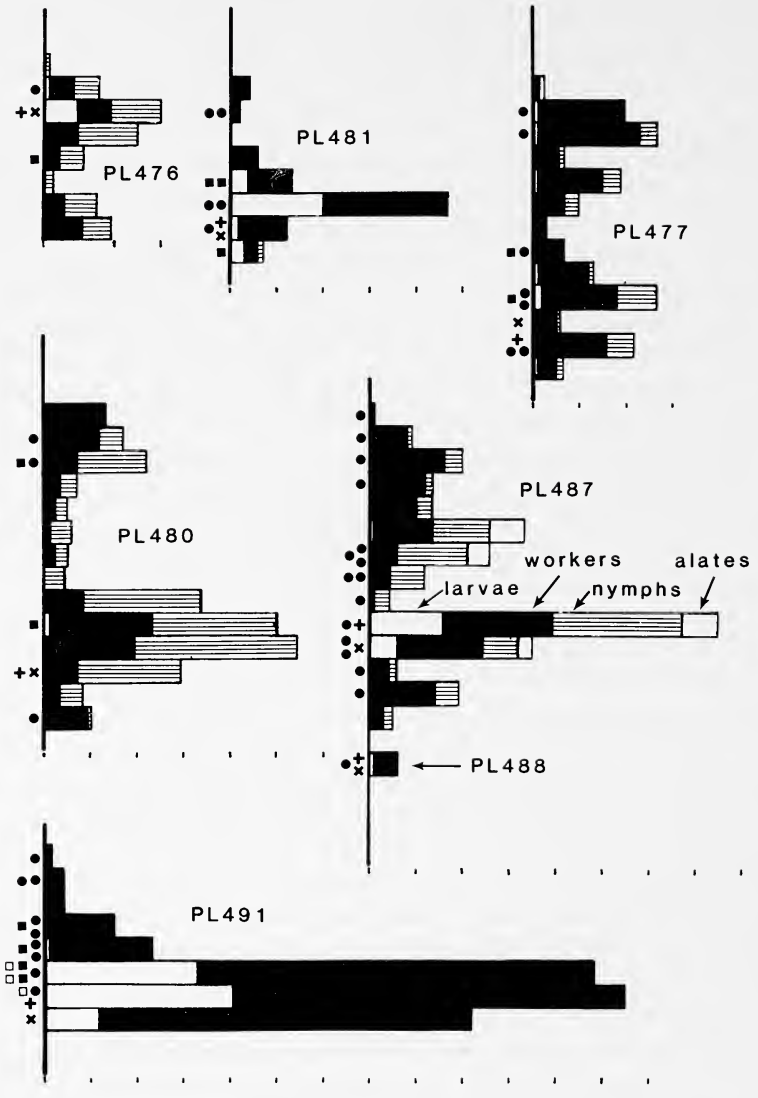
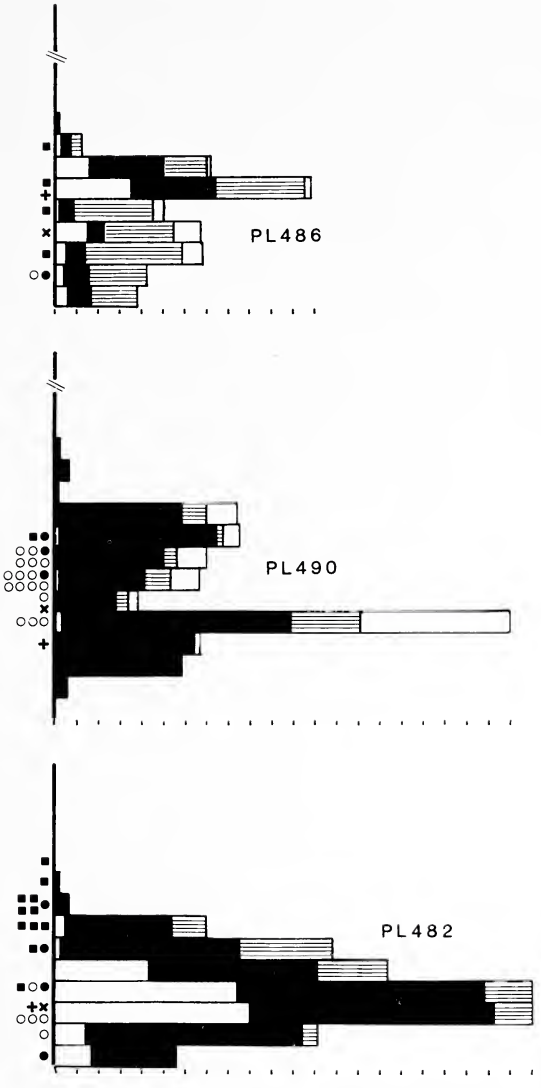


Fig. 1. Segment-by-segment distribution of castes in colonies contained in 9 pieces of wood. The base line indicates the height of the wood in each case. Represented on the left side of each colony are the numbers of individual soldiers (solid symbols) and presoldiers (open symbols)—circles, small soldiers and presoldiers;



squares, large soldiers and presoldiers. Also shown are the reproductives—+, king; ×, queen. See colony PL487 for legend for other castes. The space between successive tick-marks at the bottom of each colony represents ten individuals. Note that the scales for Figs. 1A and 1B are different.

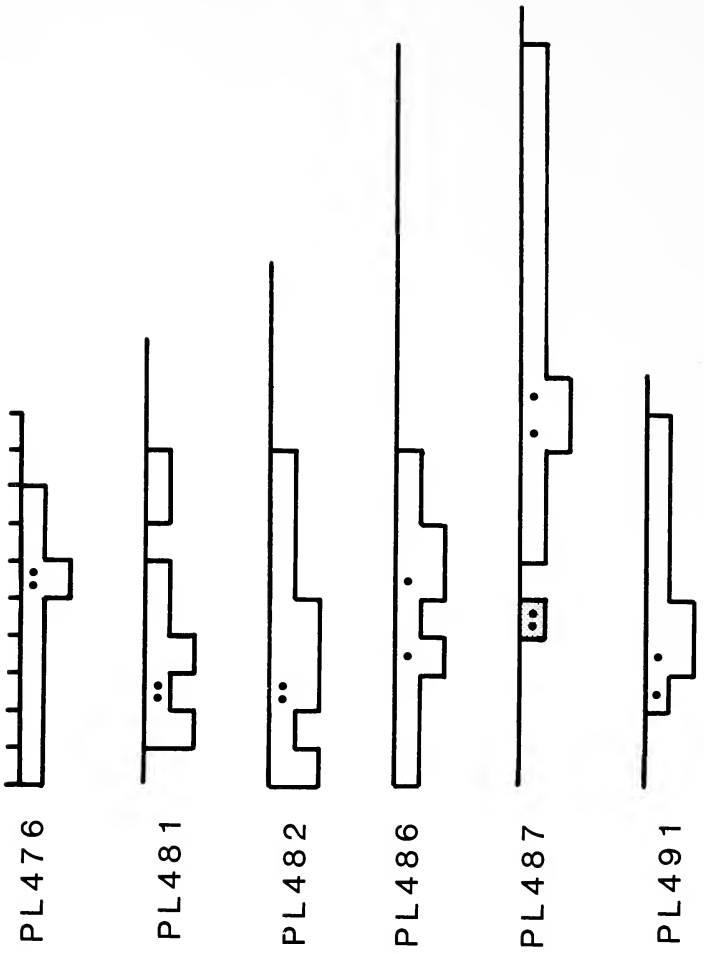


Fig. 2. Segment-by-segment distribution of larvae in relation to reproductives in 6 colonies (colonies PL477, PL480, and PL490 were omitted because they had too few larvae). The size of individual segments analyzed separately is indicated by the tick-marks on PL476. For each colony, the baseline alone indicates uninhabited wood; low boxes indicate fewer larvae, high boxes indicate more larvae than expected for that segment (based on the average number of larvae per segment for that colony). Dots represent reproductives. The shaded segment represents PL488, an incipient colony contained entirely within a single segment.

nymphs over a wider number of segments than the late-stage nymphs (Fig. 3). The variance in position of the members of a caste can be used as a measure of the dispersion or aggregation of that caste, and then compared with the position-variance for all the members of all the major castes of the colony taken together. In colony PL487, for example, the ratio of the caste variance to total colony variance was 1.30, 0.80, 0.52, and 0.40, for the workers, early-stage nymphs, late-stage nymphs, and alates, respectively. A summary of all variance ratios for all seven of the colonies with nymphs or alates is given in Fig. 4.

There was no regularity in the mean positions of the major castes in relation to each other nor in relation to the top or bottom of the colony. In several colonies (e.g., PL482, Fig. 3), the mean position of the nymphs was higher than that of the workers, but just as often the reverse was true. In colonies PL482 and PL487, the mean posi- of the early-stage nymphs was between that of the workers and of the late-stage nymphs, but in colony PL486 it was below that of those two castes. Neither was the mean position of alates (in the three colonies that had alates) consistent in relation to that of the other major castes.

The mean position of the *soldiers,* however, with the exception of those in colony PL477, was always above that for the bulk of the colony (e.g., colony PL482, Fig. 1). This makes sense in terms of the function of soldiers in defending the colony, for the wood in the upper part of the colonies is generally more deteriorated than that lower down, and presumably more susceptible to invasion by predators.

Six of the 9 colonies—PL476, PL477, PL480, PL486, PL487, and PL490—had bimodal distributions (Fig. 1). There was no clear or consistent difference between the top and bottom groups in total numbers of termites nor in overall caste composition in any of these colonies. (The excess numbers of nymphs and alates in the bottom groups of PL480 and PL486 are probably a secondary effect of the tendency of these castes to clump together.)

Discussion

The association of larvae with the reproductives has been casually noted by many students of the Kalotermitidae, but has not been

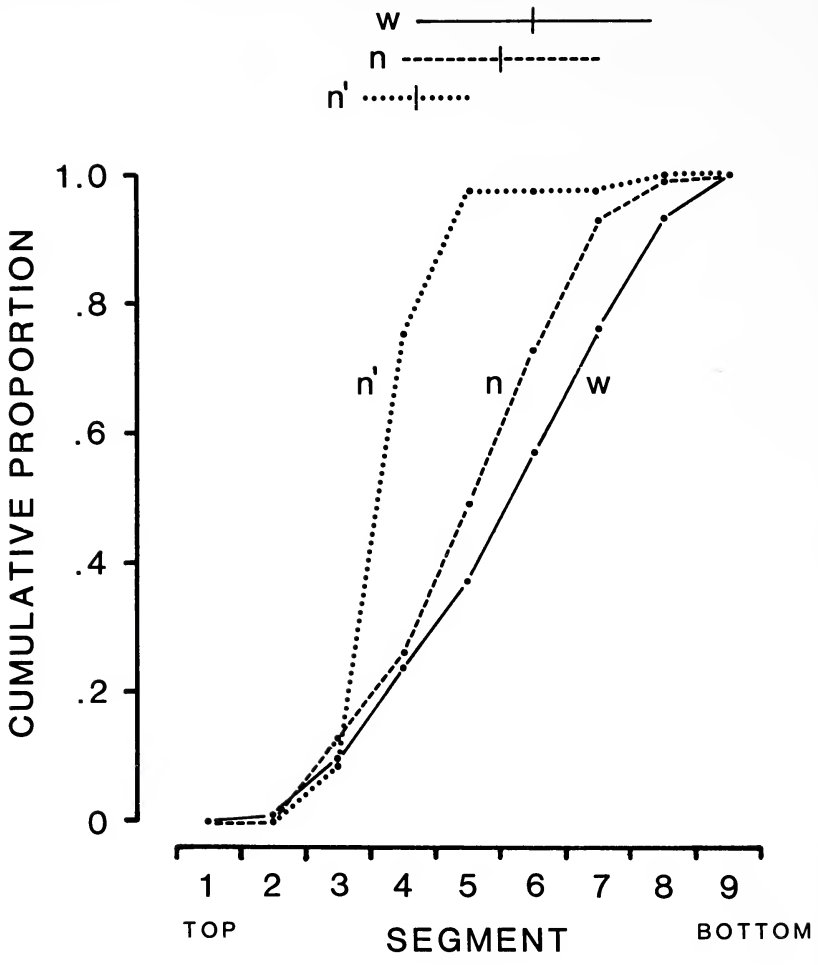


Fig. 3. Distribution of workers (w), early-stage nymphs (n), and late-stage nymphs (n') in colony PL482. The mean position and standard deviation of the distribution for each caste is indicated by the three lines at the top.

documented quantitatively until now. Certainly the larvae are mobile enough to disperse themselves more widely. Even in the laboratory, after the disruption of field-collected colonies in opening them up and transferring them to petri dishes, the larvae are often found later to have re-aggregated under one fragment of wood, often in association with the reproductives. The significance

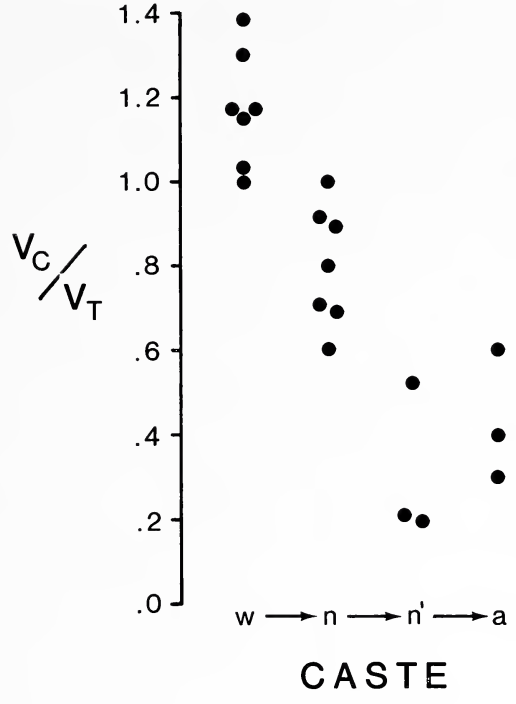


Fig. 4. Aggregation of individuals with successive developmental stage: w, workers; n, early-stage nymphs; n′, late-stage nymphs; a, alates (imagos). V_C/V_T, ratio of position-variance of members of a given caste to position-variance of all castes in the colony taken together.

of the association is not entirely clear. It is usually thought (e.g., see Wilson, 1971) that in termites the care of the youngest larvae is assumed by older siblings—this is, after all, one of the hallmarks of eusociality. It might seem surprising, therefore, that the larvae remain associated with their parents even in the presence of numerous older siblings. It may be that in some termite species, particularly among the lower termites, the parents continue to provide some essential nutrients to newly-hatched larvae, something that cannot readily be provided by older siblings. Something like this has been seen by Nalepa (1984) in family groups in *Cryptocercus punctulatus,* a subsocial wood-eating cockroach widely regarded as a model of termite ancestors.

Alternatively, the significance of the association between larvae and reproductives may be just the reverse: the larvae may be feeding the royal pair. What were classified as "larvae" in this study were approximately the first three instars. The newly hatched larvae, lacking intestinal flagellates, cannot feed themselves and therefore would not be expected to be able to feed other individuals either. But by the third instar the termites possess the intestinal symbionts, and can feed themselves. It may be that the younger instars (beyond the first or second) are responsible for the care of the reproductives. There is some evidence in other species of termites (reviewed by McMahan, 1979) that it is the younger workers that are primarily concerned with colony feeding functions, while older workers specialize in other acitivities.

These two alternatives could probably be distinguished by means of careful observations on the behavior of larvae and reproductives in laboratory colonies.

The aggregation of alates within the colony is interesting, and parallels laboratory observations on groups of alates removed from colonies. The aggregation may reflect a tendency of the alates to accumulate near an exit hole in preparation for emergence. The data in Fig. 4 demonstrate that the tendency to aggregate begins in the preceding nymphal stages. Buchli (1961) described an accumulation of late-stage nymphs and alates in the upper and peripheral regions of nests of *Reticulitermes lucifugus,* but this was apparently due to an antagonism between these stages and the main body of workers of the nest. In *I. schwarzi* nymphs and alates appear to aggregate in the main part of the colony without any mutual show of antagonism with other nestmates.

A striking feature of six of the nine colonies (PL476, PL477, PL480, PL486, PL487, and PL490) was a tendency for the termites to distribute themselves in the wood in two distinct groups. In general, the caste composition was about the same for the upper and lower groups (the excess of nymphs or alates in the bottom group in colonies PL480 and PL486 may simply be a secondary effect of the tendency of these castes to clump together). It seems unlikely, given the regular differences found in the distribution of the major castes, that this bimodal distribution is somehow an artefact of the procedure used in cutting the colony into segments with a consequent wholesale redistribution of members of the colony. It may be that as

a colony grows, the wood in the center of the colony is often used up, and the members of the colony then spread upwards and downwards from the center.

Acknowledgments

This work was supported by grant no. BSR-8119692 from the National Science Foundation. We are grateful to Dr. Steven Green for suggestions on how to evaluate the distribution of the major castes (Figs. 3 and 4), to Dr. Keith Waddington for comments on the manuscript, and to Carol A. Provost for help in preparing the figures.

Summary

Nine colonies of the dry-wood termite *Incisitermes schwarzi* were rapidly cut into segments in the field, and the numbers of individuals of different castes in each segment analyzed in order to learn something about the distribution of castes within natural colonies. The main findings are that the royal pair is usually in the lower part of the colony, associated with small larvae; the mean position of soldiers is usually higher than the mean position for the whole colony; and, relative to the pseudergates, the early-stage nymphs, late-stage nymphs, and alates are successively more clumped or aggregated within the colony.

Literature Cited

Buchli, H.

1961. Les relations entre la colonie maternelle et les jeunes imagos ailés de *Reticulitermes lucifugus*. Vie et Milieu, **12**: 627–632.

Grassé, P.-P.

1949. Ordre des isoptères ou termites. Traité de zoologie **9**: 408–544. Masson, Paris.

Imms, A. D.

1919. On the structure and biology of *Archotermopsis*, together with descriptions of new species of intestinal protozoa, and general observations on the isoptera. Phil. Trans. Roy. Soc. Lond., B., **209**: 75–180.

Luykx, P.

1987. Termite colony dynamics as revealed by the sex- and caste-ratios of whole colonies of *Incisitermes schwarzi* Banks (Isoptera: Kalotermitidae). Insectes Sociaux (in press).

LUYKX, P., J. MICHAEL AND J. K. LUYKX.
1987. The spatial distribution of the sexes in colonies of the termite *Incisitermes schwarzi* Banks (Isoptera: Kalotermitidae). Insectes Sociaux (in press).

MCMAHAN, E. A.
1979. Temporal polyethism in termites. Sociobiology, **4**: 153–168.

NALEPA, C. A.
1984. Colony composition, protozoan transfer and some life history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). Behav. Ecol. Sociobiol., **14**: 273–279.

WILSON, E. O.
1971. The insect societies. Harvard Univ. Press.

A NEW SPECIES OF *ORTHAEA*, A NEOTROPICAL MYODOCHINE GENUS WITH AN UNUSUAL HABITAT (HEMIPTERA: LYGAEIDAE: RHYPAROCHROMINAE)*

By B. J. Harrington
Department of Entomology, University of Wisconsin
Madison, Wisconsin 53706

The genus *Orthaea,* as described by Dallas (1852), was monotypic, with *O. consuta* the type species, and was treated by Stål (1874) as a subgenus of *Pamera* (Say, 1832). In 1914, Van Duzee argued against the use of the generic name *Pamera,* which Say (1832) had merely employed in a faunal list with no type or original species given, and suggested *Orthaea* as the valid generic name for a growing assemblage of myodochine species. In his subsequent catalogue of Hemiptera (Van Duzee, 1917) *Pamera* Stål (*nec* Say, 1832) 1874, *Plociomerus* A & S 1843, *Gyndes* Stål 1862, and *Diplonotus* Stål 1872 were listed as synonyms of *Orthaea,* which generally persisted as the name employed for the group in question until Barber (1939) synonymized it with *Pachybrachius* (Hahn, 1826). Harrington's 1980 monograph of the tribe Myodochini recognized the large, catch-all genus *Pachybrachius* as polyphyletic, including several genera and representing separate lineages involving three of the four male genitalic types for the tribe. In that study (Harrington, 1980), the genus *Orthaea,* with genitalic Type IV, was resurrected from synonymy with *Pachybrachius* and noted to include the type species *O. consuta* and one other species, *Orthaea procincta* (Breddin) (1901).

The present paper describes a new species, *Orthaea alveusincola,* and provides features to distinguish it and the other two known species from each other. Details of the habitat in which the type series was collected are provided since this genus apparently occupies a niche unique for members of the tribe Myodochini.

All measurements in the following description are in millimeters and the Villalobos color chart (Palmer, 1962) has been used as a standard.

*Manuscript received by the editor September 2, 1986.

Orthaea alveusincola Harrington, new species
(Figure 1)

Description. Head, anterior pronotal lobe including collar, and scutellum sooty black. Posterior pronotal lobe, background color of clavus and corium, and majority of hemelytral membrane blackish brown; posterior pronotal lobe subtly lighter, grading toward light chestnut on humeral angles. A pair of small maculae on either side of midline on anterior half of posterior pronotal lobe, anterior one-half of corial margin of clavus, adjacent base of corium, an elongate macula midlength along claval margin of corium, lateral corial margin except for apical corial angle, an elongate macula running just inside and extending less than half the length membranal margin of corium (forming a V-shape with the line-like pale lateral corial margin), and a small macula on hemelytral membrane adjacent to apical corial angle pale, between tawny and buffy yellow. A small diffuse area between cream and pale gray marking the posterior margin of the hemelytral membrane medially. Antennal segment I, distal one-fourth of segment II, distal one-half of segment III, and extreme proximal portion and distal one-fourth of segment IV dark, fuscous tinged with chestnut. Femora of all three pairs of legs pale cream basally grading to between fuscous and tawny; the extent of the dark area greatest on the forelegs, covering almost three-fourths their length. Tibiae light tawny with distal ends fuscous. Tarsi with segments I and II light tawny and segment III darker. Abdomen laterally and ventrally dark chestnut, except pygophore dark tawny.

Legs, antennae, and labium smooth; antennae with short hairs and legs and labium with sparse elongate hairs. Meso-and metatibae also with bristles along full length. Head subshining with microrugosity and numerous short, recumbent, anteriorly directed hairs. Pronotum pruinose and with fine recumbent hairs. Collar of anterior pronotal lobe and posterior pronotal lobe prominently punctate; punctures present but smaller, sparse and very shallow on anterior lobe. Scutellum pruinose, punctate, and clothed with fine hairs. Hemelytra subshining with sparse hairs emerging from punctures. Clavus with punctation in three regular rows plus an incomplete fourth. Corium with a regular row of punctures along claval suture and another parallel row along cubitus; other claval punctation randomly distributed. Abdomen ventrally and laterally subshining, clothed with numerous fine recumbent hairs.

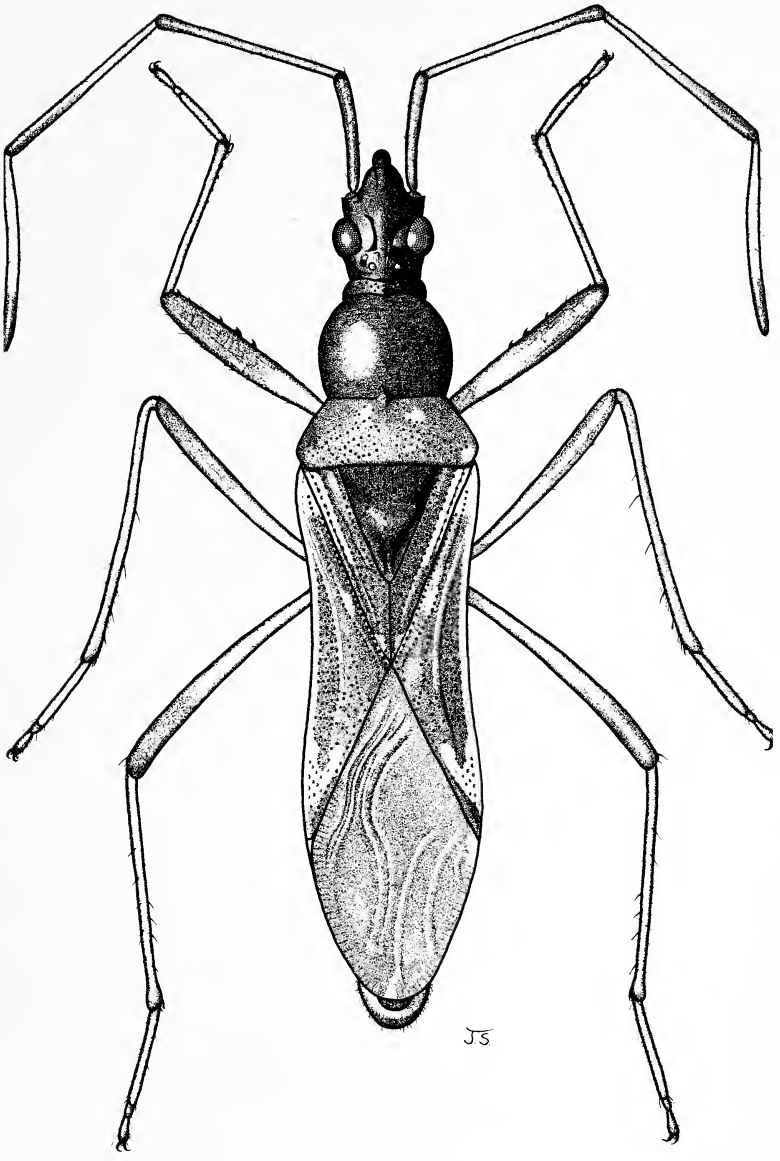


Fig. 1. *Orthaea alveusincola* Harrington, new species, holotype, dorsal view

Head barely declivent anteriorly; somewhat prolonged in postocular region, but not constricted to form a neck. Tylus not attaining midlength on antennal segment I. Vertex flattened, slightly depressed before ocelli. Ocelli behind hind margin of eyes. Eyes rounded. Length of head 1.40; postocular length 0.30; width across eyes 1.10; interocular distance 0.52. Anterior pronotal lobe rounded; anterior margin with a distinct band-like collar. Transverse pronotal impression well demarked and complete save for a narrow, median, dull carina. Posterior pronotal margin straight across base of scutellum. Humeral angles truncate, rounded. Length anterior pronotal lobe 1.22; width 1.38; width transverse impression 1.28; length posterior pronotal lobe 0.80; width across humeral angles 1.98. Length scutellum 1.20; width 1.04. Hemelytra not quite attaining end of abdomen; rounded rim of pygophore visible posteriorly beyond hemelytral membrane. Lateral corial margins vaguely sinuate at level of claval commissure. Length corium 2.06; midline distance apex corium to apex membrane 3.04; length claval commissure 0.82; midline distance apex clavus to apex corium 1.82. Labium attaining anterior margin of metacoxal cavities. Length labial segments I 1.20, II 1.30, III 1.08, IV 0.58. Bucculae short, projecting anteriorly around base of labium; buccular juncture broadly V-shaped and occurring at level of antenniferous tubercles. Antennae slender and extremely elongate; segment IV fusiform and slightly curving. Length antennal segments I 1.32, II 2.22, III 2.14, IV 2.30. Legs elongate, slender. Fore femur slightly incrassate with spines double ranked, the anterior row extending proximad two-thirds the femoral length. Middle one-half or more of fore tibia bearing a single row of small spines. Mesofemur with a single row of spines on anterior surface. Mesepimeron barely emergent. Metathoracic scent gland auricle strongly elevated from pleural surface. Total length 8.98.

Holotype. PANAMA: ♂, La Mesa above El Valle, 13-I-1974, B. J. Harrington and J. A. Slater. In American Museum of Natural History, New York.

Paratypes. 7♂, 10♀, Same data as holotype. In American Museum of Natural History, New York; United States National Museum of Natural History, Washington; British Museum (Natural History), London and private collections of P. D. Ashlock, B. J. Harrington, and J. A. Slater.

Variation. Female specimens lack spines on the foretibia and mesofemur. They also have the anterior pronotal lobe smaller, less rounded, and in a plane lower than that of the posterior pronotal lobes.

Etymology. This species is named *O. alveusincola,* "river-bed dweller", for the surprising habitat in which the type series was collected.

Diagnosis. O. alveusincola, consuta, and *procincta* can be distinguished from each other on the basis of their hemelytral color patterns. In *alveusincola* the lateral corial margin is narrowly pale complete to the subapical macula, which continues the pale area inward along the membranal margin in a characteristic V-shape. In both *consuta* and *procincta* the narrow pale area along the lateral corial margin extends posteriorly only about one-half to two-thirds the corial length stopping short of the pale subapical corial macula and that macula is broad and transverse, extending medially to the membranal margin instead of running at an angle as a stripe along the membranal margin. *O. consuta* lacks pale markings on the clavus, while both *alveusincola* and *procincta* have them, and *O. consuta* also lacks the distinctive pair of orange maculae on either side of midline on the anterior one-half of the posterior pronotal lobe that are present in the other two species. *O. consuta* and *procincta* have the lateral margins of the posterior pronotal lobe broadly marked with orange, contrasting with the dark background; in *alveusincola* these margins are not so distinctly marked and only vaguely, if at all, lighter than the background. *O. procincta* lacks foretibial and mesofemoral spines in the males as well as females, while *alveusincola* and *consuta* males have rows of spines in both areas.

Habitat. The type series of *O. alveusincola* was collected among rocks in the partially dry bed of a mountain or highland stream (approximate elevation 750 m.) in Panama. The insects were most abundant in hollows and around rocks where seeds of an overhanging tree were concentrated. They ran rapidly, often entering the edges of trapped pools of water, and flew readily when pursued, indicating full macroptery consistent with the temporary nature of the habitat. Two series of *O. procincta* from Peru that were examined in this study each also have labels reporting collection in association with a rapid stream at high elevations (500 m. and 1600 m.).

One generally would not anticipate finding rhyparochromine Lygaeidae closely associated with a stream, since their diet of seeds would be expected to either rot or germinate on moist ground. Yet a highland stream, which can by flash flooding wash and concentrate seeds and then dry rapidly, would provide a very suitable habitat with a rich concentration of a seed resource to be exploited. Members of the genus *Orthaea* have apparently adapted to capitalize on this resource, since two of the three known species have been collected in such a habitat.

Currently, known distributions for the genus include *O. consuta* from British Guiana and Colombia, *O. procincta* from Ecuador, and *O. alveusincola* from Panama. As *Orthaea* is apparently a highland genus in an unexpected habitat and thus not commonly collected, it is quite likely that additional new neotropical species may be found, having evolved as montane isolates.

Summary

A new species, *Orthaea alveusincola,* from Panama is described. Diagnostic features are presented to distinguish it and the other two species in the genus, *O. consuta* Dallas and *O. procincta* (Breddin). The type locality is described and the unusual river-bed habitat of the genus is discussed. A full dorsal view illustration of the holotype of *O. alveusincola* is provided.

Acknowledgments

I thank Dr. H. Dodge Engleman of the Coco Solo Hospital, Panama Canal Zone, who was a generous host and collecting associate during a field trip to Panama. I appreciate the loan of specimens of described species by W. R. Dolling of the British Museum (Natural History), London and P. D. Ashlock of the Snow Entomological Museum, University of Kansas, Lawrence, KS. I thank Jeffrey Sternberg, University of Wisconsin, Madison for the excellent dorsal view illustration of the holotype. This research was supported by the College of Agricultural and Life Sciences, University of Wisconsin, Madison (Project No. 2578).

Literature Cited

Barber, H. G. 1939. Scientific survey of Porto Rico and the Virgin Islands: Insects of Porto Rico and the Virgin Islands: Hemiptera-Heteroptera (excepting the Miridae and Corixidae). Sci. Surv. P. Rico **14**: 3: 263–441.

Breddin, G. 1901. Neue neotropische Wanzen und Zirpen. Soc. Entomol. **16**: 59.

Dallas, W. S. 1852. List of the specimens of Hemipterous insects in the collection of the British Museum. Part II. London: Taylor and Francis Inc. p. 580.

Hahn, C. W. 1826. Icones ad monographium Cimicum. Nurnberg: Lechner. **1**: 18.

Harrington, B. J. 1980. A generic level revision and cladistic analysis of the Myodochini of the world (Hemiptera, Lygaeidae, Rhyparochrominae). Bull. Amer. Mus. Nat. Hist. **167**:2: 45–116.

Palmer, R. S. 1962. Handbook of North American birds. Vol. I Loons through flamingos. Yale University Press, New Haven col. pl.

Say, T. 1832. Descriptions of new species of Heteropterous Hemiptera of North America. New Harmony, Indiana. **1831:** 16.

Stål, C. 1874. Enumeratio Hemipterorum pt 4. K. svenska VetenskAkad. Handl. **12**:1: 1–186.

Van Duzee, E. P. 1914. Nomenclatural and critical notes on Hemiptera. Canad. Entomol. **46**: 377–389.

Van Duzee, E. P. 1917. Catalogue of the Hemiptera of America North of Mexico (excepting the Aphididae, Coccidae and Aleurodidae). University of California Press, Berkeley. p. 183.

BLATTELLA ASAHINAI INTRODUCED INTO FLORIDA (BLATTARIA: BLATTELLIDAE).

By Louis M. Roth*

Museum of Comparative Zoology, Harvard University
Cambridge, MA 02138

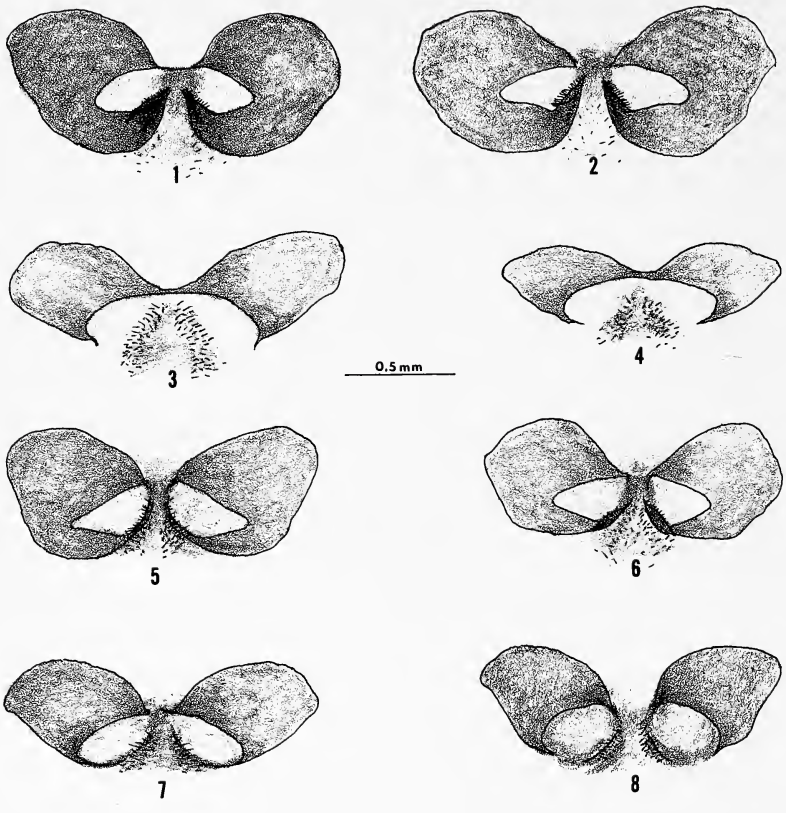
On March 3, 1986, Dr. Philip G. Koehler of the Florida Extension Service, University of Florida, sent me some cockroaches from Lakeland, Florida, for identification. These had been submitted to him by Mr. Ed Shower, a pest control worker, who referred to them as German cockroaches, but pointed out that they were unusual because they flew readily and were common outdoors. Until now only 2 species of *Blattella* occur in the United States, namely, *vaga* Hebard (India, Afghanistan, Pakistan, Sri Lanka, Mexico, and the United States [California, Arizona, Texas]), and the cosmopolitan *germanica* (Linn.), both originating from Asia (Roth, 1985).

I decided that the "unusual *germanica*" could be *Blattella beybienkoi* Roth, which is found in Sri Lanka, Andaman Islands, Burma, Chagos Archipelago, China, India, and Thailand (Roth, 1985). However, it also agreed with specimens of *Blattella asahinai* Mizukubo, described from Okinawa (Mizukubo, 1981; Asahina, 1985). I was unaware of this species when I completed my revision of *Blattella* and submitted it for publication in 1982.

I sent several Lakeland specimens to Dr. Mizukubo, who concluded that they are *asahinai.* He also made a detailed comparison of Sri Lanka paratypes of *B. beybienkoi,* and *asahinai* from Florida and Okinawa, and could find no significant differences between the two species, which I am here synonymizing.

My (Roth, 1970) attempts to cross *B. germanica* with 6 other species of *Blattella,* namely, *bisignata* (Brunner), *lituricollis* (Walker), *sauteri* (Karny), *roederi* Roth [as sp. C], *humbertiana* (Saussure) [as sp. D], and *lobiventris* [as sp. E], were generally unsuccessful. *B. germanica* males mated only once with *bisignata*

*Correspondence: 81 Brush Hill Road, Box 238, Sherborn, MA 01770
Manuscript received by the editor August 23, 1986



Figs. 1–5. Tergal gland reservoirs on abdominal segment 8 of *Blattella* spp.: Figs. 1, 2. *B. germanica* from Lakeland, Fla. Figs. 3, 4. *B. asahinai* from Lakeland and Okinawa, respectively. Figs. 5–8. F_1 males resulting from a cross between male *asahinai* and female *germanica*.

and a male of the latter mated once with a female *germanica*. No offspring resulted from these 2 crosses. However, in the laboratory, *B. asahinai* males do cross readily with *germanica* females producing F_1 offspring which, to date, have produced F_2 nymphs. Attempts to produce offspring from the opposite cross of *germanica* males and *asahinai* females, have been unsuccessful (Patterson, et al., 1986); these results suggest that the 2 species are distinct, but very closely related.

One of the best diagnostic morphological characters for distinguishing *asahinai* from *germanica* is the shape (KOH preparation)

of the male tergal gland reservoirs on the eighth abdominal segment (cp. Figs. 1 and 2 with Figs. 3 and 4). Although there is some variation in the shapes of these sacs in *germanica* (see Figs. 6, 7, *in* Roth, 1985), their posterior margins curve cephalad where they may or may not join with the anterior margins. In *asahinai* the sacs are connected anteriorly, but their hind margins are widely separated (see Figs. 12B, C, 13A–F, *in* Roth, 1985). The F_1 males resulting from crossing male *asahinai* with female *germanica* have reservoirs which are more typical of *germanica* (Figs. 5–8).

Blattella asahinai is very widely distributed. On Okinawa it is usually found among dead leaves and litter on the ground, and occasionally was collected by sweeping over tree blossoms (Mizukubo, 1981). In Florida it is considered to be a potential pest since it is found in large numbers in lawns, on bushes, and invades houses. It is now being studied by members of the USDA-ARS, and the University of Florida, Household Insects Project (Patterson et al., 1986).

Acknowledgments

I thank the following: Dr. Takayuki Mizukubo, National Institute of Agro-Environmental Sciences, Japan, for his opinions concerning *B. asahinai* from Florida and *B. beybienkoi;* Dr. Syoziro Asahina, retired, for specimens of *B. asahinai* from Okinawa; Mr. Donald Azuma, Academy of Natural Sciences of Philadelphia for sending paratypes of *B. beybienkoi* to Dr. Mizukubo at my request; Dr. R. S. Patterson, Dr. R. J. Brenner, and Dr. P. G. Koehler, USDA-ARS, Gainesville, Florida, and the University of Florida, for specimens and biological information of *asahinai* from Florida and for F_1 specimens resulting from a cross between *asahinai* and *germanica.*

I am grateful to The American Philosophical Society for partial support.

References

Asahina, S.

1985. Taxonomic notes on Japanese Blattaria, XIV. Descriptions of one new and four little-known species. Chô Chô, pub. by Gen-Gen Sha, Kitakyushu-shi, Wakamatsu, Miyamaru, Nippon, **8**: 19–26.

Mizukubo, T.

1981. A revision of the genus *Blattella* (Blattaria: Blattellidae) of Japan. 1. Terminology of the male genitalia and description of a new species from Okinawa Island. Esakia, **17**: 149–159.

PATTERSON, R. S., P. G. KOEHLER, AND R. J. BRENNER.
1986. Personal communication.
ROTH, L. M.
1970. Interspecific mating in Blattaria. Ann. Ent. Soc. Amer. **63**: 1282–1285.
ROTH, L. M.
1985. A taxonomic revision of the genus *Blattella* Caudell (Dictyoptera, Blattaria: Blattellidae). Entomol. scand. Suppl. No. **22**: 1–221.

SUBSTITUTE NAMES FOR THE EXTINCT GENERA *CYCLOPTERA* MARTYNOVA (MECOPTERA) AND *PARELCANA* CARPENTER (ORTHOPTERA)*

By Frank M. Carpenter
Museum of Comparative Zoology
Harvard University, Cambridge, Mass. 02138

In 1958 Dr. Olga M. Martynova described a fossil mecopteron belonging to a new genus, *Cycloptera,* and representing a new family, Cyclopteridae. Since the name *Cycloptera* turns out to be preoccupied, a substitute name is needed. Dr. Martynova has asked me to propose a replacement name, and, following her suggestion for the name, I propose the following:

Cyclopterina, *nomen novum, pro Cycloptera* Martynova, 1958, p. 85, *non* Audinet-Serville, 1839, p. 439. The type species, *Cycloptera autumnale* Martynova, 1958, original designation, becomes *Cyclopterina autumnalis* (Martynova), new combination. The new generic name is derived from *Cycloptera* with the addition of the feminine suffix *-ina* and is considered feminine. The genus is known only from the Permian of the Kuznetz Basin, near the Tom River, Kemerovsk Region, USSR.

The family name, Cyclopteridae Martynova, 1938, p. 84, is herein replaced by Cyclopterinidae. *Cyclopterina* is the only genus known in the family at present.

In 1966 I described a Permian orthopteron, placing it in a new genus, *Parelcana,* of a new family, Parelcanidae. I have only recently realized that the name *Parelcana* is preoccupied and I take this opportunity to propose the following substitute name:

Anelcana, *nomen novum pro Parelcana* Carpenter, 1966, p. 84, *non* Handlirsch, 1906, p. 420. The type species, *Parelcana dilatata* Carpenter, 1966, original designation, becomes *Anelcana dilatata* (Carpenter), new combination. The new generic name is derived from *Elcana* with the prefix *an* ("not"). The genus is known only from the Permian of Kansas, U.S.A.

*Research supported by National Science Foundation grant DEB 8205398, F. M. Carpenter, Principal Investigator.

The family name, Parelcanidae Carpenter, is herein replaced by Anelcanidae. The genus *Petrelcana* Carpenter (1966), from the same locality, is the only other genus in the family.

References

Audenit-Serville, J. G.
1839. Histoire naturelle des insectes, Orthoptèrés. Paris Libraraire Encyclopédique de Roret, p. 1–776, pl. 1–14.

Carpenter, F. M.
1966. The Lower Permian insects of Kansas. Part 11. The orders Protorthoptera and Orthoptera. Psyche, **73**: 48–88, Pl. 4–7, text-fig. 1–20.

Handlirsch, Anton
1906. Die fossilen Insekten und die Phylogenie der rezenten Formen. P. 1–640, pl. 1–26, Engelmann (Leipzig).

Martynova, O. M.
1958. Novye nassekomye ix permskikh i mezozojskikh ot lozxgenij SSSR. Materialy k Osnovam Paleontologii, **2**: 69–94, text-fig. 1–23.

PSYCHE

A Journal of Entomology

Volume 93

1986

Editorial Board

F. M. CARPENTER, *Editor*
W. L. BROWN, JR.
E. O. WILSON
H. W. LEVI
M. D. BOWERS
J. M. CARPENTER
B. K. HÖLLDOBLER

Published Quarterly by the Cambridge Entomological Club

Editorial Office: Biological Laboratories

16 Divinity Avenue

Cambridge, Massachusetts, U.S.A.

The numbers of PSYCHE issued during the past year were mailed on the following dates:

Vol. 92, no. 4, April 27, 1986
Vol. 93, nos. 1–2, October 10, 1986

PSYCHE

INDEX TO VOLUME 93, 1986

INDEX TO AUTHORS

INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room 154, Biological Laboratories, Divinity Avenue, Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

BACK VOLUMES OF PSYCHE

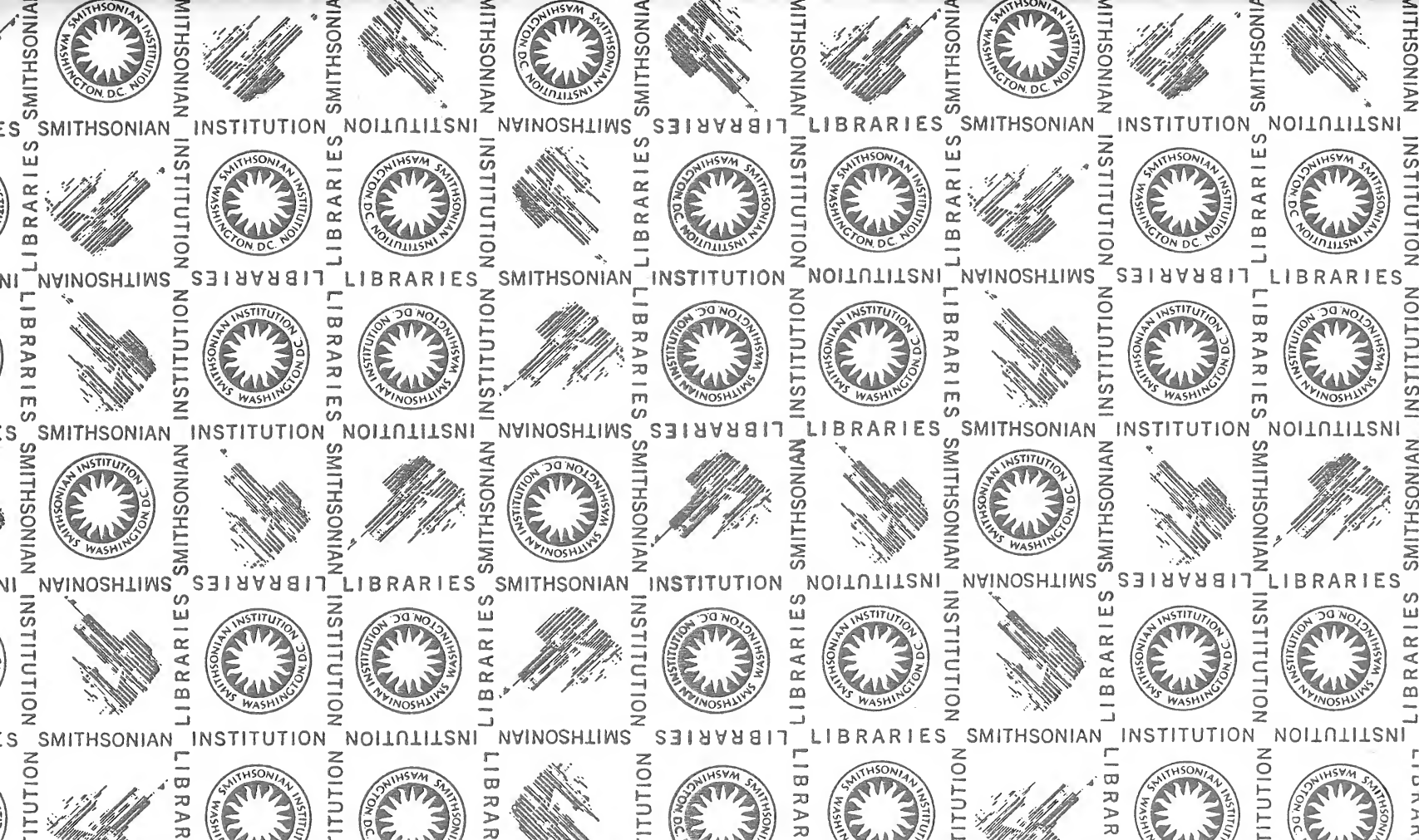
Requests for information about back volumes of Psyche should be sent directly to the editor.

F.M. Carpenter
Editorial Office, Psyche
16 Divinity Avenue
Cambridge, Mass. 02138

FOR SALE

Reprints of articles by W. M. Wheeler

The Cambridge Entomological Club has for sale numerous reprints of Dr. Wheeler's articles that were filed in his office at Harvard University at the time of his death in 1937. Included are about 12,700 individual reprints of 250 publications. The cost of the reprints has been set at 5¢ a page, including postage; for orders under $5 there will be an additional handling charge of 50¢. A list of the reprints is available for $1.00 from the W. M. Wheeler Reprint Committee, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138. Checks should be made payable to the Cambridge Entomological Club.


SMITHSONIAN INSTITUTION LIBRARIES

SMITHSONIAN INSTITUTION LIBRARIES

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 00844 9787