The PAN-PACIFIC ENTOMOLOGIST

Volume 68 January 1992 Number 1

Published by the PACIFIC COAST ENTOMOLOGICAL SOCIETY
in cooperation with THE CALIFORNIA ACADEMY OF SCIENCES
(ISSN 0031-0603)

The Pan-Pacific Entomologist

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THE PAN-PACIFIC ENTOMOLOGIST (ISSN 0031-0603) is published quarterly by the Pacific Coast Entomological Society, c/o California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599. Second-class postage is paid at San Francisco, CA and additional mailing offices. Postmaster: Send address changes to the Pacific Coast Entomological Society, c/o California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599.

This issue mailed 7 February 1992

The Pan-Pacific Entomologist (ISSN 0031-0603)

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044, U.S.A.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PAN-PACIFIC ENTOMOLOGIST
68(1): 1–7, (1992)

EVOLUTION OF OVIPOSITION HABITS IN *APHODIUS* DUNG BEETLES (COLEOPTERA: SCARABAEIDAE)

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Abstract.—Oviposition habits of nine species of *Aphodius* dung beetles common in Sapporo, Hokkaido, northern Japan, were studied under laboratory conditions using glass cages supplied with soil and fresh cattle dung. Four types of oviposition habits were recognized. Type I: Eggs were laid singly in the dung on the ground. Type II: Eggs were laid singly in the soil beneath the dung. Type III: Each egg was laid in a small dung mass stuffed in a shallow burrow excavated beneath the dung. Type IV: Each egg was laid in the soil near the terminal end of a sausage-shaped dung mass buried beneath the dung. Although Types III and IV were similar in that females provided food for larvae, behavioral sequences of oviposition and provisioning were distinctly different between the two types. In Type III, an egg was laid after a dung mass was provided; whereas, in Type IV, an egg was laid before a dung mass was buried. Provisioning habits of Type III and Type IV seemed to have evolved independently from more primitive Types I or II, and from Type II, respectively. Oviposition habits of *Aphodius* were compared with those of two major groups of scarabaeid dung beetles, Geotrupinae and Scarabaeinae. Our Type III oviposition habit is analogous to those of certain species of Geotrupinae and Scarabaeinae, and Type IV to some Geotrupinae, indicating parallel evolution of dung burying habits in several lines of scarabaeid beetles.

Key Words.—Insecta, Scarabaeidae, *Aphodius,* dung beetles, oviposition, behavioral sequence, evolution

Reproductive biology of dung beetles belonging to the subfamily Aphodiinae has had little attention until recently, in spite of their dominance in the number of species and individuals in the north temperate zone (Balthasar 1964). Scattered records show that oviposition habits of Aphodiinae are diverse. Many species lay eggs directly in dung on the soil surface, or in the soil beneath the dung (Hafez 1939, White 1960, Landin 1961, Hanski 1980). A few species bury dung masses for larval food in the soil under droppings (Paik 1968; Hosogi et al. 1979, 1980). Obligatory or facultative kleptoparasitic species are also known (Hammond 1976 [and the references therein], Klemperer 1980, Kiuchi 1987).

Due to this diversity, the Aphodiinae may offer invaluable information for studying evolutionary origin of more elaborated oviposition habits found in two major groups of dung beetles: Geotrupinae and Scarabaeinae (for reviews, Halffter & Matthews 1966, Halffter & Edmonds 1982, Doube 1990). Unfortunately, however, oviposition habits of Aphodiinae species have not been studied in detail, except for a few species such as *Aphodius rufipes* (L.) (Madle 1934, Holter 1979, Klemperer 1980). For many species, only the scattered descriptions of egg site and/or larval feeding sites were available. Furthermore, there have been no quantitative studies specifically dealing with oviposition behavior or evolutionary trends in Aphodinae species.

In this paper, we will examine four types of oviposition habits distinguished for nine Japanese species (all belonging to *Aphodius*) on the basis of the results obtained by rearing under laboratory conditions.

Table 1. Types of oviposition habits and egg distributions of nine *Aphodius* species together with their reproductive periods and female body size. S: desiccated dung surface, U: moist upper half layer of dung, L: moist lower half layer of dung, M: margin between dung and soil, G: soil under dung.

Type	Species	*n*	% of eggs laid in					Total[a]	Reproduction[b]	Body size[c] (mm)
			S	U	L	M	G			
I	*A. brachysomus*	23[d]	1.2	76.1	22.2	0.4	0.0	1417	spring	7.8 ± 0.58
I	*A. haemorrhoidalis*	35[e]	4.4	26.5	38.9	23.0	7.1	113	spring	4.7 ± 0.23
I	*A. breviusculus*	18[e]	16.7	40.3	37.5	5.6	0.0	72	spring	4.6 ± 0.34
I	*A. pratensis*	22[e]	11.4	48.6	37.1	2.9	0.0	35	autumn	4.6 ± 0.31
II	*A. sordidus*	28[e]	0.0	0.0	0.0	0.0	100.0	70	autumn	6.5 ± 0.43
II	*A. rectus*	59[e]	0.0	0.0	4.9	7.6	87.6	185	spring	5.8 ± 0.42
II	*A. pusillus*	38[e]	0.0	2.8	8.3	11.1	77.8	36	spring	3.7 ± 0.28
III	*A. elegans*	45[d]	0.0	0.0	0.0	0.0	100.0	1576	autumn	11.6 ± 0.92
IV	*A. haroldianus*	48[d]	0.0	0.0	0.0	0.0	100.0	329	spring	9.4 ± 0.81

[a] Total number of eggs laid in all glass cages.
[b] Reproductive period (all species are univoltine in Japan).
[c] Female body length (mean ± SD, $n > 30$).
[d] Number of females separately reared.
[e] Number of adults reared (sex unknown).

Materials and Methods

The nine *Aphodius* species listed in Table 1 were reared. Each species was collected, at the peak of reproductive activity (Yoshida & Katakura 1985), from cattle dung at pastures in Hokkaido Agricultural Experiment Station (42°59′ N, 141°24′ E) in Sapporo, northern Japan, approximately 10 km from the laboratory of Hokkaido University, where the rearing was performed.

Of these species, *A. haroldianus* Balthasar and *A. elegans* Allibert have been known to bury dung and lay eggs near (*A. haroldianus*) or in (*A. elegans*) the buried dung masses (Paik 1968; Hosogi et al. 1979, 1980). Other species are considered to lay eggs directly in droppings on the ground, or in the soil under the droppings (Yoshida & Katakura 1985; M. Kiuchi, personal communication).

Beetles were reared in glass cages consisting of two vertical glass plates and a narrow wood frame, which formed the bottom and the two sides of the cage. One of the glass plates was fixed to the wood frame, but the other plate was removable permitting food changes and periodical inspections. The lower half of the cage was filled with humid sand, and then fresh cattle dung was placed on sand to a depth equal to one-quarter volume of the cage. The top of each cage was sealed with cotton cloth and 3 mm mesh nylon net to prevent escape of beetles. Several rearing cages were placed together in a wood box and were shaded by black sheets so as to keep them dark except for the top. Two sizes of glass cages were used according to the body size of beetle species (length × width × height: large cage, 19.0 × 1.4 × 25.0 cm; small cage, 12.5 × 0.6 × 10.0 cm).

The females collected at the peak of reproductive activity were assumed mated prior to collection (Yoshida & Katakura 1985). Then, a female of each of the three larger species (*A. elegans, A. haroldianus* and *A. brachysomus* Solsky, which were easily sexed) was released separately and individually into large glass cages. The other six species were difficult to sex externally, and so one to four adults (unknown sex) per small cage, or five to ten adults (unknown sex) per large cage, were released.

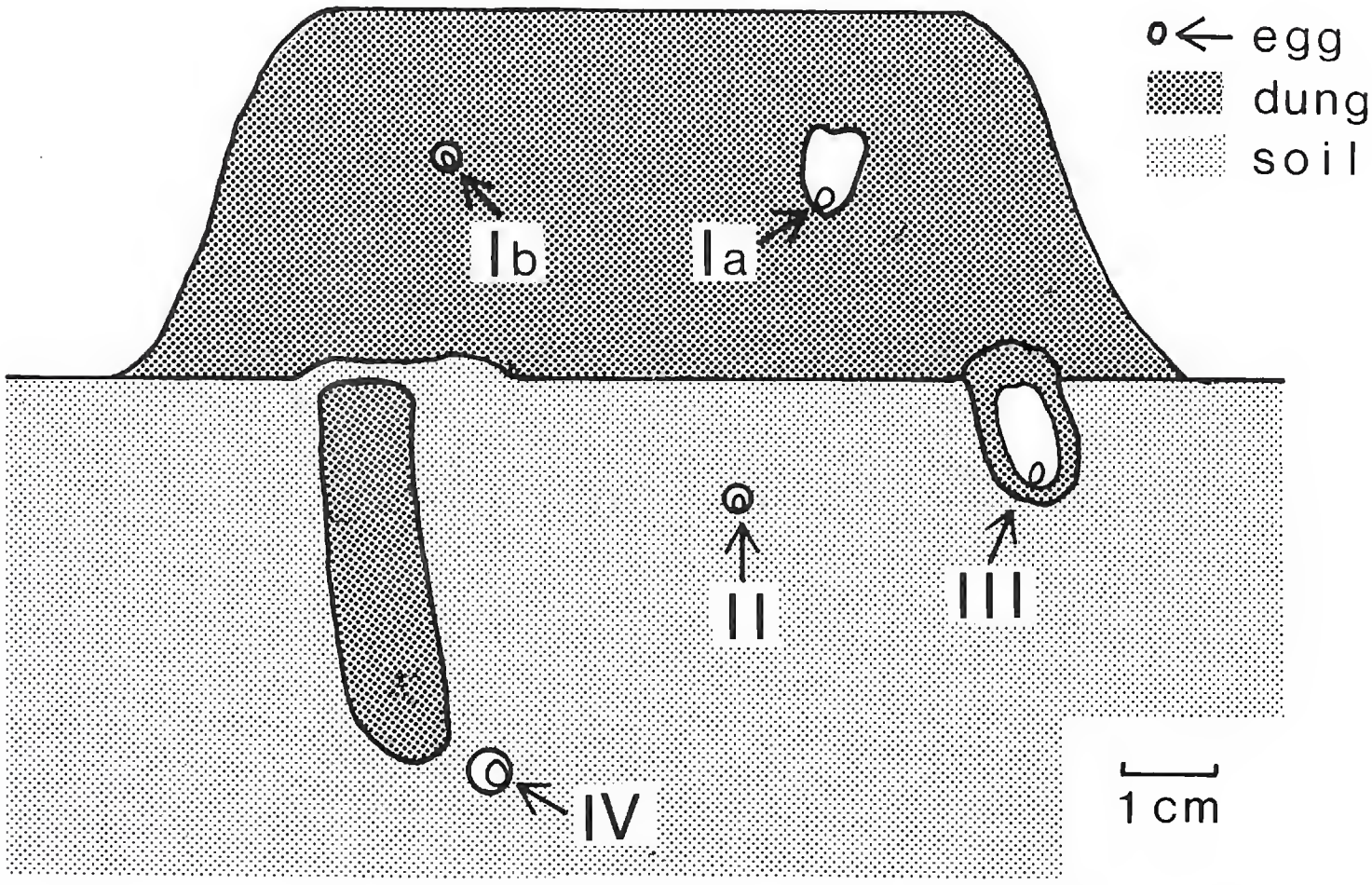

Figure 1. A scheme of oviposition sites of four types of oviposition habits distinguished for nine *Aphodius* species. I–IV: type of oviposition habits defined in the text; Ia, *A. brachysomus*; Ib, *A. haemorrhoidalis, A. breviusculus, A. pratensis.*

The dung and soil in each cage were changed every two or three days, after they were thoroughly examined to detect the oviposition sites and the number of laid eggs. In addition, position of laid eggs was traced, when necessary, on the transparent Saran Wrap®, which was placed on the glass plate. For the two species that bury dung for larvae, the dung burying process was also observed through the glass plate.

Species that reproduce in the spring (Table 1) were reared under long day conditions (LD 16:8) at 15 ± 1° C or 18 ± 1° C, and species that reproduce in the autumn were reared under short day conditions (LD 12:12) at 18 ± 1° C or 23 ± 1° C.

Results

Oviposition habits of the nine *Aphodius* species were classified into four types according to egg sites and presence or absence of provisioning for larvae (Table 1, Fig. 1).

Type I.—Four species were classified as Type I: *A. brachysomus, A. haemorrhoidalis* (L.), *A. breviusculus* (Motschulsky), *A. pratensis* Nomura & Nakane. Eggs were laid singly in round or oval spaces in the dung on the soil surface (Fig. 1, Ia, Ib).

The following is a summary of oviposition habits of *A. brachysomus,* the most intensively studied species of this type: Most eggs were laid in the middle part of cattle dung placed in the rearing cages (Table 1). Almost all eggs were laid in oval spaces (98.3%, n = 1264); the remainder were laid directly on the surface of tunnels left behind by the adults' passage. These spaces (Fig. 1, Ia) are probably egg chambers prepared by the mother beetles for oviposition. The spaces were

relatively large (6.7 ± 1.16 mm long, 4.4 ± 0.66 mm wide; mean ± SD, $n = 47$) and their inner wall was smooth, except for one side that was rough and protruded somewhat inwards into the space. No such space had more than one egg. Each egg was stood on end at the side opposite to the rough side of the space. It seems that the mother beetle makes an egg chamber, lays an egg, and closes it with rough dung fragments.

Eggs of the remaining three species of this type were also found singly in round or oval spaces, 1.3–2.4 mm diameter, inside of the dung (Fig. 1, Ib; Table 1). Whether these spaces were specially prepared egg chambers or mere spaces left behind by the adults' movement was not determined for these smaller species.

Type II.—Three species were classified as Type II: *A. sordidus* (Fabr.), *A. rectus* (Motschulsky), *A. pusillus* (Herbst). Eggs were laid singly in spaces in the soil beneath dung (Table 1; Fig. 1, II).

The spaces were simple and round, 1.5–3.0 mm diameter and not coated with dung. Because these spaces were apart from tunnels that were left behind by the adults' passage, they were probably specially prepared egg chambers. Most of the eggs were deposited at a depth shallower than 30 mm as follows: *A. sordidus,* 13.5 ± 11.28 mm; *A. rectus,* 11.1 ± 10.14 mm; *A. pusillus,* 10.3 ± 9.73 mm. Some eggs of *A. rectus* and *A. pusillus* were laid at the boundary between dung and soil, and a few others were in the lowest part of dung.

Type III.—One species was classified as Type III: *A. elegans.* Each egg was laid in a small dung mass stuffed into a shallow burrow in the soil beneath the dung (Fig. 1, III).

Dung masses were found shallower than 30 mm deep, and its top usually connected with the bottom of the above dung. The periphery of buried dung masses was mixed with grains of soil. Dung masses were 17.3 ± 3.6 mm long and 9.6 ± 1.6 mm wide ($n = 83$). There was a space in each mass, in which a single egg was usually laid (97.0% of masses with one egg, 0.4% with two eggs, and 2.6% with no egg, $n = 533$). The space (egg chamber) was 10.5 ± 2.79 mm long and 5.9 ± 1.37 mm wide ($n = 45$). The inner surface of the egg chamber was smooth at the bottom and sides, but rough at the top, sometimes protruding inwards. The dung wall was thin at the bottom (1.7 ± 1.41 mm) and sides (2.6 ± 0.92 mm) but thick at the top (4.4 ± 1.85 mm). Most eggs were laid on the lower one-half of the wall of egg chambers (58.5% of laid eggs; $n = 94$) or on the bottom (36.6%). Sometimes a few dung masses were fused together at their sides.

In the provisioning and oviposition processes, a female excavated a shallow burrow in the ground beneath dung, carried dung fragments from above, and plastered the wall of the burrow with dung so as to form a chamber. Although we could not trace subsequent processes, the female must smooth the inner surface, lay an egg and close it from above with dung fragments, judging from the condition of buried egg masses.

Type IV.—One species was classified as Type IV: *A. haroldianus.* Each egg was laid in the soil beneath the dung; after oviposition, the parental females buried a dung mass near the egg (Fig. 1, IV).

Buried dung masses were found in the soil up to 8 cm deep. They were similar to a sausage and often somewhat curved; 34.8 ± 8.4 mm long and 14.3 ± 3.2 mm wide ($n = 106$). Dung sausages were made of stratified compact dung and had no spaces within them. An egg was laid in a space in the soil 5–8 mm apart from the terminal end of each dung sausage. The space was on the average 6.6

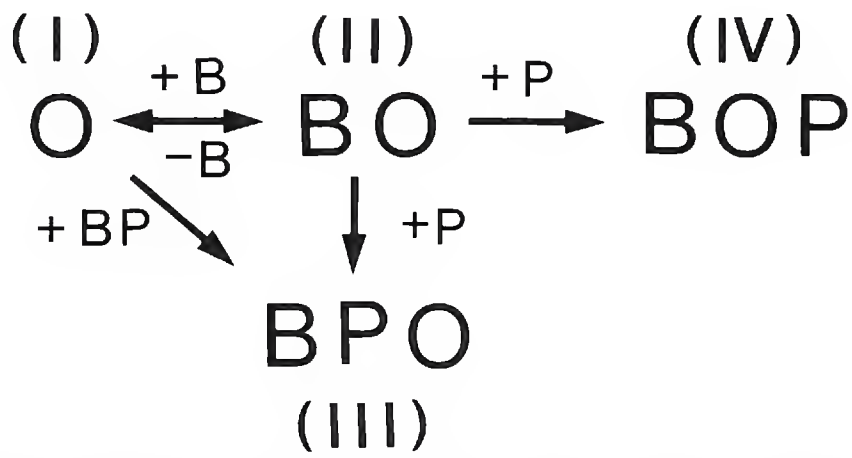

Figure 2. Suggested evolutionary relationships among four types of oviposition habits in *Aphodius*. I–IV: type of oviposition habits, O: oviposition, B: burrowing soil, P: provisioning dung into burrow.

mm long, 4.0 mm wide, and without any coating. Two or three masses sometimes fused together at the sides or at the terminal ends, at least in the narrow rearing cages.

In the provisioning and oviposition processes, a female excavated a vertical shaft beneath the dung and constructed an egg chamber near the end of the shaft. (Then, she probably lays one egg in the chamber and closes the chamber with soil, but these processes could not be confirmed in this study.) After oviposition, she filled the shaft with dung, mixed her own excrements with dung, and then she closed the shaft with soil. Sometimes, however, the dung sausage was not entirely buried but remained in contact with above unburied dung.

Discussion

Evolutionary Trends among Oviposition Habits.—Although it is yet uncertain which behavior type is most primitive among the four, Types I and II are evidently simpler and more primitive than Types III and IV. In Types III and IV, dung is supplied for the young, but the behavioral sequence of provisioning and oviposition is distinctly different between the two species. In Type III, a dung mass is first prepared in the soil, and then an egg is laid in the dung mass. On the other hand, in Type IV egg is laid in the soil before dung is buried to form a dung sausage. Because the sequence of oviposition and provisioning is thus inverted between the Types III and IV behaviors, it is likely that these two types evolved independently (Fig. 2).

Type IV behavior seems to have evolved from Type II; in both behaviors eggs are laid in the soil near (but not in) the larval food resource, and the behavioral sequence of oviposition habits in Type IV can be easily evolved from the simpler Type II, by adding provisioning behavior to the behavioral sequence of the latter (+P).

On the other hand, two alternative interpretations are possible for the evolution of Type III behavior: (1) this type may have evolved from Type II, by inserting provisioning behavior (P) between burrowing (B) and oviposition (O); or (2) Type III behavior may be introduced from Type I, by inserting burrowing and provisioning to the behavioral sequence of the latter (+BP). The first interpretation seems more parsimonious, but the second interpretation may be supported by the fact that in both Type III and Type I behaviors eggs are laid in the larval food resource.

Parallel Evolution of Dung Burying Habits.—Klemperer (1983) coined the term

"rummagers" for the *Aphodius* species that lay their eggs directly in droppings (synonymous with endocoprids sensu Hanski 1986, not sensu Bornemissza 1969), and contrasted them with "buriers" (paracoprids) that excavate burrows and fill them with dung masses in each of which an egg is laid, and with "rollers" (telocoprids) which roll away a ball of dung some distance before being buried in a chamber where the ball is either eaten or converted to a brood ball. According to this classification, species with Type I behavior are typical rummagers. Type II behavior species can also be called rummagers because their larvae freely feed on the dung on the soil surface, although they lay eggs outside of the dung.

On the other hand, species of Types III and IV behavior are buriers, in that both place dung in the soil for larvae. However, the prepared dung masses are small in behaviors of both Types III and IV, as described above. Larvae of species with Type III behavior cannot complete the growth with buried dung masses (second and third instars eat freely in droppings on the soil; Hosogi et al. 1979; NY, unpublished data). Larvae of species with Type IV behavior can complete the growth in the buried dung masses, but often depart from it and eat freely in unburied dung (third instars; NY, unpublished data). Accordingly, it seems more appropriate to treat behaviors of Types III and IV as intermediate states between rummagers and typical buriers completing growth only with buried dung masses.

Anyhow, behaviors of Types III and IV could be regarded as representing two basic types of oviposition habits found in buriers. Type III is analogous to the oviposition habits of many species of Scarabaeinae (e.g., the Oniticellini and Onthophagini; in particular, *Oniticellus egregius* Klug) and Geotrupinae (e.g., *Geotrupes spiniger* Marsham, *G. cavicollis* Bates) laying eggs in buried dung masses (Halffter et al. 1985, Klemperer 1979, Davis 1989). Type IV is essentially the same as the oviposition habits of some Geotrupinae, typically represented by *Typhoeus typhoeus* (L.) (Palmer 1978, Brussaard 1983) and *Ceratophyus hoffmannseggi* Fairmaire (Klemperer 1984), which lay each egg near the terminal end of a dung sausage buried in the soil.

Diversification of brood caring habits is prominent in two major groups of scarabaeid beetles, Scarabaeinae and Geotrupinae (Halffter & Matthews 1966, Halffter & Edmonds 1982). Almost all species of these two groups are presocial, and even in the most primitive type, adults provide foods for larvae. Ironically, this makes it difficult to seek the evolutionary origin of their presociality among these two groups of beetles. For the evolutionary origin of brood caring in dung beetles to be clarified, it is more preferable to concentrate our effort to the groups which include both species showing brood caring and those not. The present study showed that *Aphodius* beetles are particularly suitable for such purpose. We expect that closer ethological and ecological studies of *Aphodius* beetles will thus facilitate our unbiased understanding of the diverse brood caring habits evolved in coprophagous beetles of the family Scarabaeidae.

Acknowledgment

Makoto Kiuchi kindly informed us of his unpublished observations on oviposition habits of some *Aphodius* species. Terumitsu Miyashita and other members of the staff of the Hokkaido Agricultural Experiment Station made available the facilities of the Experiment Station. The rearing of *Aphodius* beetles was carried out at Center for Experimental Plants and Animals, Hokkaido University.

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Received 31 January 1991; accepted 20 May 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 8–11, (1992)

SURVEY OF *MYZUS PERSICAE* (SULZER) (HOMOPTERA: APHIDIDAE) INFESTATIONS ON BEDDING PLANTS FOR SALE IN EASTERN IDAHO

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Abstract.—A survey of bedding plants commercially available in all potato seed production areas of eastern Idaho revealed that they remain a potential source of infestation of *Myzus* (*Nectarosiphon*) *persicae* (Sulzer), the green peach aphid. Cole crops, eggplant, forget-me-not, peppers, and petunia showed 18, 53, 36, 42, and 41% infestation, respectively. A survey involving 476 green peach aphids showed that none transmitted PLRV to test plants.

Key Words.—Insecta, Aphididae, *Myzus persicae,* bedding plants, PLRV

Potato leafroll virus (PLRV) can be a major problem in Idaho potato production, especially for certified potato seed growers. PLRV is spread by vegetative propagation of infected potato seed or transmission by aphid vectors, the most important being *Myzus* (*Nectarosiphon*) *persicae* (Sulzer), the green peach aphid.

Myzus persicae has a broad summer host range, but in Idaho it overwinters holocyclicly only on peach and apricot trees (Bishop & Guthrie 1964). These overwintering hosts will not withstand the severe winters in most Idaho potato seed production areas. Work by Tamaki et al. (1979) suggested that anholocyclic overwintering may occur in Washington during mild winters, but this is very unlikely under severe Idaho winter conditions in seed production areas. Prior to the 1960s, it was assumed that aphid infestations on seed potatoes were initiated each year by alatae that immigrated from warmer areas; however, subsequent work indicated that this might not be the case. Bishop (1965) showed tht seed potato fields closest to towns had the most *M. persicae* and highest PLRV incidence. Home gardens in the towns were found to be sources of both virus and vector. Bishop & Guthrie (1964) strongly implicated bedding plants imported from surrounding states as the major source of *M. persicae* and showed that virus inoculum built up in home grown potatoes as gardeners used their own crop for seed year after year.

A successful integrated pest management program for potato seed production involving elimination of winter hosts, distribution of free certified seed potatoes to home gardeners, and insecticide treatment of bedding plants was implemented in the Grace area of Idaho in the 1960s (Bishop 1967). More recently, prophylactic insecticide treatments have supplanted this integrated program. Because of new restrictions on insecticide use, assessment of the feasibility of integrated pest management has become attractive. The source of *M. persicae* in seed production areas that are too cold for survival of primary hosts is thus a matter of scientific and applied interest. Though bedding plants have been suspected as a major source of aphids, there is no published survey objectively documenting frequency of infested bedding plants in a major potato seed production area. There is also no published information as to whether or not aphids on bedding plants are virulifer-

Table 1. *Myzus persicae* infestation of commercially available bedding plants in eastern Idaho seed potato production areas. Survey conducted 14–18 May 1990.

City/area[a]	Plant examined	No. salable units examined	No. infested with GPA	PLRV transmission[b]
American Falls/Aberdeen (2)	eggplant	11	8	0/30
	pepper	24	15	0/30
Arco/Mackey (4)	cole crops	33	11	0/30
	pepper	34	21	0/50
Ashton/St. Anthony (4)	cole crops	24	12	0/5
	eggplant	20	11	—
	forget-me-not	3	0	—
	pepper	46	14	0/10
	petunia	12	3	—
Burley (2)	cole crops	2	0	—
	eggplant	18	12	0/9
	pepper	21	10	0/17
Idaho Falls (7)	cole crops	35	6	0/10
	eggplant	54	25	0/47
	pepper	109	31	0/37
Pocatello (5)	cole crops	12	2	—
	eggplant	28	12	0/10
	pepper	99	54	0/32
Resburg (6)	cole crops	62	10	0/25
	eggplant	8	0	—
	forget-me-not	9	0	—
	pepper	87	27	0/40
Soda Springs/Grace (3)	cole crops	40	4	0/4
	eggplant	11	11	0/10
	pepper	42	13	0/20
	petunia	12	10	—
Teton basin (3)	cole crops	37	0	—
	forget-me-not	10	8	0/30
	pepper	28	19	0/30
	petunia	8	0	—

[a] Number in parentheses is the number of commercial outlets surveyed. The information is pooled by community/area. Not every business had infested plants.

[b] Number of aphids transmitting/number tested. Readings on concurrent controls were: aphids with no access to PLRV, 0/20; no aphids, 0/20; aphids fed on known PLRV source, 12/20.

ous. This survey tried to determine if commercially available bedding plants are presently a source of *M. persicae* and if they are a potential source of PLRV inoculum in Idaho's major seed production areas.

Methods and Materials

The survey was carried out from 14–18 May 1990, in all major eastern Idaho potato seed production areas and nearby larger cities (Pocatello, Idaho Falls and Rexburg). Bedding plants originating from nurseries in Idaho and surrounding states were inspected in 36 commercial outlets in 14 communities.

Only those plants known to be good hosts of *M. persicae* were examined: cole

Table 2. *Myzus persicae* infestation of commercially available bedding plants in eastern Idaho seed production areas summarized by plants. Survey conducted 14–18 May 1990.

Plant	Salable units		
	No. examined	No. infested	% infested
Cole crops	245	45	18.4
Eggplant	150	79	52.7
Forget-me-not	22	8	36.4
Pepper	490	204	41.6
Petunia	32	13	40.6
Totals	939	349	37.2

crops, eggplants, peppers (green and chili) and certain ornamentals. Results were scored in terms of salable units rather than individual plants (i.e., if plants were sold in trays of six plants, the number recorded would be number of trays infested out of number examined).

Aphids infesting bedding plants might originate on hosts other than those examined at commercial outlets allowing for the possibility, however slight, of previous PLRV acquisition. To examine this possibility, at each location where infested plants were found, three infested plants were purchased, individually caged and returned to the laboratory. The aphids were then transferred to *Physalis floridana* L. seedlings for a 72 h inoculation access period. After removing the aphids with an insecticide spray, the plants were held for three weeks in the greenhouse and observed for PLRV symptoms.

Results and Discussion

Plants infested with *M. persicae* were found in every community/area surveyed (Table 1), but not in every store. In all, infested plants were found in 72% of the outlets surveyed. Percentages varied from 25% in Ashton/St. Anthony to 100% in American Falls/Aberdeen, Burley and Pocatello. Overall, approximately 42% of the peppers and 53% of the eggplants were infested with green peach aphids (Table 2). Forget-me-nots and petunias (mostly very young petunia plants) were similarly infested, and cole crops (Brussels sprouts, broccoli, cabbage and cauliflower) were less frequently infested. This survey indicates that commercially available bedding plants remain a major source of *M. persicae* in the eastern Idaho seed production areas.

None of the plant species examined in this survey are known hosts of PLRV. Although these plants provided a significant source of *M. persicae,* they were not a source of viruliferous aphids that may have originated on PLRV hosts. Testing of 476 aphids for PLRV transmission revealed none transmitted the virus to *P. floridana* seedlings.

As restrictions on insecticide use increase, there is a need to return to an integrated approach to aphid management. Success of Bishop's (1967) pilot program depended, in part, upon control of aphids on bedding plants. It is likely that interdiction of infested bedding plants, coupled with elimination of volunteer peach and apricot seedlings and distribution of free certified potato seed to home gardeners would significantly reduce aphid infestation levels and PLRV incidence in Idaho seed production areas.

Blackman (1987) and Blackman & Paterson (1986) have shown that *M. persicae,* in its historical sense, is actually a complex of morphologically similar species. It would be problematic if sibling species in the *M. persicae* complex have differential vectoring abilities for PLRV. Future work should be done to assess the ability of aphids originating on bedding plants to colonize potato and their efficiency in transmitting PLRV.

Acknowledgment

We thank Joyce Sorrell for technical assistance and the Idaho Potato Commission for financial support. This is Idaho Agricultural Experiment Station scientific paper 90762.

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Received 4 March 1991; accepted 15 May 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 12–14, (1992)

RATES OF PREDATION BY *CHRYSOMYA RUFIFACIES* (MACQUART) ON *COCHLIOMYIA MACELLARIA* (FABR.) (DIPTERA: CALLIPHORIDAE) IN THE LABORATORY: EFFECT OF PREDATOR AND PREY DEVELOPMENT

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Abstract.—*Chrysomya rufifacies* (Macquart) is a blow fly that was recently introduced to North America. Because the larvae of this species are facultative predators on other maggots, native North American carrion flies probably will be negatively affected by the invasion. *Cochliomyia macellaria* (Fabr.), the native calliphorid with the greatest bionomic similarity to the invader, was selected as the prey species for a laboratory study of predatory behavior. We investigated the influence of both predator and prey development on predation rates when single predators and prey were paired in the laboratory. Third instar *C. rufifacies* consumed third and, at a lesser rate, second instar *C. macellaria*. Earlier instars were not predaceous. Both relatively small and relatively large third instar *C. rufifacies* consumed the same number of mid-size prey.

Key Words.—Insecta, Calliphoridae, *Chrysomya* invasion, predatory behavior, *Cochliomyia* prey, effect of development

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The Old World blow fly *Chrysomya rufifacies* (Macquart) was apparently introduced to Costa Rica around 1978 (Jirón 1979). Since that time it has been collected in Baja California and Caifornia (Greenberg 1988), Texas (Richard & Ahrens 1983), and Arizona (Baumgartner 1986). *Chrysomya rufifacies* is an important parasite of newborn calves in extremely wet areas of Hawaii (Shishido & Hardy 1969) and concern has been expressed about the economic impact of this species in its new range (Schmidt & Kunz 1985). *Chrysomya rufifacies* larvae are facultative predators on other maggots including parasitic species (Fuller 1934). Because of this habit, and because *C. rufifacies* is typically a secondary invader of both carrion and live mammals (Fuller 1934, Norris 1959), the net economic effect of this fly is often unclear.

Carrion arthropod species display a continuous succession in a carcass (Schoenly & Reed 1987). Two species occupying the same carcass may avoid particular interactions simply because the necessary developmental stages do not meet. It is of interest, then, to know what interactions are possible between various life stages. Both second and third instar *Chrysomya rufifacies* have been described as predaceous (Goodbrod & Goff 1990), but the relative behavior of the different instars and the size of the prey that can be subdued have not been reported. As part of a study of the ecology of this fly and its impact on native Diptera, we investigated the effect of both predator and prey development on *C. rufifacies* predation rates in a laboratory setting. The prey species was *Cochliomyia macellaria* (Fabr.), the North American fly with the greatest bionomic similarity to the invader (Nicholson 1934, James 1947, Hall 1948, Bohart & Gressitt 1951, Denno & Cothran 1975, unpublished data), and presumably its closest ecological homolog.

Methods and Materials

Experiment 1.—Single *C. rufifacies* and *C. macellaria* larvae were confined together in 55 × 13 mm plastic petri dishes lined with moistened filter paper. Dishes were placed on a laboratory bench at 23° C with lights on. Larvae from laboratory colonies had been reared on an excess of ground beef. Treatments were the nine possible combinations of the three larval instars of each species. Approximate body lengths of the larvae used were 2.3, 7.4 and 10.5 mm for first, second and third instar *C. rufifacies,* and 2.3, 7.0 and 16.8 mm for first, second, and third instar *C. macellaria.* Twenty pairs were created for each treatment. The dishes were simultaneously arranged in a random pattern within 20 rows and nine columns. The larvae were constantly scanned for 5 h and instances of successful predation (*C. macellaria* consumed) by *C. rufifacies* were recorded for every hour (*C. rufifacies* curls around and pierces its prey which struggles violently in response). Following this, the larvae were left in place with the lights off for 17 h and again examined for evidence of predation.

Experiment 2.—Larvae were confined as in experiment 1, but in this case we examined the effect of predator size when third instar *C. rufifacies* attack third instar *C. macellaria.* Predator size was either relatively small (approx. 10.5 mm) or relatively large (approx. 16.2 mm) matched with one prey size (approx. 12.5 mm). Care was taken that post-feeding larvae were not used for the larger predators. Again, 20 dishes for each treatment were set up and arranged at random within a pattern of 10 rows and four columns. Because the great majority of predaceous acts in experiment 1 occurred within the first hour (see below), the larvae were constantly scanned for 1 h and instances of predation were recorded for each 0.5 h.

Results and Discussion

The numbers of dishes with predation in experiment 1 were 17 of the paired third instars, seven of third instar *C. rufifacies* with second instar *C. macellaria,* and zero for all other treatments. All acts of predation between third instars occurred within the first hour, but some from the second treatment occurred in hours two (two dishes) and three (one dish). After the dishes were left overnight in darkness a second instar *C. rufifacies* was observed feeding on a dead second instar *C. macellaria.* This may have been either predation or scavenging. In experiment 2 there was no difference in the number of prey taken by small versus large *C. rufifacies* (15 each).

The conditions in this investigation were, of course, highly artificial and might not represent true predation rates within a carcass. Still, the relative differences in behavior seen here may exist in the field. Although second instar *C. rufifacies* may be predaceous as reported, they were much less so than third instars.

Chrysomya rufifacies typically behaves as a secondary fly in that oviposition occurs on carcasses already occupied by other larvae (Fuller 1934, Bohart & Gressitt 1951, Early & Goff 1986). Our results suggest that an ecological refuge exists for native Diptera that reach the post-feeding stage before third instar *C. rufifacies* are present. We have found that all *C. rufifacies* instars are present in goat carcasses when the food is exhausted (unpublished data), indicating that no similar refuge could exist for species following *C. rufifacies* in succession.

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Received 16 January 1991; accepted 18 May 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 15–26, (1992)

NEST BIOLOGY OF *OSMIA* (*DICERATOSMIA*) *SUBFASCIATA* CRESSON IN CENTRAL TEXAS (HYMENOPTERA: MEGACHILIDAE)

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Abstract.—Nests and provisioning behavior of *Osmia* (*Diceratosmia*) *subfasciata* Cresson, a widely distributed, polylectic, cavity nesting bee were studied in central Texas. Most study nests were in borings in pine blocks, but field observations suggest snail shells also are used. Nest plugs and partitions are formed of a mixture of masticated plant material and coarse sand with both materials collected and mixed on the same foraging trip. Provisioning series consist of a mix of long and short foraging trips, with six to ten long trips required to provision a cell. Details of the structure of the four layered cocoon are discussed and figured. Biologically novel features included the initiation of the outermost cocoon layer while the larva is still feeding with the margins of this layer being extended along the cell wall as feeding continues. Larvae spend part of the summer in an extended prepupal diapause before pupating and eclosing to overwinter within their natal cocoons. Floral pollen and nectar sources are listed and observations on the biology of *Chrysura pacifica* (Say) (Chrysididae), a nest parasite, are presented.

Key Words.—Insecta, bee, nest biology, provisioning rate, cocoon, diapause

The subgenus *Diceratosmia* has been considered the most generalized group of North American *Osmia* (Sinha 1958). Although American workers long considered *Diceratosmia* to be a distinct genus, it was reduced to a subgenus of *Osmia* by Sinha (1958) in a treatment followed by most modern workers (Mitchell 1962, Hurd 1979, Michener 1979). *Osmia* (*Diceratosmia*) *subfasciata* Cresson is a widespread but little studied member of this assemblage with most observations on its biology consisting only of brief reports of its use of beetle burrows in wood as nest sites (Linsley 1946, Mitchell 1962), and collection records suggesting its use of mud wasp nests and plant stems as nest sites (Cockerell 1911). The only report yielding any details on its nesting biology is a brief note by Krombein (1967: 311–312) that described a single nest from Arizona, but gave little indication there is anything distinctive about the biology of this bee. Our observations agree in general outline with those of Krombein but differ significantly from his observations in several aspects of nest biology such as materials used in nest construction and duration of prepupal diapause. These differences, coupled with new data on provisioning behavior and timing of cocoon formation, suggest that *O. subfasciata* is biologically more interesting than previously indicated.

MATERIALS AND METHODS

Observations on foraging behavior and nest construction were conducted from 1979 to 1990 at several sites in central Texas with most of the studies done between 1986 and 1990 at the Brackenridge Field Laboratory (BFL) of the University of Texas, Austin, Texas. Artificial pine block trap-nests with diameters of 2.8, 3.2, 4.8 and 6.4 mm were set out at BFL as well as at Sayersville, Bastrop

Co., and Charco, Goliad Co. Additional nests with bores of 5.8, 7.9 and 9.5 mm were also set out at BFL. All 2.8 mm and some 3.2 mm diameter nests had bore depths of 45 mm. Most 3.2 mm nests and nests of all other diameters were bored to a depth of 120 mm. Nests were set out in both large, shaded domiciles with 40 to 60 nests per domicile or in smaller exposed clusters of 12 to 16 nests at BFL. Roughly equal numbers of nests of each diameter were used in each cluster or domicile. Nests in the large domiciles, but not in the small clusters, were replaced when empty nests were filled. The domiciles were placed 1 m from the ground on poles equiped with various sticky traps and moats to exclude fire ants. Nest clusters were taped or wired to tree limbs at 1 or 2 m above the ground as well as mounted on stakes at a height of 15 cm above the ground. Four sets of nest clusters were set out at Charco and Sayersville with two nest clusters on stakes and two on tree limbs at each site. All nests were aligned with their long axes horizontal to the ground.

Individual nests, or provisioning females, from BFL were coded by the year followed by the nest number. Data on phenology and floral hosts were based on the general collections and observations of JLN in central Texas from 1979 through 1989. Data are presented as the mean ± one standard deviation. Plant nomenclature follows Correll & Johnston (1970) and Johnston (1988). Insect vouchers are deposited at the Brackenridge Field Laboratory, Austin, Texas and the Snow Museum, University of Kansas, Lawrence Kansas.

Observations on larval development were based on trap-nests opened in the laboratory and maintained at room temperature (24° C to 8° C summer and 15° C to 22° C winter). Torchio (1989) found that in several *Osmia* spp., the first larval molt occurs before hatching so that the first evident instar is actually the second yielding a total of five larval instars. Our methods were inadequate for detecting if such an early molt occurs in *O. subfasciata* so our discussion refers to the number of instars assuming the eclosing larva is the first instar although we recognize this may be incorrect.

Pollen collection records were based on field observations and analyses of samples of scopal loads and nest provisions. Pollen from scopal loads was mounted in glycerine for microscopic examination and sorted to plant morphospecies with the aid of a reference pollen collection. Crude pollen volume per morphospecies was estimated from pollen volume per grain times number of grains per sample (minimum of 200 grains for total sample). As a conservative measure, only pollens of species constituting 10% or more of the volume of a sample were considered to have been actively collected because some pollen will be picked up incidental to nectaring and many flowers may show high levels of "contamination" of foreign pollen which may be unintentionally collected by a bee.

Results

Phenology and Floral Hosts.—Osmia subfasciata is a strictly vernal species in central Texas. Collection records suggest the species is weakly protandrous with females having much greater longevity than males (Fig. 1). We have collected males from 3 Mar to 14 May in central Texas with most records from the last half of March, although females were collected from 14 Mar to 19 Jun with most activity from the last half of March through April. Lifespans of individual bees are unknown.

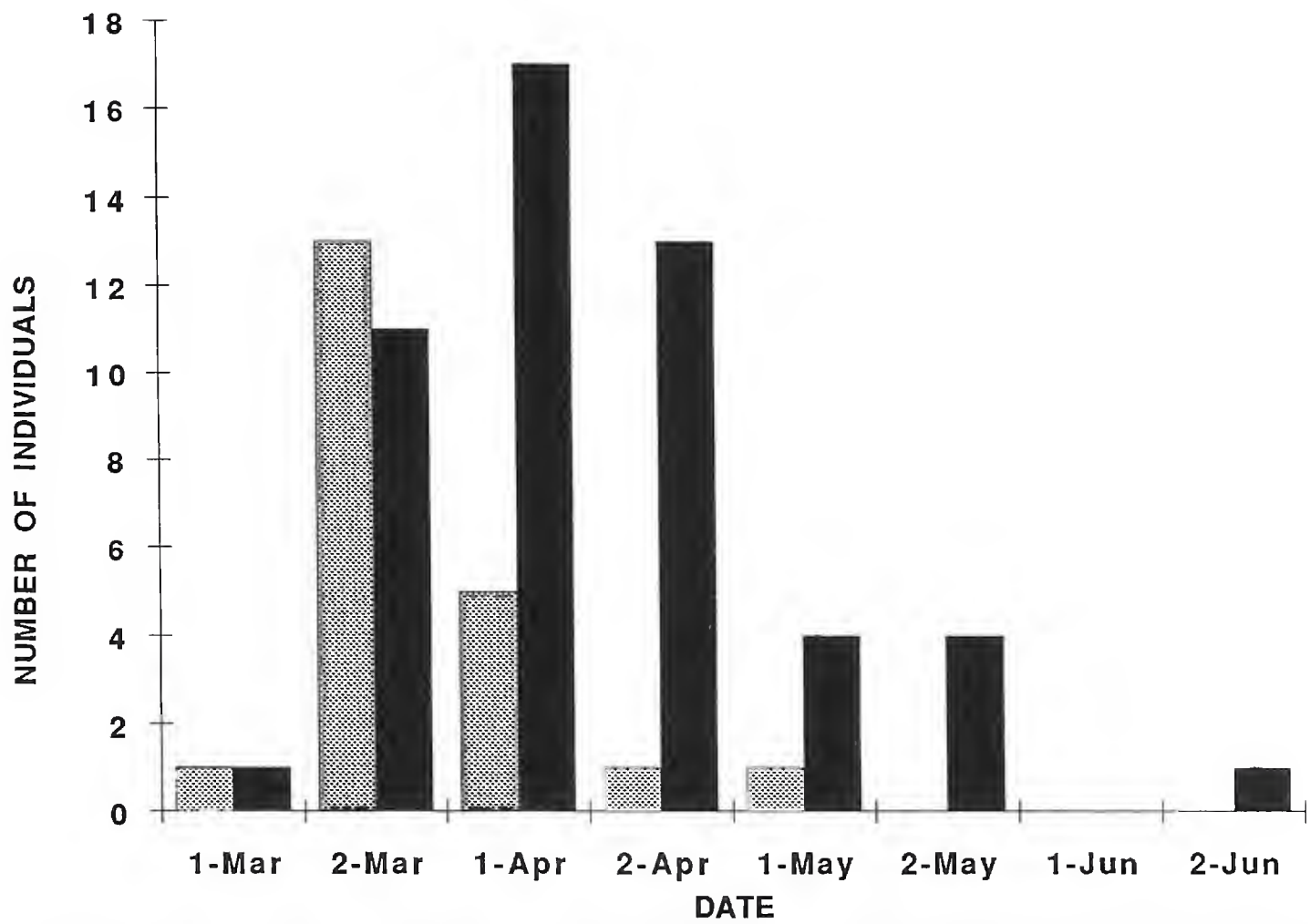


Figure 1. Central Texas collections records for *O. subfasciata* indicating pattern of seasonal abundance. Males = hatched bars. Females = solid bars. Horizontal axis in 2 week periods.

Females of *Osmia subfasciata* are clearly polylectic, collecting pollen from a wide array of plants. We recorded *O. subfasciata* visiting flowers of 32 genera in 14 families in central Texas (Table 1). Hurd & Michener (1955) listed an additional three families and nine genera of plants visited by *O. subfasciata* in Texas. NonTexas records (Hurd & Michener 1955, Mitchell 1962) bring the total to 18 families and 48 genera. *Osmia subfasciata* collected pollen of at least 13 genera in nine families in central Texas (indicated by the letter P in Table 1). Analysis of pollen loads and nest contents from trap-nests indicated 54% (14 of 26) of the scopal loads contained mixtures of pollens (two or more pollens each representing at least 10% of pollen load volume).

Nest Structure.—Considerable variation in body size is seen in central Texas *O. subfasciata* with males usually smaller than females. Males were 7.1 ± 0.8 mm (range 5.8–8.7; n = 25) in length with thoracic widths of 2.2 ± 0.2 mm (range, 1.8–2.6; n = 25). Females were 8.5 ± 0.8 mm (7.0–9.7; n = 25) in length with thoracic widths averaging 2.7 ± 0.5 mm (2.2–3.1; n = 25). Females initiated nests in wooden traps with bore diameters of 3.2 (n = 4), 4.8 (n = 11) and 6.4 mm (n = 2). Only the long 120 bores were used by *O. subfasciata.* Our sample of nests suggests diameters of 3.2 to 4.8 mm, a size best fitting observed female cross-sectional area, were the preferred nest diameters for *O. subfasciata.* Unlike many taxa collected during trap-nesting programs, *O. subfasciata* is apparently not gregarious as we never found more than one female active at a given trap-nest station.

As is common in *Osmia,* but not in some trap-nesting *Hoplitis,* nest walls were unlined, even in nests with diameters significantly larger than that of the cross-

Table 1. Central Texas floral records for *Osmia subfasciata.*

Plant family	Plant taxon	Visited by
Asteraceae	*Chaetopappa bellioides* (A. Gray) Shinners	♂
	Crepis sp.	♀
	Engelmannia pinnatifida Nuttall	♂
	Coreopsis nuecensis Heller	♀
	Coreopsis basalis var. *wrightii* (A. Gray) Blake	♀
	Erigeron sp.	♀
	Gaillardia pulchella Fougeroux	♀
	Hymenoxys scaposa (DC) Parker	♀P, ♂
	Krigia occidentalis Nuttall	♂
	Lindheimera texana Gray & Engelmann	♂
Berberidaceae	*Berberis swaseyi* Buckley	♂
Brassicaceae	*Lesquerella grandiflora* (Hooker) Watson	♀P
	Lesquerella argyraea (A. Gray) Watson	♀
Cactaceae	*Opuntia macrorhiza* Engelmann	♀
Commelinaceae	*Tinantia anomala* (Torrey) Clarke	♀P
Fabaceae	*Cercis canadensis* L.	♀, ♂
	Desmanthus velutinus Scheele	♀P
	Lupinus texensis Hooker	♀P
	Prosopis glandulosa Torrey	♀P, ♂
	Vicia villosa Roth	♂
Hydrophyllaceae	*Nama hispidum* A. Gray	♀P
	Nemophila phacelioides Nuttall	♀P, ♂
	Phacelia congesta Hooker	♀P
	Phacelia patuliflora (Engelmann & A. Gray) A. Gray	♀
Lamiaceae	*Brazoria* sp.	♀
	Monarda citriodora Cervantes	♀P
	Teucrium cubense Jacquin	♀, ♂
Malvaceae	*Callirhoe leiocarpa* Martin	♀
	Callirhoe involucrata (Torrey) A. Gray	♀P, ♂
	Sida abutifolia Miller	♀
	Sphaeralcea lindheimeri A. Gray	♀P
Onagraceae	*Oenothera speciosa* Nuttall	♀P
Rubiaceae	*Hedyotis nigricans* (Lamark) Fosbery	♀P
Sapindaceae	*Ungnadia speciosa* Endlicher	♂
Solanaceae	*Chamaesaracha sordida* (Dunal) A. Gray	♀
Verbenaceae	*Verbena bipinnatifida* Nuttall	♀
	Verbena officinalis L. ssp. *halei* (Small) Barber	♀, ♂

[1] P indicates known pollen host.

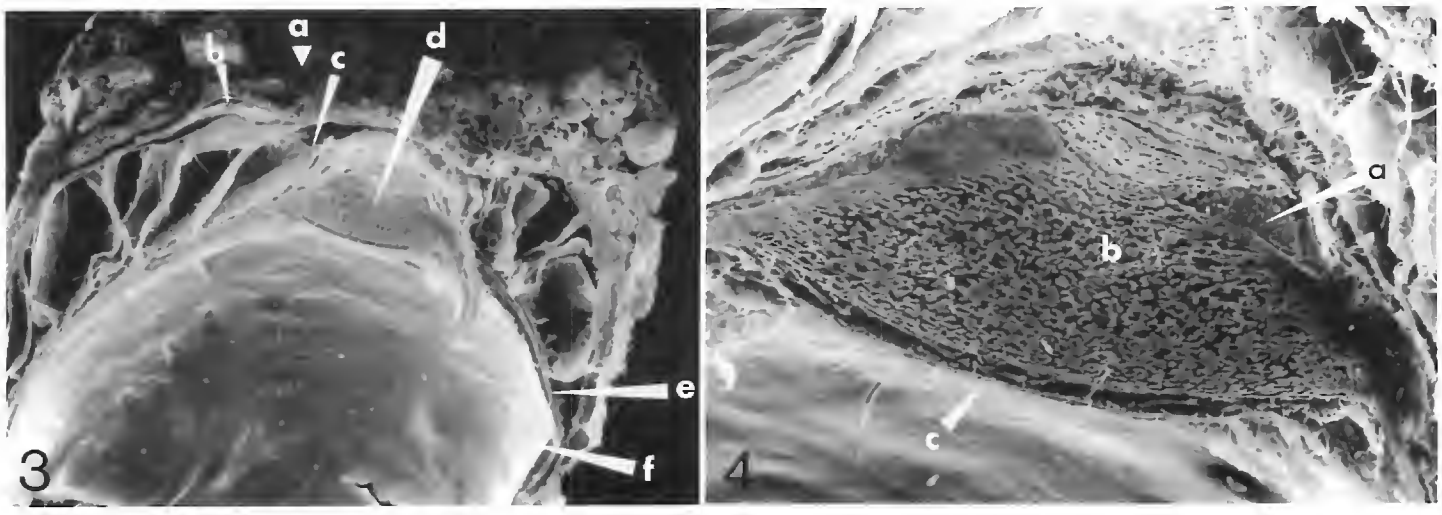
sectional diameter of the bee. Partitions, basal plugs and entrance plugs were constructed of a mixture of coarse sand and masticated plant material (Figs. 2, 3). The entrance plug was single layered, 3–6 mm thick, and had a smooth, concave outer surface. The margins of the plug were usually flush with, or more rarely recessed 3–6 mm from, the nest entrance. The entrance plug was followed by one or two vestibular cells of 6–47 mm in length. The partition between the vestibular cells, or the outermost cell partition, if only one vestibular cell was present, was consistently thicker than the inner brood cell partitions and sometimes thicker than the entrance plug. Partitions between inner cells were quite thin medially (0.2–0.3 mm) but thicker along the cell wall (0.5–1.0 mm). In one case, a female was found to have used a nest previously occupied by a eumenid wasp and had

Figure 2. Female *O. subfasciata* adding soil to masticated leaf material (7×).

used portions of some of the remaining mud partitions as bases for her own nest partitions.

Nests consisted of linear series of 2–12 brood cells. These cells varied from 5.5–12.0 mm in length or 60.0 to 322.0 mm^3 in volume depending on nest diameter. Lengths of brood cells averaged 8.4 ± 0.6 mm (7.5–9.7; $n = 21$) in nests with diameters of 3.2 mm and 7.9 ± 1.3 mm (5.5–12.0, $n = 52$) and 7.9 ± 1.4 mm (6.5–12.0, $n = 11$) for 4.8 and 6.4 mm diameter nests respectively. No consistent pattern was evident between brood cell length and its position within a nest. Too many bees escaped from nests without being sexed or were detroyed by parasites to allow accurate estimates of sex ratio or position of sexes within nests. Limited available data suggest that, as is common in sexually dimorphic, trap-nesting species with large females, females are produced primarily in the innermost cells. Only males were produced from the two 3.2 mm diameter nests. The provision mass was firm and uniformly moist (except for dry loose pollen along the walls), filling most of the cell. The outer face of the provision mass slanted towards the cell entrance, the upper part of the mass being the furthest from the entrance. Females inserted the posterior end of the egg in a moistened area on the upper third of the slanted face with the anterior portion of the egg remaining free but curving down over the provisions.

In addition to trap-nests, we observed females of *O. subfasciata* investigating



Figures 3–4. *O. subfasciata* cell and cocoon structure. Figure 3. Cross-section of anterior portion of cocoon with attached nest partition (12.2×). (a) partition of coarse sand and masticated plant material. (b) outer cocoon layer adhering to partition. (c) outer sheets of inner cocoon. (d) fibrous layer of nipple. (e) middle layer of inner cocoon. (f) innermost layer of inner cocoon. Figure 4. Cross-section of cocoon nipple (49×). (a) elaboration of middle layer of inner cocoon. (b) fibrous inner layer of nipple. (c) innermost layer of cocoon.

various small, empty snail shells at BFL where a single-celled bee nest was found in one of these shells by A. Hook (personal communication). Although the nest was destroyed when opening the shell, the plug was of the characteristic sand/plant mastic mix. This, along with its small size, suggests it was a *Disceratosmia* nest. *Osmia subfasciata* is the only *Diceratosmia* known to occur at BFL, and other small megachilines occurring there use different materials in their nest partitions. It thus seems likely that *O. subfasciata,* like *Osmia conjuncta* Cresson (Rau 1937), occasionally constructs nests in snail shells.

Nest Construction.—Nests were initiated by placing a thin layer of the sand/masticated plant material mix at the end of the burrow. Sand and plant material were collected on the same trip. At Sayersville, we repeatedly observed female *O. subfasciata* chewing leaf margins of *Helianthemum georgianum* Chapman (Cistaceae), forming a small ball which was held beneath the mandibles. The bee then moved to an area of loose sand and dropped the ball of chewed leaf material on the sand surface where she proceeded to chew and knead the ball as she rolled it over the soil surface incorporating soil/sand particles into the mass (Fig. 2). Individuals were observed to return to the same small one or two m^2 areas for five or more consecutive leaf-soil loads. Source of the plant material at other sites is unknown but presumably a variety of plant taxa is utilized. Upon returning to the nest, the female laid down a low rim of the soil/leaf masticate mix which served as the base of the partition separating the first two cells of the nest. Construction of such a rim, known as Fabre's threshold (Malyshev 1936) is widespread among megachiline bees (Frohlich 1983; JLN, personal observation). After provisioning and ovipositing in the first cell, the female closed the cell delimited by the initial rim and constructed another rim. This pattern continued until the final cell of the nest was completed.

Bee 87-7 required 11 trips and 97.7 minutes to finish a partition and construct a new rim. During this period she averaged 6.3 ± 1.73 min (2.82–9.63; $n = 11$) in the nest and 2.58 ± 2.34 min (0.76–8.78; $n = 11$) away from the nest. Female *O. subfasciata* apparently are able to construct and provision two cells per day.

The female observed in 1989 at BFL took six days to complete a 12 cell nest (89-7) and then six days for a nine cell nest (89-18).

Provisioning Behavior.—Because females in the small 3.2 and 4.8 mm diameter nests had to exit the nest to turn around to deposit pollen, time in the nest after pollen trips could be separated into nectar and pollen deposition components. Female 89-7 averaged 0.76 ± 0.19 min ($n = 11$) in the nest for nectar deposition and 1.00 ± 0.30 ($n = 11$) for pollen deposition. Female 87-7 was somewhat faster, averaging 0.31 ± 0.14 ($n = 9$) for nectar deposition and 0.71 ± 0.21 for pollen deposition. The preceding times for pollen deposition exclude the long final period of a provisioning sequence which presumably represents final pollen mass preparation and oviposition. This final period was 5.35 min for bee 87-7, and 4.45 min for bee 89-7.

Interpretation of foraging patterns was complicated by the lack of consistency in the duration of pollen trips. A complete provisioning series for a male cell in nest 89-7, provisioned on 19 Apr 1989 required 192 minutes. This entailed 10 or possibly 13 pollen trips. The variable estimate stems from the fact that most pollen trips were relatively long, averaging 16.05 ± 2.78 min (12.04–22.29; $n = 9$) but there were also three short trips averaging only 2.74 ± 1.22 min (2.02–4.15; $n = 3$) when the bee returned with pollen. It is likely the short trips were not true pollen trips but we cannot be sure as we were not able to tell if the bee's scopa still contained pollen when she exited the nest. The female behaved as if she were depositing pollen prior to leaving for the apparent short pollen trips. Another cell provisioned on 1 Apr 1987 showed the same pattern. This cell required only 88 minutes and six long trips with a mean of 15.07 ± 4.66 min (6.12–19.90) and four short ones with a mean of 1.46 ± 0.85 min (0.89–2.71). A similar mix of long and short trips was observed in other partial provisioning series noted in 1987, 1989, and 1990. The short trips may have been nectar trips or perhaps represent a form of defensive behavior against nest parasites which oviposit in open cells.

Development and Cocoon Structure.—Larvae fed without moving from the initial position of egg insertion during the first three instars. The conspicuously setose fourth instar occurs six to seven days after hatching and then begins moving over the provision mass. Defecation is initiated one to two days after molting to the fourth instar. The pale, flattened fecal pellets are initially placed on the distal portions of the cell, particularly the distal walls and outer margins of the cap. Individual pellets free from the wall are curved, have tapered ends, and are 0.6–0.7 mm long. The curved, ventral surface of an individual pellet had a weakly defined, shallow, longitudinal groove. Pellets produced later become strongly flattened, even ribbon-like, as they are closely appressed to the cell wall or outer layer of the cocoon.

The cocoon consists of four layers in two distinct structures, an inner and outer cocoon (Fig. 3). The outer cocoon is single-layered and is initiated two to three days after molting to the final larval instar, well before the completion of feeding as two-thirds to three-fourths of the provision mass remains at that time. The initial portion of the outer cocoon layer consists of a tough translucent membrane placed over, and closely adhering to, the cell cap and anterior portions of the cell wall up to the edges of the remaining provisions. This portion of the cocoon is laid over the initial layer of fecal pellets. The outer cocoon is extended along the

cell walls, sometimes after the deposition of more fecal pellets, as the walls are exposed by continued feeding. Additional fecal pellets are deposited on the inner surface of this cocoon layer. The provisions are completely consumed roughly four to five days after the initiation of the outer cocoon. The outer cocoon is completed by covering the base of the cell after the completion of feeding.

The inner cocoon, initiated after the completion of the outer, required two or three days to construct and consisted of three layers. The outermost is formed by a series of thin, translucent sheets with a few embedded threads. These sheets are apparently laid down as overlapping series which are attached both to one another and to the outer cocoon. The innermost of these translucent sheets forms the foundation for the relatively thick (0.02 mm), tough, brown, opaque middle layer. Closely appressed to the inner surface of the middle layer is a thin, translucent inner layer.

The anterior end of the inner cocoon is elaborated into a nipple (Figs. 3, 4), a complex structure which apparently serves as an air exchange mechanism for the otherwise impervious cocoon. Seen from within, the innermost portion of the nipple appears as an opaque, smooth brown disk surrounded by a paler ring. In cross section, it can be seen that the disk is formed by a tightly packed region of the tough brown fibers which fill the mesal, hemispherical region of the nipple. The thick layer of tough threads is covered by, and grades into, the thickened continuation of the opaque middle layer of the cocoon. This thickened opaque layer is not continuous, having a central opening of approximately 0.3 mm. This central opening is filled with a continuation of the inner layer of coarse threads which in turn intergrades with dense translucent sheets covering the outer surface of the nipple.

Osmia subfasciata is univoltine in central Texas. After the completion of cocoon spinning, there is a relatively long larval diapause of approximately 90 to 110 days before pupation. Larvae completing cocoon construction by 6 May pupated by 5 Aug when kept in the lab at room temperature (23.3°–27.7° C). However larvae from a nest constructed at the same time but left in the field did not pupate until 30 Aug. Individuals overwinter as adults within their natal cocoons.

Mating Behavior.—Mating was rarely observed although males are commonly observed patrolling female pollen and nectar sources such as flowers of *Cercis, Nemophila* or *Berberis* during the initial portions of the flight season. Mating, including a period of post-copulatory mate guarding, was prolonged and was observed only at flowers. Males were never observed at nest sites or areas of female emergence when occupied trap nests were placed in the field. It is likely that female *O. subfasciata* mate only once, or at most a few times, during a brief receptive period.

Predators and Parasites.—Nest parasitism was not extensive with only two species of nest parasites reared. Bombyliid larvae were reared from two outer cells of BFL trap-nests. Pupal morphology indicated they were Anthracinae, presumably *Anthrax,* but neither individual was able to pierce the nest closure to exit and both failed to eclose. The other nest parasite was the small chrysid wasp, *Chrysura pacifica* (Say) which was reared from nests from Sayersville set out in 1986 and 1989. *Chrysura pacifica* has not been collected at BFL. Our observations of *C. pacifica* larval development agreed with earlier observations of *C. pacifica* attacking *Osmia pumila* Cresson (Krombein 1967: 446). The four-celled Sayers-

ville 89 nest included six *C. pacifica*: two cells with two *C. pacifica,* and two with one. The eggs have a thick, tough chorion and are deposited near the basal portion of the provisions. In a cell where larval development was followed completely, the *C. pacifica* egg hatched one day after the *O. subfasciata* egg (three to four days after *O. subfasciata* oviposition). The *C. pacifica* larva remained quiescent for three days before beginning to move forward over the provision mass, aided by an unusual bifurcate caudal segment. After two days of movement it reached and attached itself with its mandibles to the still sessile, third instar *O. subfasciata* larva. A second *C. pacifica* larva, previously hidden on the opposite side of the cell, attached itself to the *O. subfasciata* larva on the following day. The *O. subfasciata* larva molted to the fourth instar the following day (seven days after hatching) and both larvae were detached, with only one reattaching to the now setose, free moving *O. subfasciata* larva. The remaining first instar *C. pacifica* larva remained inactive but attached to the *O. subfasciata* larva for an additional 12 days, during which the *O. subfasciata* larva completed constructing its cocoon. It then began feeding on the *O. subfasciata* larva and its own growth became obvious. Feeding continued for five days, after which the *O. subfasciata* larva was badly shriveled. Unfortunately, the *C. pacifica* larva was killed by a laboratory infestation of *Chaetodactylus* mites which almost certainly came from infested nests of *Osmia ribifloris* Cockerell stored nearby. Mites developed from egg to adult on provisions and feces of *O. subfasciata* but no infestations were observed in field collected nests nor were mites present on adults.

Miltogrammine flies were common at the BFL nest site but apparently were associated with various sphecid and eumenid wasps using the domicile as none were observed at bee nest entrances. The surface of the pollen mass from one cell in nest 89-18 in which the egg failed to hatch was encrusted with the black fruiting bodies of *Ascosphaera.* The fungus was not noted in other cells. The only observation of predation was a female captured by the common red assassin bug, *Apiomerus spissipes* (Say), at flowers of *Verbena officinalis* Linnaeus ssp. *halei* (Small) Barber, at Pedernales Falls State Park, Blanco Co., Texas.

Discussion

Our observations on nest structure and cocoon structure of *O. subfasciata* agree with those of the only previous study by Krombein (1967) in many features of general nest architecture but differ in a number of important aspects. Krombein reported that partitions in his nest from Scottsdale, Arizona, were constructed only of masticated leaf material rather than the sand/plant mix we found in Texas. Use of a combination of sand or soil and masticated leaf material for nest construction is common in the *Hoplitis-Anthocopa-Proteriades* complex, particularly in the subgenera *Penteriades, Hoplitina, Xerosmia, Acrosmia, Atoposmia, Eremosmia* and *Hexosmia* (Parker 1975, 1978a, b). However, it apparently is uncommon in *Osmia* (sensu Sinha 1958). Published accounts indicate the vast majority of *Osmia* species use either soil or plant masticate in nest construction but not both (Iwata 1976, Rust 1974). Exceptions among American species include *Osmia* (*Cephalosmia*) *californica* Cresson, which constructs nest plugs and partition of a mix of mud and masticated plant material (Levin 1966, Rust 1974, Torchio 1989), and *Osmia* (*Trichinosmia*) *latisulcata* Michener, which uses a sand/plant masticate mix for cell partitions and plant masticate and pebbles for

nest plugs (Parker 1984). Both mud and plant masticate are used in constructing the urn-like cells of some members of subgenus *Acanthosmioides* (Rust et al. 1974). The use of a sand/plant masticate mix in nest construction appears to be unusual even within *Diceratosmia*. Nest construction materials in various species of *Diceratosmia* have been described as leaf paste (*O. conjuncta* [Rau 1937]), leaf pulp (*Osmia gallarum* Spinola [Iwata 1976]), and green putty (*Osmia versicolor* Latreille [Fabre 1915]). If *Diceratosmia* is actually the sister group of all other *Osmia* (sensu Sinha 1958), it is tempting to suggest that the sand/plant pulp mixture is the primitive nest construction material for this lineage, but the occurrence of mud, plant masticate, or various mixes as nest construction materials by taxa scattered throughout the genus renders this highly speculative.

Initiation of cocon spinning before the completion of feeding also appears to be unusual among megachilines. Although production of a few threads, which aid in holding the feces in place prior to cocoon completion, is common among megachilines (Stephen et al. 1969, Torchio 1989), production of a distinct sheet as produced by *O. subfasciata* is not. Unfortunately, there are relatively few studies of development which would allow one to ascertain accurately when cocoon-spinning is initiated. The only other megachiline we are aware of that regularly initiates cocoon construction well before completing feeding is *Hoplitis* (*Robertsonella*) *simplex* (Cresson) (JLN, personal observation).

There is considerable variation in cocoon structure within *Osmia*. The cocoon of *O. subfasciata* is a distinctive combination of elements found elsewhere in the genus. The tough, nippled, multilayered cocoons of *Osmia* s. str. (Rust 1974; JLN, personal observation) appear to be virtually identical to the inner cocoons of *O. subfasciata*. The presence of a well formed anterior layer of the outer cocoon is apparently more unusual in *Osmia* although a very similar structure is present in cocoons of *O. latisulcata* (Parker 1984). A well defined anterior portion of the outer cocoon is present in at least some species of *Hoplitis* and *Chelostoma* (Parker 1988; JLN, personal observation).

The extended prepupal diapause we observed in *O. subfasciata* also appears to be unusual among megachilines which overwinter as adults. A review of published reports suggests most *Osmia* larvae pupate within thirty days of cocoon completion. Significant exceptions are the two year individuals of parsivoltine species, which typically spend their first winter as prepupae (Torchio & Tepedino 1982) and larvae of *Osmia nigrifrons* Cresson that have prepupal diapause lasting 130–150 days (Rust et al. 1974). In addition, we have found that central Texas populations we studied of *Osmia ribifloris* have an extended prepupal diapause of 100–150 days (unpublished data) even though populations from northern Nevada have a brief prepupal diapause (Rust 1986). Although we are unaware of conclusive proof, it is generally believed that the prepupal stage of bees has lower metabolic requirements and is more resistant to environmental stress than the adult. Presumably this explains why the prepupal stage is the one most commonly used for overwintering or extended diapause.

Nonetheless, overwintering as an adult is common among cool-temperate bees which emerge in the early spring (Stephen et al. 1969). Overwintering as an adult presumably facilitates early emergence and avoidance of pupation under cold or otherwise unsuitable conditions. However, overwintering as an adult by vernal bees may regularly expose diapausing adults to potentially lethal temperatures

and/or moisture stress in areas of high summer temperatures. A recent study has shown that diapausing adult *Osmia cornifrons* Radoszkowski kept at 22° C had a survivorship rate (76%) nearly twice that of individuals maintained at 30° C (39.9%) (Maeta 1978). Excluding *Osmia,* most osmiine bees overwinter as prepupae so it is possible that the extended prepupal diapause we observed in *O. subfasciata* simply reflects retention of the plesiomorphic state. However, we believe that in *Osmia,* extended prepupal diapause is a derived condition facilitating tolerance of extended hot conditions, particularly those with high night temperatures such as are commonly encountered during central Texas summers. Average minimum monthly temperature exceeds 18° C from May through September in central Texas (Conway & Liston 1974). We expect extended prepupal diapause will be found in other *Osmia* spp. of central Texas as well as in other regions with high night temperatures. *Osmia subfasciata* larvae from Scottsdale, Arizona reared in a Washington, D.C. laboratory had a prepupal diapause of roughly 45 days (Krombein 1967). The pattern of overwintering as an adult during the winter before spring emergence, appears to be universal in *Osmia* and may be an important factor limiting the southern distribution of the genus. Two year old individuals in parsivoltine species of *Osmia* spend their first winter as prepupae, but their second as adults (Torchio & Tepedino, 1982). These cases represent an extreme form of extended prepupal diapause for some individuals. Extended prepupal diapause appears to be a mechanism which minimizes exposure of diapausing adults to the temperature and moisture stress in warm climes yet retains the flexibility for early spring emergence.

Acknowledgment

We thank Gregg Dieringer for assistance with SEM work, and the Texas Department of Parks and Wildlife for permission to collect at Pedernales State Park (permits 17-89 and 10-90). Gregg Dieringer also read the manuscript and made many helpful suggestions.

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Received 18 January 1991; accepted 1 June 1990.

PAN-PACIFIC ENTOMOLOGIST
68(1): 27–37, (1992)

OBITUARY: JAMES WILSON TILDEN (1904-1988)

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James Wilson "Bill" Tilden, entomologist, lepidopterist, naturalist, professor emeritus at San Jose State University, died on 27 Dec 1988, four days before his 84th birthday, in San Jose, California, of injuries resulting from a fall at his home. Memorial services were held at the Methodist Church in Philo, California, on 27 May 1989, and his ashes were buried at Philo in the Ruddock family cemetery.

Bill Tilden is known to many through his research and publications on Lepidoptera and ecology, including the books *Butterflies of the San Francisco Bay Region* (Tilden 1965), *A Field Guide to Western Butterflies* (Tilden & Smith 1986), and *California Butterflies* (Garth & Tilden 1986); through teaching for 22 years at San Jose State University; and through his membership in many societies, including the Pacific Coast Entomological Society. He was a member of this society for 49 years—elected to membership at the 158th meeting on 30 Sep 1939—and served as president in 1960. Several articles have been published on Bill's life (Anonymous 1989; Helfer 1989; Moreno 1989; Opler & Smith 1990; Smith 1990a, b), and this article complements information given in the others.

Bill Tilden was born 31 Dec 1904 in a shake cabin constructed by his father in the hills above Philo and Anderson Valley, in Mendocino County, California. He was the second of four children (he had an older sister and two younger brothers) of Thomas Jefferson Tilden (6 Jul 1871–3 Jun 1945) and Charlotte Almira Tilden, née Ruddock (13 Apr 1887–7 Apr 1966).

Bill's grandfather, James Wilson Tilden (17 Sep 1827–2 Nov 1878), a mate on a sailing ship, jumped ship in San Francisco to join in the Gold Rush. His grandmother, Susan Dickerson Tilden (26 Jan 1844–6 Mar 1875), died at the early age of 31, leaving her husband with three small children to raise. Upon the death of Bill's grandfather, three years later in a boating accident in Sacramento, the orphaned children were supported by the Independent Order of the Odd Fellows.

Bill's father, a lumberman and carpenter, was born in Shingle Springs, in the foothills of El Dorado County, California. He ran away from his foster home when he was 14 and supported himself thereafter by his own resources. He worked near Philo lumbering in the redwood forests with oxen teams. It was here that he met Bill's mother, the youngest daughter of Albert G. Ruddock (1839–1895), and Permelia Curtis Ruddock (1846–1932). Albert Ruddock was a road supervisor and the first postmaster of Philo. Bill's father and mother were engaged to be married for seven years while his father acquired the land and built his cabin. They were married on 15 Aug 1900.

Bill's family moved from Philo in 1906, following the death, from diphtheria, of his sister, Naomi Alice (1902–1905), just before her fourth birthday. This move was not financially advantageous to the family but was necessitated by the grief

Figures 1–5. Figure 1. Thomas Jefferson Tilden, ca. 1900. Figure 2. Charlotte Ruddock Tilden, ca. 1900. Figure 3. Bill Tilden ten years old with two brothers—Thomas C. Tilden, four years old, and Earl R. Tilden, two years old. Figure 4. Bill Tilden, high school graduation picture, 1922. Figure 5. Bill Tilden, San Jose State College graduation picture, 1942.

of his mother, who wanted to move elsewhere because of the loss of her daughter, and concern over Bill's poor health.

Bill attended public schools in Philo, Turlock, Fresno, and Hilmar. At Hilmar, a small town located south of Turlock in Merced County, the family lived on a 20 acre ranch between Tegner and Hilmar. Bill graduated from Hilmar High School in 1922, completing his high school requirements in three years. Bill wanted, at the time of his graduation, to attend the University of California at Berkeley and to major in English Literature, but no funds were available for him to do so.

In 1923, his father purchased 86 acres of second growth redwoods in Santa Cruz, at Route 1, box 710 (now 3363 Branciforte Drive). About 10 acres were available to grow garden produce and to plant an orchard. In Santa Cruz, his father also worked as a carpenter. Bill was to make the family home his headquarters for the next 16 years, whenever he was not working elsewhere.

Figures 6–11. Figure 6. Thomas and Charlotte Tilden, at Santa Cruz ranch, 1942. Figure 7. Bill Tilden and Hazel Irene Miller Tilden, wedding day, San Francisco, California, 19 Jun 1943. Figure 8. Field day, 200th meeting of the Pacific Coast Entomological Society, Rock City, Mount Diablo, California, 18 Apr 1948. Left to right, John R. (Jack) Walker, Bill Tilden, John P. Harville, and Richard M. Bohart (photo by Edgar A. Smith). Figure 9. Vector Control Staff of Santa Clara County Health Department: back row, left to right, Edgar Smith, Robert Cunningham, Roy Eastwood, Tal Lloyd, Dean Ecke, and James St. Germaine; front row, left to right, Bill Tilden, Tom Sexton, Jerry Kraft, Bruce Eldridge, and Rocci Pisano, 1954. Figure 10. Bill Tilden with children (left to right) James, Janice and Bruce, Christmas picture, 1954 (photo by Hazel I. Tilden). Figure 11. Bill Tilden, while on Vector Control Staff of Santa Clara County Health Department, 1954.

Bill's employment at this time included working for the Southern Pacific Railroad Company in San Francisco, in canneries, and as a fruit tramp with his brothers, Tom and Earl. While following the fruit season from California to Idaho, they managed a side trip to see Yellowstone National Park. Bill belonged to the Musician's Union and played trombone in a band on the Santa Cruz Boardwalk. That also included several engagements with The Miss America pageants, and playing in San Francisco and elsewhere. He was proud of his association with jazz groups and he later reminisced of participating in a jam session after a Santa Cruz concert with Jack Teagarden, the famed trombonist. With his brother, Tom, he collected insects of all orders for L. M. McQuesten of the National Insect Company, of Davis, California. On one occasion, McQuesten loaned Bill and Tom his car so that they could collect in the Sierra Nevada for him. Tom recalls they returned by way of Madera, where they also collected insects from dead sheep. McQuesten also loaned them a 410-gauge sawed-off shotgun, so that they could shoot wild game for food. As Tom has commented, "These were the depression years and employment was hard to come by."

Bill became interested in natural history at an early age. He started an insect collection when seven years old. He also enjoyed drawing birds with crayon, and an aunt subscribed to *Bird Lore* for him. As was the custom for those who lived on farms at that time, he shot robins and squirrels for food. His early correspondents included the entomological promoter, James Sinclair of San Diego, the then Kansas lepidopterists William D. Field and Virgil F. Calkins, and the twin brothers Arthur C. and Edgar A. Smith, of Los Banos, California, in 1933. His first exchange was made with Hugh Gibbon of Miniota, Manitoba, and early exchanges were made also with Lionel Paul Grey. Bill told me that in 1927 he seriously began to study Lepidoptera, aided by the Santa Cruz resident lepidopterists Edgar A. Dodge and John P. Strohbeen. In his first publication, "Preliminary list of the butterflies and skippers of Santa Clara and Santa Cruz counties, California" (Tilden 1940), Bill acknowledged the help of Dodge, Strohbeen, Art and Ed Smith, and George S. Mansfield. Between 1940 and 1987, Bill published over 100 articles (Smith 1990b) on Lepidoptera, Coleoptera, life histories, ecology, flies of public health importance, etc. Some of these he wrote with co-authors, including John C. Downey, Carl D. Duncan, John S. Garth, James St. Germaine, David H. Huntzinger, George S. Mansfield, William A. Palmer, Ernest R. Schoening, Arthur C. Smith, and Bruce A. Tilden.

In 1938, 16 years after his graduation from Hilmar High School, and when 33 years of age, Bill enrolled at San Jose State College. This was made possible, in part, by financial support from a friend, Charles "Chas" Bowles, a retired civil engineer who lived along Indian Creek near Philo. He was a general naturalist who had an interest in birds. Bill had an avid interest in birds as well as insects, and it was evident to Bowles and others how knowledgeable Bill was, in spite of the fact that he did not have a college education. Bowles told Bill that "you simply have to go to college." Bill helped Bowles by being the driver on automobile trips, including one to the deserts of southern California and Arizona. Bowles, in turn, placed some funds in a bank account to get Bill started in college. In his freshman year at San Jose State College, Bill roomed in an apartment at 72 South 6th Street with his earlier entomological correspondents Art and Ed Smith, who were then in their senior year. It was Art and Ed Smith who earlier made arrangements for

Bill to meet Carl D. Duncan on the annual field day of the Pacific Coast Entomological Society that was held at Alum Rock Park, San Jose, on 8 Apr 1938. That was the 152nd meeting of the Society, during which year Duncan was president. On the basis of this meeting, Bill decided to attend San Jose State College.

Bill graduated in 1942 from San Jose State College, receiving a Bachelor of Science degree in Biological Sciences. This was at the height of the Second World War, and he had applied for deferment so that he might attend medical school at Stanford University. Because he did not receive word on his request, he decided to enlist in the U.S. Navy in August 1942, rather than be drafted into the Army. (Bill later received his letter of deferment when he was overseas!) After six weeks of basic training on Treasure Island in San Francisco Bay, he served as a Pharmacist's Mate on the troop evacuation ship "Bloemfontaine," in the Pacific Theater, until V-J Day in 1945. His long-time friend Art Smith, who served with an Air Force intelligence unit attached to Admiral Nimitz's headquarters (CincPac), recalls how he was usually able to meet and visit with Bill, whenever his ship docked at Pearl Harbor. Bill did some entomological collecting during his military service, but this was hampered by travel restrictions.

Bill married Hazel Irene Miller in San Francisco on 19 Jun 1943, at which time she was teaching elementary school at Tupman, in Kern County, California. Later, Hazel taught in Redwood City in order to be close to Stanford University when Bill was enrolled there. They first met, in their junior year at San Jose State College, when in an ornithology class given by Gayle Pickwell. Bill and Hazel were two of three students who made perfect scores on one of Pickwell's examinations.

On his return from military service, utilizing his "G. I. bill," Bill made arrangements to commence graduate work in the Department of Biology at Stanford University, under the guidance of Gordon Floyd Ferris. He was assigned a graduate student office in a wing of the Leland Stanford Junior Museum that served for many years as the Natural History Museum (housing primarily Botany, Entomology, and Ichthyology). Bill completed his Master of Arts degree in 1947, with the thesis topic, "The comparative morphology of the larval head in Lepidoptera" (44 pages, and 14 plates). Ferris wanted him to continue work in morphology but Bill strongly resisted. Bill was permitted to study "The insect community on *Baccharis pilularis* De Candolle," and completed a Doctoral Dissertation (Tilden 1948) of 408 pages. This was published in part in *Microentomology* (Tilden 1951b) and in additional papers (see a listing in Smith 1990b: 50–55). With the completion of his doctoral degree in 1948, Bill became a member of the staff of the Department of Biology, at the then San Jose State College (now University). He taught about 30 different courses in the 22 years before his retirement as Emeritus Professor, in June 1970. His primary assignment, however, was Entomology.

Starting in the early 1950s, Bill not only worked each summer for the Vector Control program of the Santa Clara County Health Department, which was under the management of Edgar A. Smith, but he also served as a consultant in the identification of insects and other arthropods of public health importance throughout the years.

According to C. Don MacNeill, Bill pioneered in the study of our western North American skippers. As MacNeill commented, most lepidopterists had avoided

Figures 12–17. Figure 12. 12th Annual meeting of the Lepidopterists' Society held at the Santa Barbara Museum of Natural History. Left to right, Fred T. Thorne, Charles L. Remington, John A. Comstock, and Bill Tilden (photo Santa Barbara News Press). Figure 13. Tilden family on deck of "Matsonia" leaving San Francisco, July, 1963. Figure 14. Left to right, Bill Tilden and Lloyd M. Martin, Prescott, Arizona, 30 Mar 1972 (photo by Hazel I. Tilden). Figure 15. Roy O. Kendall's Open House, San Antonio, Texas, 22 Jun 1972. Left to right, Harry K. Clench, Charles V. Covell, Jr., Kenelm W. Philip, and Bill Tilden (photo by Hazel I. Tilden). Figure 16. San Antonio, Texas, June, 1972. Left to right, Mrs. Wilbur S. McAlpine, Bill Tilden, John C. Downey, and Wilbur S. McAlpine (photo by Hazel I. Tilden). Figure 17. Lepidopterists' dinner on river boat, San Antonio, Texas, June, 1972. Left side of table, left to right—Harry K. Clench, Hazel I. Tilden, Bill Tilden, Jerry A. Powell, Mignon Bush, Don R. Davis, and Julian P. Donahue; right side of table, left to right—Madeleine Field, Lloyd M. Martin, Dorothy Martin, Stanley S. Nicolay, name unknown, and W. Donald Duckworth.

the skippers because "they were difficult to catch, difficult to spread, and difficult to classify." This only made them more interesting to Bill, and he collected these and other butterflies extensively in California and Arizona. Because of his commitment to prepare a book on the western butterflies in the Peterson Field Guides series, Bill took many field trips from 1969 through 1986. He covered over 200,000 miles of road travel throughout western North America from Texas and the Mexican border east to Kansas and north to western Canada and Alaska (three trips).

From July to August of 1963, Bill and his family spent six weeks on a sabbatical travelling to four islands of Hawaii (Hawaii, Kauai, Maui, and Oahu). They arrived in Honolulu aboard the "Matsonia" on 20 Jul and were met by their friend Richard Kong and their landlord, Mr. Lum. The rent of $10 per day was charged for their three bedroom house with sitting room, kitchen, washroom, two bathrooms, and included the use of a 1953 Chevrolet. Bill was able to consult with J. Linsley Gressitt and G. Allan Samuelson at the Bernice P. Bishop Museum. With Walter C. Mitchell, University of Hawaii, Alan Thistle, State Department of Agriculture, and other entomologists, he was able to observe and discuss problems concerning termites, armyworms, cactus moth (*Cactoblastis cactorum* (Berg)), southern green stink bug (*Nezara viridula* (L.)), sterilization of male fruit flies, etc. He became acquainted with new methods of biological and vector control, information that he incorporated in his course instruction at San Jose State University. He also studied the Lepidoptera of the Hawaiian Islands.

In March 1978, Bill and Hazel were able to spend two weeks in Great Britain, studying the Lepidoptera collection at the British Museum (Natural History) in London, and visiting Scotland. They were able to meet the retired Keeper of Entomology, Norman D. Riley, who had been away from the museum for months because of a serious illness but was fortunately at the museum on one of the days of their visit. This permitted them to have their copy of *A Field Guide to the Butterflies of the West Indies* autographed by Riley. Richard I. Vane-Wright made the Lepidoptera collection available for Bill's study of certain western North American skipper types, including those of W. H. Evans.

Bill built a superb personal collection of North American butterflies, certain moth families, and favorite Coleoptera families (Buprestidae, Cerambycidae, and Meloidae). He maintained, at his home, a very carefully organized and curated collection housed in California Academy of Sciences drawers and cases, and in Schmitt-sized boxes. The development of this major collection was undertaken in a private manner without fanfare and came as a surprise to some of his students when they later learned of its size, scope, and perfection.

Of the six taxa described as new by Bill, primary types of four of them are deposited in the Academy's collection: the holotype and allotype of *Callophrys lemberti* Tilden (CAS Entomol. Type No. 7239) (Tilden 1963: 292); the holotype and allotype of *Glaucopsyche lygdamus incognita* Tilden (CAS Entomol. Type No. 12171) (Tilden 1974: 213); the holotype and allotype of *Mitoura siva mansfieldi* Tilden (CAS Entomol. Type No. 7240) (Tilden 1951b: 96); the holotype and allotype of *Euphilotes rita pallescens* (Tilden & Downey) (CAS Entomol. Type No. 6237) (Tilden & Downey 1955: 25; as *Philotes*). The holotype of *Tharsalea arota schellbachi* (Tilden) is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Tilden 1955: 72; as *Lycaena*), and

Figures 18–22. Figure 18. Bill Tilden's 75th Birthday party at his home in San Jose, California, 31 Dec 1979. Left to right, Paul H. Arnaud, Jr., Hugh B. Leech, Dick Mewaldt, and Bill Tilden (photo by Hazel I. Tilden). Figure 19. Bill Tilden, with drawer of Lepidoptera at his home in San Jose, California, ca. 1980 (photo by Hazel I. Tilden). Figure 20. Bill Tilden with net, Palo Alto Bay lands, California, ca. 1980 (photo by Hazel I. Tilden). Figure 21. Book signing at Book Café, Capitola, California, 12 Oct 1986. Left to right, Arthur C. Smith and Bill Tilden (photo by Hazel I. Tilden). Figure 22. Book signing at Willow Glenn Tattler, San Jose, California, 22 Nov 1986. Left to right, Madeline M. Arnaud, Paul H. Arnaud, Jr., Arthur C. Smith, Bill Tilden, John S. Garth (photo by Hazel I. Tilden).

the holotype of *Philotiella speciosa bohartorum* (Tilden) is deposited in the Los Angeles County Museum of Natural History, Los Angeles (Tilden 1968: 281; as *Philotes*).

The paratypes of butterflies contained in Bill's collection, when received by the Academy in 1989, totaled 85 specimens representing 30 species, as follows: Family Hesperiidae: 2, *Agathymus dawsoni* Harbison; 3, *Erynnis telemachus* Burns; 1, *Hesperia miriamae* MacNeill; 2, *Hesperia pahaska martini* MacNeill; 2, *Hesperia comma tildeni* H. A. Freeman; 2, *Hesperia uncas macswaini* MacNeill; 2, *Megathymus coloradensis louiseae* H. A. Freeman; 2, *Megathymus coloradensis reinthali* H. A. Freeman; 3, *Pholisora gracielae* MacNeill; and 2, *Stallingsia maculosa* (H. A. Freeman). Family Papilionidae: 1, *Papilio cresphontes pennsylvanicus* F. & R. Chermock. Family Pieridae: 2, *Colias gigantea mayi* F. & R. Chermock. Family Lycaenidae: 3, *Callophrys lemberti* Tilden; 2, *Epidemia dorcas megaloceras* Ferris; 2, *Euristrymon ontario violae* (D. Stallings & Turner); 13, *Everes comyntas texanus* R. Chermock; 2, *Glaucopsyche lygdamus jacki* D. Stallings & Turner; 4, *Mitoura siva mansfieldi* Tilden; 2, *Mitoura thornei* J. W. Brown; 4, *Philotes enoptes bayensis* (Langston); 1, *Philotes enoptes tildeni* (Langston); 11, *Euphilotes pallescens* (Tilden & Downey); 1, *Philotiella speciosa bohartorum* (Tilden); and 2, *Tharsalea arota schellbachi* (Tilden). Family Nymphalidae: 2, *Basilarchia archippus lahontani* (Herlan); 2, *Phyciodes orseis herlani* Bauer; 2, *Speyeria aphrodite manitoba* (F. & R. Chermock); 1, *Speyeria cybele pseudocarpenteri* (F. & R. Chermock); and 1, *Vanessa anabella* (Field). Family Satyridae: 6, *Enodia portlandia missarkae* (J. R. Heitzman & dos Passos). The collection also contained 12 specimens labelled as paratypes in the genera *Boloria, Euphyes,* and *Plebejus* that appear to be manuscript names, as they cannot be confirmed in current Lepidoptera checklists.

As commented by Helfer (1989), Bill was the first lepidopterist to investigate the occurrence of the Lotis blue (*Lycaeides idas lotis* (Lintner)) colony that was discovered south of Caspar, in Mendocino County. Bill also published on San Francisco's vanishing butterflies (1956). He knew the locality, in the Santa Cruz Mountains, where the now possibly extinct Strohbeen's parnassian (*Parnassius clodius strohbeeni* Sternitzky) occurred and encountered his first specimen there on 12 Jun 1933 (Tilden 1941). He collected only a few specimens and the two given to the Academy bear his collection dates of 21 Jun 1936 and 1 Jul 1958. The latter may be one of the last collected specimens. The Tilden bequest contained four specimens of this taxon, which Bill had earlier emphasized to me that he wanted deposited in the Academy collection (Bill had recently declined an offer of $3,000 for these four rare specimens.)

Bill Tilden had a long association with the Department of Entomology of the California Academy of Sciences. Letters indicate that Hartford H. Keifer and Edward P. Van Duzee identified Microlepidoptera and larger moths (noctuids and geometrids) for him in 1933, and in 1936 beetles were identified by Edwin C. Van Dyke. Before his entry into military service in 1942, Bill had made an agreement with the Academy Director, Robert C. Miller, and Entomology Curator, Edward S. Ross (Tilden letters: 4 and 31 Mar 1942), for the presentation of his collection to the Academy, but there appeared to be a problem of delivery: Bill did not have transportation, Ross was about to leave for his military duty, and there was strict gasoline rationing for civilians during the war. The collection was

then stored in Santa Cruz, but unfortunately was somewhat damaged while being fumigated during his absence.

After World War II, from 1946 through 1988, Bill donated portions of his collection, totaling 35,607 specimens (27,087 Lepidoptera, 7091 Coleoptera, and 1429 miscellaneous insects and arachnids), to the Academy. Following his death, the receipt of 20,274 additional specimens of Lepidoptera (16,460 pinned and spread; 3814 papered) gives a total of 47,361 Lepidoptera received through 1991. In addition, with nearly 8000 specimens of Coleoptera still to be accessioned, the final Tilden donations will total approximately 64,000 specimens.

The California Academy of Sciences has been indeed fortunate to have such loyal support of Bill and his family for nearly half a century. Bill became a member of the California Academy of Sciences on 13 Apr 1948, at a time when there were fewer than fifteen hundred active members. He was elected a Fellow of the Academy in 1968. Bill's reprint library on Lepidoptera was donated to the Department of Entomology, California Academy of Sciences, with the stipulation that if papers were duplicate to Academy holdings they would be sent to the Department of Entomology, Bernice P. Bishop Museum. Bill's correspondence files are also stored in the Archives section in the Special Collections of the Academy's Library.

Prior to his retirement, Bill also donated about 100 drawers of Lepidoptera and miscellaneous insects, including Odonata, Diptera, and Coleoptera, to the Entomology Museum at San Jose State University (a collection that now houses about 600,000 specimens in the Carl D. Duncan Hall of Science).

Bill Tilden lived a full and active life devoted to family, friends, and institutions. He overcame the limitations of the depression years and a delayed higher education to fully dedicate his exceptional talents to teaching, researching, publishing, and collection making. Shortly after his retirement, Bill faced heart problems that included open heart surgery, valve replacement; eventually he had a pacemaker installed. Yet he did most of his extensive field collecting program for the Guides following this surgery. The development of his collection and its donation to the Academy places a responsibility on the Academy to oversee its proper storage, make it available to the scientific community, and to preserve it for use by future generations.

Bill Tilden is survived by his wife, Hazel Irene Tilden, of San Jose, California; two sons, Bruce Allen Tilden of San Jose, California, and James Wilson Tilden, Jr. of Phuket, Thailand; one daughter, Janice Elaine Tilden of Denver, Colorado; and two brothers, Thomas C. Tilden of Santa Cruz, California, and Earl R. Tilden of Dillingham, Alaska.

Acknowledgment

For information, loan of photographs, and review of this manuscript I am especially grateful to Hazel I. Tilden of San Jose, California; Thomas C. Tilden of Santa Cruz, California; and Arthur C. Smith of Watsonville, California; Donald J. Burdick, California State University, Fresno, California; Helen K. Court, Vincent F. Lee, C. Don MacNeill, and Keve J. Ribardo of the Department of Entomology, California Academy of Sciences. I would also like to thank Caroline Kopp and Charlotte Fiorito of the Photography Department, California Academy of Sciences, for their photographic assistance with the illustrations.

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Received 18 April 1991; accepted 24 May 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 38–45, (1992)

PREVALENCE OF TWO *BACILLUS POPILLIAE* DUTKY MORPHOTYPES AND BLUE DISEASE IN *CYCLOCEPHALA HIRTA* LECONTE (COLEOPTERA: SCARABAEIDAE) POPULATIONS IN CALIFORNIA

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Abstract.—The milky disease bacterium, *Bacillus popilliae* Dutky, and the blue disease rickettsial organism, *Rickettsiella popilliae* (Dutky & Gooden), were isolated from larval populations of *Cyclocephala hirta* LeConte in California. Two morphological types of *B. popilliae,* characterized by the size of sporangia, spores, and parasporal bodies, were recovered. The typical *Cyclocephala* strain had a sporangium averaging 5.5 × 2.1 μm, a spore averaging 2.1 × 0.9 μm, and a primary parasporal body averaging 1.9 × 0.7 μm. Multiple parasporal bodies occurred in up to 50% of this strain. The smaller atypical *Cyclocephala* strain had a sporangium averaging 4.4 × 1.3 μm, a spore averaging 1.9 × 0.8 μm, and a parasporal body averaging 1.0 × 0.7 μm. *Bacillus popilliae* was recovered from seven of eight sample sites located in southern and northern California. The typical *Cyclocephala* strain of *B. popilliae* was predominant in larvae at two sites from southern and one site from northern California, whereas the atypical strain was predominant in larvae at five sites from northern California. *Rickettsiella popilliae* was recovered from larvae at two sites in northern California.

Key Words.—Insecta, Scarabaeidae, *Cyclocephala hirta, Bacillus popilliae, Rickettsiella popilliae,* milky disease, blue disease, turfgrass

Scarabaeid larvae are the most serious pests of turfgrass throughout much of the United States (Tashiro 1987). In the northeastern United States, introduced scarabaeid species, notably the Japanese beetle, *Popillia japonica* Newman, the oriental beetle, *Anomala orientalis* Waterhouse, and the Asiatic garden beetle, *Maladera castanea* (Arrow), cause severe damage to turfgrass. In the midwestern states, the Japanese beetle and native species of May and June beetles, *Phyllophaga* spp., and masked chafers, *Cyclocephala* spp., are more prevalent. In California, a complex of *Cyclocephala* species occurs (Saylor 1945, Endrodi 1985), some of which cause extensive turf damage. These pestiferous species include *Cyclocephala hirta* LeConte, *C. lurida* Bland (= *immaculata* (Olivier)), *C. longula* LeConte, *C. melanocephala* (Fabr.), and *C. pasadenae* Casey (Ali 1989). In 1988, we observed that scarabaeid larvae caused considerable damage to turfgrass at a golf course in northern California. Moreover, we detected larvae infected with the bacterium *Bacillus popilliae* Dutky, the causal agent of milky disease, and *Rickettsiella popilliae* (Dutky & Gooden), the causal agent of blue disease. Because of the biological control potential of these microorganisms, in particular the milky disease

bacterium (Klein 1988), we determined their prevalence in scarabaeid populations in California.

Materials and Methods

Second- and third-instar scarabaeids were sampled during the spring and fall of 1989 and 1990 from northern and southern California. In the towns of Fairfax, Moraga, San Rafael, and Santa Rosa, larval density was determined by taking at least three 18 × 18 × 10 cm soil samples and counting the number of larvae in each. Counts were averaged and the number of larvae per 0.1 m^2 was determined. In the town of Walnut Creek, only one larval density was taken because of the small area of infestation. In the town of Chino, larval density was determined by taking ten 0.1 m^2 samples or by estimating the number of larvae per 0.1 m^2. Larval density was estimated because it was too low and a wide area was sampled to collect sufficient larvae for examination.

Larvae were collected from areas of golf courses and parks where no chemical insecticides had been applied. Larvae were held either individually in 35 ml plastic cups or in groups of eight to 10 larvae with field soil in a 210 ml plastic cup. Groups of larvae were placed in field soil and were held for three to 10 days in cold storage (10° C) before they were examined. Individually held larvae were examined immediately upon return to the laboratory or placed in 35 ml cups with 31 grams of sterilized dry soil (75% sand, 18% silt, 7% clay, pH 6.9, organic matter 0.3%), 4.75 ml of distilled water, and perennial rye grass seeds. These larvae were held for 19 days at 25 ± 2° C to allow further development and expression of disease symptoms before they were examined.

Each larva was bled by inserting a sterilized size-2 insect pin through the integument behind the head and a drop of hemolymph was placed on a microscope slide. The hemolymph was examined for bacterial or rickettsial infection using phase contrast microscopy at 400×. Measurements of *B. popilliae* sporangia, spores, and parasporal bodies at their longest and widest points were made with an interference contrast microscope system at 9000× and computer software image analyzer. Data for measurements of *B. popilliae* (lengths and widths of the sporangia, spores, and parasporal bodies) were analyzed using SAS program (*t*-test) (SAS Institute 1988).

Two steps were used in identifying the scarabaeids. Raster patterns were used to identify larvae to genus, and a subset of larvae was reared to adults. Adults were identified to species by examination of the male genitalia (Saylor 1945, Endrodi 1985).

Results and Discussion

Only one scarabaeid genus, *Cyclocephala,* was recovered during this study and adult male specimens from each site were identified as *C. hirta.* Distribution of larvae in turfgrass was patchy with infested areas ranging from <1 to 38 larvae/ 0.1 m^2 (Table 1).

Bacillus popilliae was recovered from *C. hirta* in seven out of eight sites in California and the prevalence of infection ranged from none to 71% (Table 1). Even within a site, the prevalence of infection varied greatly indicating the uneven distribution of spores in the soil. Thus, in Santa Rosa, we sampled two adjacent areas (Santa Rosa 1A and 1B) which were separated by about 50 m. *Cyclocephala*

Table 1. Prevalence of *Bacillus popilliae* and *Rickettsiella popilliae* from *Cyclocephala hirta* in California.

Collection			% larvae infected with		
Site[a]	Date	No. larvae	*Bacillus*	*Rickettsiella*	Larval density/0.1 m² ± SD
Chino 1	5 May 89	21	61.9	0	<1
	3 Oct 89	199	28.1	0	19 ± 5.1
	23 Apr 90	12	41.7	0	<1
Chino 2	5 May 89	8	25.0	0	<1
Fairfax	3 Oct 90	39	2.6	0	<1
Moraga A	25 Sep 89	511	17.8	4.7	22 ± 15.5
	2 Oct 89[b]	81	11.1	22.2	ND[c]
Moraga B	24 Sep 90	33	3.3	3.3	38 ± 4.0
Moraga C	24 Sep 90	19	0	94.7	<1
San Rafael	19 Sep 90	63	17.5	0	9 ± 3.0
Santa Rosa 1A	19 Sep 90	40	0	0	4 ± 1.7
Santa Rosa 1B	19 Sep 90	62	71.0	0	6 ± 5.1
Santa Rosa 2	4 Oct 90	57	15.8	0	10 ± 4.6
Walnut Creek	24 Sep 90	37	0	16.2	18[d]

[a] Moraga A, B, and C are samples from the same golf course. Larvae were collected from areas separated by more than 300 m. Santa Rosa 1A and 1B sites were located in the rough of a golf course no more than 50 m from each other. Site 1A was on a slope and Site 1B was a level area.

[b] Only larvae showing signs of a frank infection were bled and examined for *B. popilliae* or *R. popilliae* infection. The remaining 54 larvae were held individually for 17 days before they were examined (see text for data).

[c] ND = no data.

[d] Only one larval density measurement taken. Larvae were concentrated in a small area.

hirta larvae from one area had a high prevalence (71%) of *B. popilliae* infection, whereas larvae from the other area were apparently free from infection (Table 1). Similarly in Moraga, the prevalence of infection ranged from none to 17.8% at three different areas within the same golf course.

Although milky disease bacteria have been isolated from other *Cyclocephala* species on a number of occasions (White 1948, Harris 1959, Warren & Potter 1983, Boucias et al. 1986, Hanula & Andreadis 1988, Cherry & Boucias 1989), we believe that this is the first report of milky disease bacteria in *C. hirta* populations. We also recovered two morphological types of *B. popilliae* from diseased larvae (Fig. 1). In Chino (southern California) and Moraga (northern California), the spores and parasporal bodies are primarily typical of those isolated from other *Cyclocephala* species (Klein 1981). They have large and often multiple parasporal bodies located adjacent to or overlapping the spore (Figs. 1B, 1C). When multiple parasporal bodies occurred, there was a primary parasporal body with a maximum of three secondary bodies observed (Table 2). Multiple parasporal bodies were found in up to 50% of these milky disease bacteria. A second type (Fig. 1A), isolated primarily from northern California, had a single parasporal body which was significantly smaller than the typical *Cyclocephala* strain (Table 2) and resembled *B. popilliae* from the Japanese beetle (Dutky 1940). We refer to this isolate as the atypical *Cyclocephala* strain of *B. popilliae* and, as far as we are aware, it is the first report of this morphological variant from a *Cyclocephala* species.

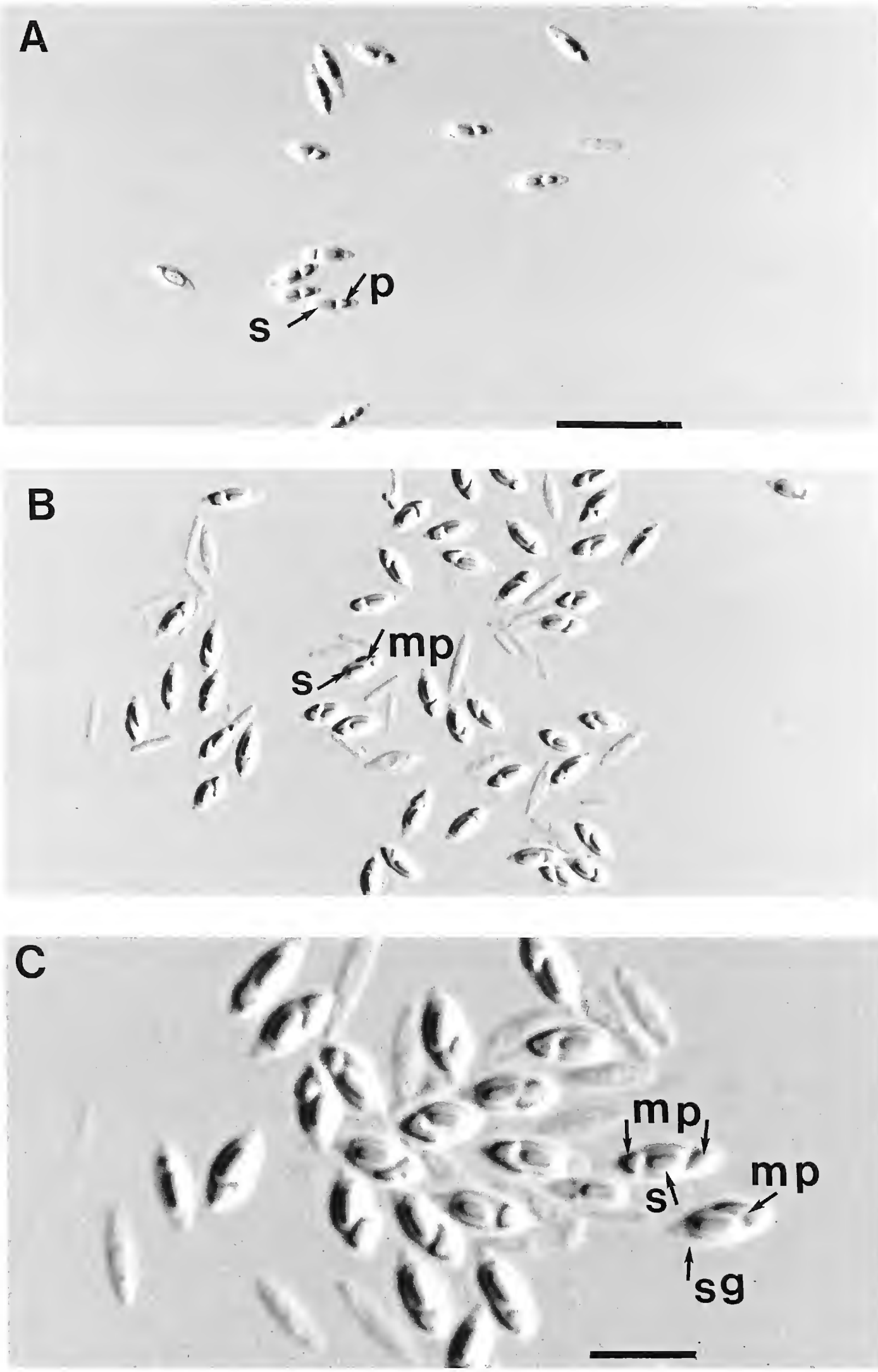

Figure 1. *Bacillus popilliae* spores from *Cyclocephala hirta.* A. Atypical *Cyclocephala* strain with single parasporal body (p) and spore (s). B. Typical *Cyclocephala* strain with a mixture of single (p) and multiple parasporal bodies (mp) and a single spore (s). Bar for A and B indicate 10 μm. C. Typical *Cyclocephala* strain with multiple parasporal bodies (mp) distributed within a sporangium (sg). Bar indicates 5 μm.

Table 2. Mean measurements in micrometers (±SD) of the sporangium, spore, and parasporal body from the typical and atypical *Cyclocephala* strain of *Bacillus popilliae* from *Cyclocephala hirta* in California.

	B. popilliae strain[a]			
	Typical		Atypical	
	Length	Width	Length	Width
Sporangium (μm)	5.5 (± 0.6)A	2.1 (± 0.2)a	4.4 (± 0.02)B	1.3 (± 0.1)b
Spore (μm)	2.1 (± 0.3)A	0.9 (± 0.1)a	1.9 (± 0.05)B	0.8 (± 0.1)a
Parasporal body (μm)				
Primary	1.9 (± 0.1)A	0.7 (± 0.1)a	1.0 (± 0.1)B	0.7 (± 0.1)b
Secondary	1.0 (± 0.5)	0.5 (± 0.2)	—	—

[a] Means followed by different upper or lower case letters within a row are significantly different ($P < 0.001$). Comparison was made only with the primary parasporal body.

The sporangium length ($F = 1015.5$; df = 24; $P = 0.0001$) and width ($F = 4.05$; df = 24; $P = 0.0001$), the spore length ($F = 35.86$; df = 24; $P = 0.0017$), and the primary parasporal body length ($F = 19.47$; df = 24; $P = 0.0001$) and width ($F = 2.61$; df = 24; $P = 0.0001$) of the typical *B. popilliae* strain were significantly longer or wider than the atypical *B. popilliae* strain. Only the width of the spores was not significantly different.

The isolation of different morphological bacterial spores responsible for milky disease from the same insect species is not unusual (Milner 1981), but the difference relates to the presence or absence of the parasporal body (Dutky 1940). For example, Boucias et al. (1986) and Hanula & Andreadis (1988) isolated milky disease bacteria with and without a parasporal body from the same species of scarabaeid larvae. In our study, we did not observe milky disease bacteria without parasporal bodies. We isolated milky disease bacteria which were different in size and in the number of parasporal bodies. The reason for the differences between the two morphological spore/parasporal body complexes isolated from *C. hirta* is unknown. Although the majority of sites contained either the typical or atypical strain, we did observe an occasional larva with the typical strain at a site which had the atypical strain and vice versa (HKK, unpublished data). A caveat is that the typical *Cyclocephala* strain appears very much like the atypical strain during early stages of sporogenesis, and when classifying the spore/parasporal body complex, sporogenesis must be complete.

Rickettsiella popilliae was only recovered from *C. hirta* larvae in Walnut Creek and the three sample areas at Moraga (Table 1). This restricted occurrence of *Rickettsiella* infection confirms earlier observations by other workers who also recovered the disease from larvae at only a small proportion of sites examined (Dutky & Gooden 1952, Hanula & Andreadis 1988). Larvae infected with *Rickettsiella* were easily detected by their bluish color, and upon examination of dissected tissues with phase contrast microscopy, by the presence of crystals and Brownian movement of the *Rickettsiella* cells in the fat body and hemolymph. Moreover, we confirmed the *Rickettsiella* infection by transmission electron microscopy (Fig. 2).

Some larvae infected with *Rickettsiella* did not appear blue during the early stages of infection, but Brownian movement of particles was evident in the he-

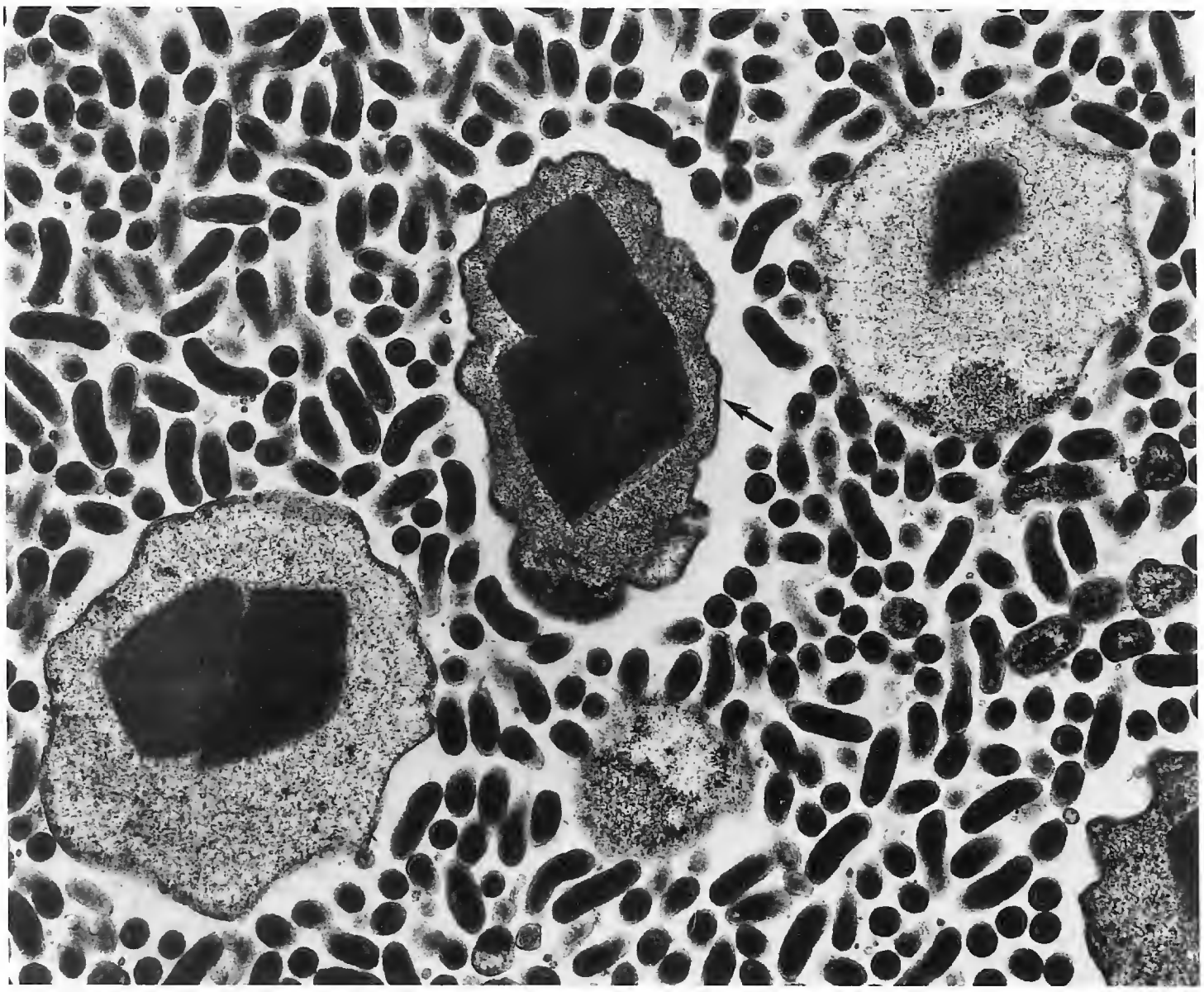

Figure 2. Transmission electron micrograph of *Rickettsiella popilliae* (kidney-shaped particles) from *Cyclocephala hirta* and crystals (arrow) which are associate with the infection. 24,000×.

molymph. Larvae collected in the field in an advanced stage of *Rickettsiella* infection appeared milky due to the turbidity of the hemolymph (Dutky & Gooden 1952). Without a microscopic examination, the larvae in early and late stages of infection may be erroneously diagnosed as healthy or as *B. popilliae* infection, respectively.

The importance of examining the hemolymph for bacterial and rickettsial infection was shown when 81 *C. hirta* larvae collected in Moraga A on 2 Oct 1989 were separated visually into "healthy," "milky" and "blue" (Table 1). Those diagnosed as "milky" or "blue" were bled and examined to confirm the disease and in all cases were infected with *B. popilliae* or *R. popilliae.* Fifty-four larvae classified as "healthy" were held individually for 17 days in sterilized soil before they were bled and examined for pathogens. Of the 54 larvae, four (7.4%) were infected with *B. popilliae,* 11 (20.3%) were infected with *Rickettsiella,* and eight (14.8%) died from unknown causes. Thus, the pooled data for the 2 Oct collection ($n = 81$) should be higher for *B. popilliae* (11.1% on 2 Oct vs 16.0% on 19 Oct) and *R. popilliae* (22.2% on 2 Oct vs 35.8% on 19 Oct). In another example, only 5.5% of the larvae collected at Chino 1 on 3 Oct 1989 had apparent milky disease symptoms. Microscopic examination of the hemolymph revealed the true rate of infection to be 28% (Table 1).

We detected both milky and blue diseases in *C. hirta* populations, but the most prevalent disease throughout California was milky disease. Although the prevalence of infection of milky disease was not related to larval density, a long term study may show density dependent relationships. The isolation of two morphotypes of *B. popilliae* containing parasporal bodies (either multiple or single) was a unique feature of our study. The natural occurrence of milky disease and its high prevalence in some *C. hirta* populations indicate that these bacteria (i.e., the typical and atypical *Cyclocephala* strains of *B. popilliae*) are important in suppressing localized populations. Our data suggest that the milky disease organisms may offer potential as effective biological control agents if they are introduced into areas where they do not occur.

Acknowledgment

We thank Jean Adams for the electron micrograph, Bruce Jaffe for the interference contrast photomicrographs, Kirk Smith for the species identification of *Cyclocephala hirta,* Graham Thurston for the statistical analysis, and the golf superintendents for their assistance in this study. This study was funded, in part, by the California Statewide Integrated Pest Management Project.

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Received 29 May 1991; accepted 31 July 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 46–51, (1992)

THE GENETIC RELATIONSHIP BETWEEN *BOMBUS FRANKLINI* (FRISON) AND OTHER TAXA OF THE SUBGENUS *BOMBUS* S.STR. (HYMENOPTERA: APIDAE)

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Abstract.—*Bombus franklini* (Frison) has either been regarded as a distinct species or has been synonymized with *B. occidentalis* Greene. We surveyed 21 enzymes by vertical starch-gel electrophoresis and compared *B. franklini* with *B. occidentalis* and nine other species of the subgenus *Bombus* sensu stricto. We found that *B. franklini* differs from *B. occidentalis* at three enzyme loci and there was no evidence of intergradation in areas of sympatry. According to the electrophoretic data *B. franklini* is close to two species groups which comprise: (a) *B. cryptarum* (Fabr.), *B. magnus* Vogt, *B. moderatus* Cresson and *B. hypocrita* Pérez; and (b) *B. occidentalis, B. terricola* Kirby and *B. lucorum* (L.), while *B. terrestris* auct., *B. affinis* Cresson and *B. sporadicus* Nylander are more distant.

Key Words.—Insecta, Apidae, enzyme electrophoresis, bumble bee genetic relationships

Among the North American bumble bee species, *Bombus franklini* (Frison) has by far the smallest area of geographical distribution. All recent records have been taken within a 60 mile radius of Grants Pass, Oregon (Thorp 1970). *Bombus franklini* has puzzled entomologists for a long while. It was described from the Oslar collection (Frison 1921) and the holotype was apparently erroneously recorded from Nogales, Arizona, as discussed by Thorp (1970), who proposed Gold Hill, Jackson County, Oregon, as the new type locality. Milliron (1971) considered *B. franklini* conspecific with *B. occidentalis* Greene. Thorp et al. (1983), however, had collected *B. franklini* at several localities sympatrically with *B. occidentalis* and did not find intergrades between them. Plowright & Stephen (1980), working on a multivariate analysis of wing venation data taken from queens, were able to show a clear separation of *B. franklini* from other species within the subgenus. They furthermore indicated that the male genitalia of *B. franklini* are markedly different from those of *B. occidentalis* and advocated retention of specific status for *franklini,* they concluded (Plowright & Stephen 1980: 479): "The origin of *B. franklini* is mysterious. The results from the present study give no indication that it is closely related to any of other nearctic representatives of its subgenus."

In a recent study, Scholl et al. (1990) investigated the genetic relationships of Nearctic and Palaearctic representatives of the subgenus *Bombus* s.str. by enzyme electrophoretic data with special reference to *B. moderatus* Cresson, another problematical taxon in this group. *Bombus franklini* unfortunately could not be included in this analysis because it was not available at that time. We now have been able to collect *B. franklini* in northern California and in Oregon and we have compared it electrophoretically with the previously studied representatives of the subgenus *Bombus* s.str.

Material and Methods

Specimens Analyzed.—Bombus franklini: CALIFORNIA. *SISKIYOU Co.:* Hilt, 29 Jul 1989, 12 workers; 6.4 km (4 mi) E of Yreka, 29 Jul 1989, 2 workers. OREGON. *JACKSON Co.:* Ashland, 29 May 1990, 4 queens and 1 worker; Ruch, 29 May 1990, 12 workers; Central Point, 30 May 1990, 2 workers; Gold Hill, 30 May 1990, 12 workers.

Frozen homogenates of previously studied material [*B. affinis* Cresson, *B. cryptarum* (Fabr.), *B. hypocrita* Pérez, *B. lucorum* (L.), *B. moderatus, B. occidentalis, B. terrestris* auct., *B. terricola* Kirby and *B. sporadicus* Nylander] (Scholl et al. 1990) and additional specimens, including one queen, nine workers and one male of *B. occidentalis* from the same localities where *B. franklini* was collected and 10 queens, 38 workers and two males of *B. occidentalis* from eight other localities in northern California have been used for electrophoretic comparison. This material is summarized in Table 1. Californian *B. occidentalis* included the nominate subspecies and *B. o. nigroscutatus* Franklin along with their intergrades, these are not listed separately because the electrophoretic data did not indicate any difference.

Electrophoresis.—We have used the same methods (vertical starch-gel electrophoresis) and enzymes (21 loci) as Scholl et al. (1990). These enzymes are: Aconitase, 2 loci: Acon-1 and Acon-2; Arginine kinase, Apk; Hydroxybutyric dehydrogenase, Bdh; Esterase, Est-1; α-Glycerophosphate dehydrogenase, 2 loci: α-Gpd-2 and α-Gpd-3; Glutamic-oxaloacetic transaminase, Got-2; Glutamic-pyruvic transaminase, Gpt; Hexokinase, 2 loci: Hk-1 and Hk-3; Isocitrate dehydrogenase, 2 loci: Idh (NAD) and Idh (NADP); Leucine aminopeptidase, Lap; Malate dehydrogenase, 2 loci: Mdh-1 and Mdh-2; Malic enzyme, Mod; Peptidase, Pep; Phosphoglucose isomerase, Pgi; Phosphoglucomutase, Pgm; Superoxide dismutase, Sod (for details see Scholl et al. 1990). A phenogram of the genetic relationships of the species investigated was constructed by average linkage cluster analysis (UPGMA) (Nei 1987) using Nei's (1972) standard coefficient of genetic identity (I).

Results and Discussion

Ten of the 21 loci scored were found invariant in all species surveyed. These loci are: Acon-2, Apk, Bdh, α-Gpd-1, α-Gpd-2, Idh (NADP), Lap, Mdh-2, Mod, and Sod. Eleven loci showed interspecific variation. The zymograms observed are schematically shown in Fig. 1, where the designation of electromorphs is based on mobilities (in mm) relative to the electromorph of *B. lucorum* (= index 100), as in previous electrophoretic studies on bumble bees (e.g., Scholl & Obrecht 1983, Scholl et al. 1990).

Bombus franklini was monomorphic in all loci scored, except Pep, where one worker was heterozygous. Minor polymorphisms were observed in some loci of other species. These are: Acon-1 in *B. lucorum, B. terrestris* and *B. sporadicus*; Est-1 in *B. lucorum* and *B. terricola,* Got-2 in *B. cryptarum, B. magnus, B. lucorum, B. occidentalis, B. terrestris* and *B. sporadicus*; Hk-1 in *B. occidentalis*; Mdh-1 in *B. terrestris.* The level of polymorphism, however, was usually very low ($H < 0.05$), as also observed previously in other bumble bee species (Obrecht & Scholl 1981, Pamilo et al. 1984), except in Got-2 of *B. occidentalis,* where the

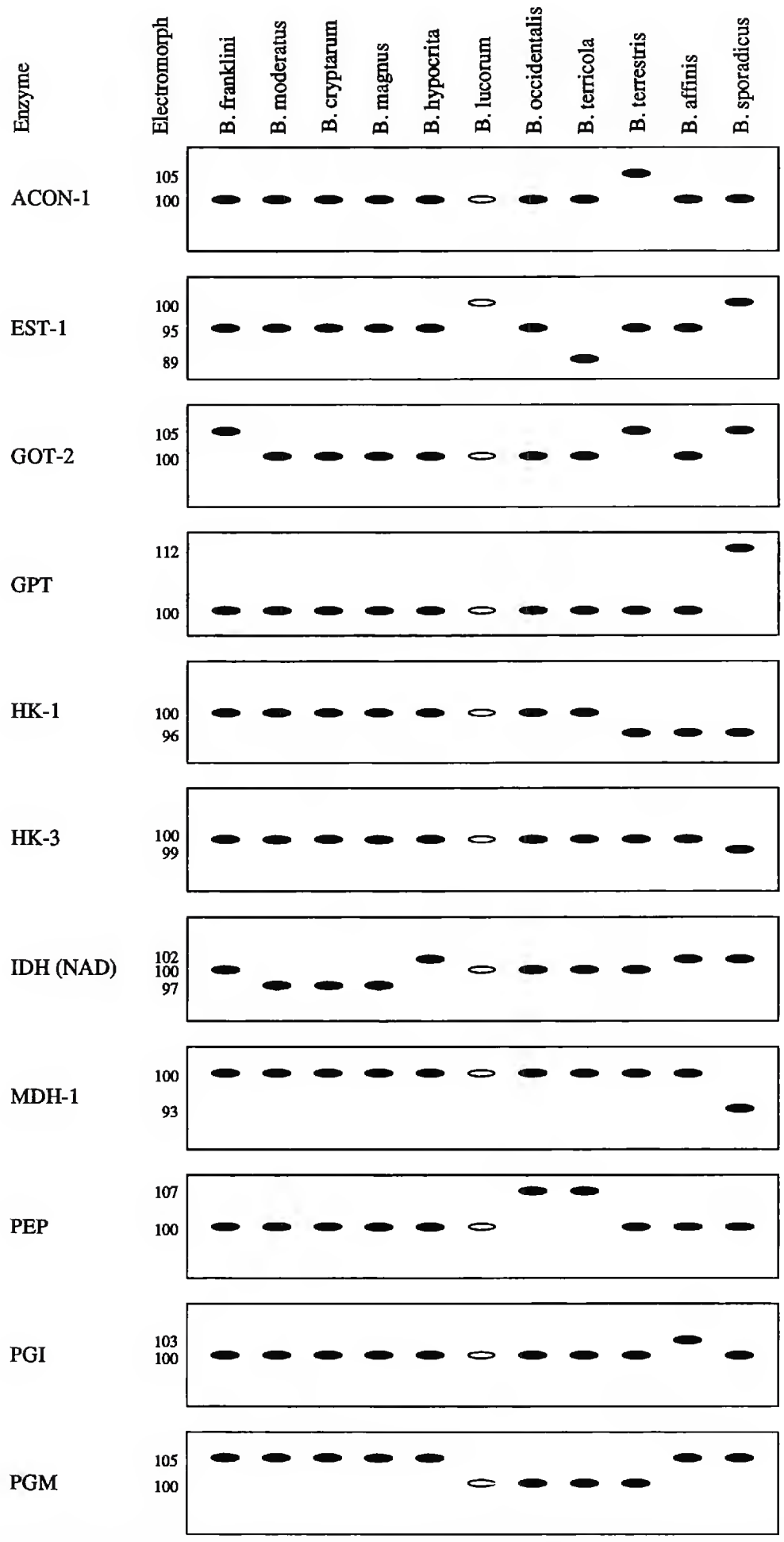

Figure 1. Schematic illustration of enzyme phenotypes in *Bombus* s.str. species. (Note: *B. lucorum* is the reference, assigned mobility index = 100 for each enzyme.)

frequency of a minor allele Got-2^{105} ranged between 0.05 and 0.25 at three sampling sites in Alberta, Calgary, Barrier Lake and Fortress Mountain respectively, while allele Got-2^{100} was fixed in samples from other areas (Table 1).

We have not found an electromorph that is unique to *B. franklini.* However,

Table 1. Specimens analyzed and origin of material.

		California	Oregon	Alaska	British Columbia	Alberta	Ontario	Japan	N-Europe	E-Europe	C-Europe	S-Europe	Total
B. franklini	♀	14	31	—	—	—	—	—	—	—	—	—	45
(*n* = 45)													
B. moderatus	♀	—	—	—	—	8	—	—	—	—	—	—	8
(*n* = 9)	♂	—	—	—	—	1	—	—	—	—	—	—	1
B. cryptarum	♀	—	—	—	—	—	—	—	2	—	13	—	15
(*n* = 22)	♂	—	—	—	—	—	—	—	5	—	2	—	7
B. magnus	♀	—	—	—	—	—	—	—	5	—	11	—	16
(*n* = 17)	♂	—	—	—	—	—	—	—	—	—	1	—	1
B. hypocrita	♀	—	—	—	—	—	—	8	—	—	—	—	8
(*n* = 8)													
B. lucorum	♀	—	—	—	—	—	—	—	2	2	41	4	49
(*n* = 57)	♂	—	—	—	—	—	—	—	6	—	2	—	8
B. occidentalis	♀	54	2	8	1	36	—	—	—	—	—	—	101
(*n* = 110)	♂	2	—	—	—	7	—	—	—	—	—	—	9
B. terricola	♀	—	—	—	—	4	11	—	—	—	—	—	15
(*n* = 18)	♂	—	—	—	—	—	3	—	—	—	—	—	3
B. terrestris	♀	—	—	—	—	—	—	—	—	3	29	8	40
(*n* = 40)													
B. affinis	♀	—	—	—	—	—	11	—	—	—	—	—	11
(*n* = 11)													
B. sporadicus	♀	—	—	—	—	—	—	—	15	—	—	—	15
(*n* = 15)													

N-Europe = Finland, Norway, Scotland, England; E-Europe = Hungary; C-Europe = Switzerland, France, Belgium; S-Europe = Spain, Italy.

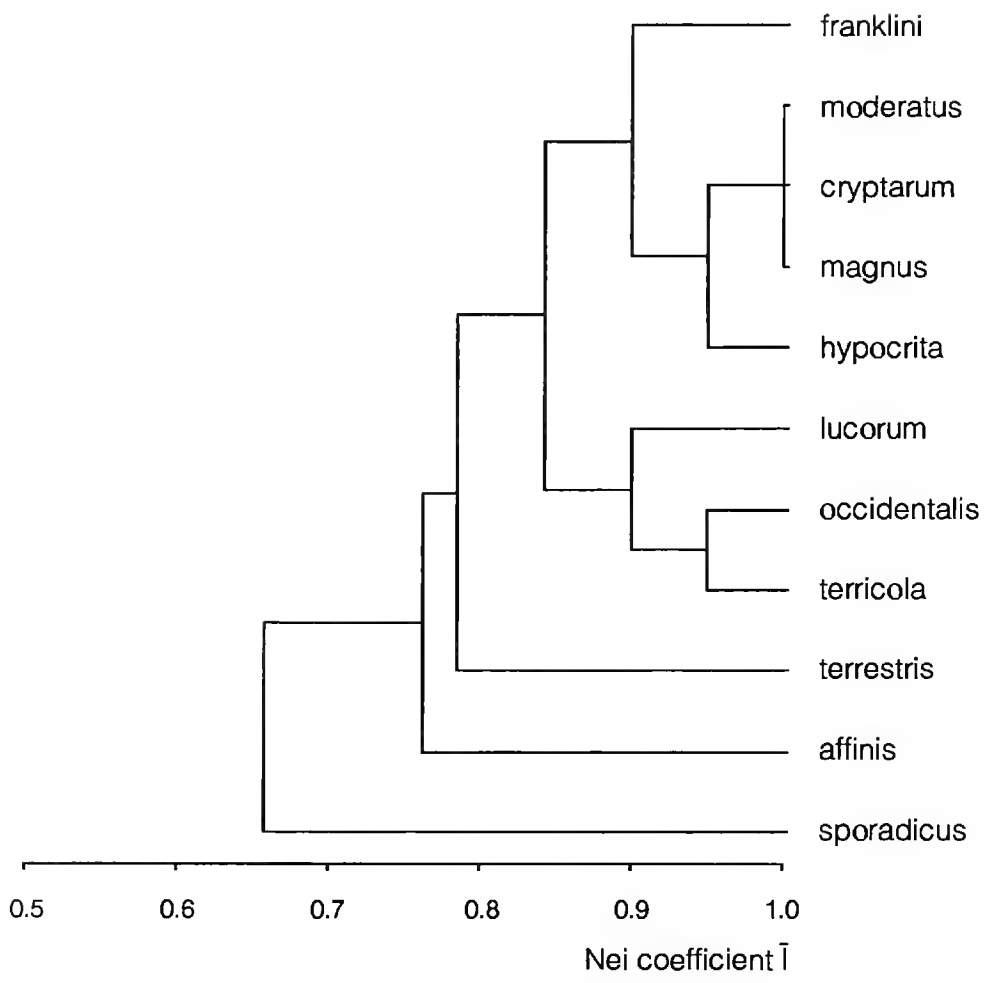

Figure 2. Phenogram showing the genetic relationship between *B. franklini* and other taxa of the subgenus *Bombus* s.str., as revealed by the electrophoretic data.

it is the electrophoretic pattern of enzymes that is unique to *B. franklini* (Fig. 1). Thus, *B. franklini* differs from *B. moderatus* in GOT-2 and IDH (NAD); *B. terrestris* is identical with *B. franklini* in GOT-2 and IDH (NAD), but these species differ in ACON-1, HK-1 and PGM, etc. *Bombus franklini* differs from *B. occidentalis* in GOT-2, PEP and PGM; the Got-2 locus, however, was found weakly polymorphic in three *B. occidentalis* samples from Southern Alberta, as mentioned above. In our material from California and Oregon, there was always a clear separation on the basis of these three enzymes and the electrophoretic data did not provide any evidence of intergradation of *B. franklini* and *B. occidentalis.*

The genetic relationships of *B. franklini* and other Nearctic and Palaearctic representatives of its subgenus, as revealed by the enzyme electrophoretic studies, are presented in Fig. 2 as a phenogram that is based on a similarity matrix (Nei coefficient I) calculated in pairwise species comparisons from the 21 loci surveyed. According to these data, *B. franklini* is close to two species groups that comprise: (a) the European *B. cryptarum* and *B. magnus,* the North American *B. moderatus* and the Japanese *B. hypocrita*; and (b) the European *B. lucorum* and the North American *B. terricola* and *B. occidentalis,* while the European *B. terrestris* and *B. sporadicus* and the North American *B. affinis* are more distant. This new information adds to, but does not alter the basic genetic relationships among species of the subgenus *Bombus* as determined by Scholl et al. (1990).

The narrow endemism of *B. franklini* is intriguing. As Thorp (1970) pointed out, all recent records have been taken within a 60 mile radius of Grants Pass, Oregon. *Bombus franklini* is keyed out from sympatric *B. o. occidentalis* by its

coat color. But Stephen (1957) found that separation is often difficult. The northwestern coast is an area where several bumble bee species, including *B. occidentalis,* show gradation from one color form to another resulting in color convergence toward local Müllerian mimicry groups (Plowright & Owen 1980, Thorp et al. 1983). However, *B. occidentalis* females do not have yellow anterolaterally on the scutum, extending back beyond the tegulae, and *B. franklini* females are uniform in color throughout the known range (Thorp et al. 1983). One might speculate that *B. franklini* has in fact a more widespread distribution, but becomes hidden within the color variation of *B. occidentalis.* The electromorphetic data presented here provide an opportunity to test this hypothesis.

Acknowledgment

The competent assistance of Mrs. V. Siegfried and Mrs. L. Frauchiger in the electrophoretic studies is gratefully acknowledged.

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Received 25 June 1991; accepted 13 August 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 52–61, (1992)

OCCURRENCE OF *DIURAPHIS* (*HOLCAPHIS*) *FREQUENS* (WALKER) (HOMOPTERA: APHIDIDAE) ON WHEAT, NEW TO IDAHO, AND A KEY TO NORTH AMERICAN *DIURAPHIS*

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Abstract.—Colonies of a species of *Diuraphis* (*Holcaphis*) were found on wheat near Parma, Idaho in 1986. Morphologically, the species best fits the description of *Diuraphis* (*Holcaphis*) *frequens* (Walker), though the process terminalis is longer with respect to the base of the sixth antennal segment than is reported for European *D. frequens.* The host range of the Idaho *Diuraphis frequens* is also consistent with that reported for *D. frequens* in Europe, except that the populations found in Idaho multiply much more quickly on wheat than on *Elytrigia repens* (L.) Beauvois. In spite of these differences, we think this *Diuraphis* sp. is *D. frequens.* We do not expect that it will become a serious pest in Idaho.

Key Words.—Insecta, Aphididae, *Diuraphis frequens, Diuraphis noxia*

In surveys of wheat (*Triticum aestivum* L.) in 1986, colonies of an unusual *Diuraphis* (*Holcaphis*) were found near Parma, Idaho. Isolated plants were severely stunted and contorted, their rolled and twisted leaves containing hundreds of wax-covered aphids. The same species was collected in suction trap samples from Parma, Rockland Valley and Arbon in 1986, from Parma in 1988 and 1989, and from Kimberly and Moscow in 1990. We think this aphid is *Diuraphis (Holcaphis) frequens* (Walker). We discuss its identity, based upon morphology and host range. We also compare its ability to colonize the plants with that of *Diuraphis* (*Diuraphis*) *noxia* (Mordvilko), which is the only other species of *Diuraphis* known to occur in Idaho, and with *Rhopalosiphum padi* (L.) and *Schizaphis graminum* (Rondani), which are both common pests in the U.S. with wide host ranges among the Gramineae.

METHODS AND MATERIALS

Twenty apterous viviparae from a colony of *D. frequens,* collected in Canyon County, Idaho on *T. aestivum* propagated on *T. aestivum* cv. ID0232, were mounted and measured using a Zeiss compound binocular microscope equipped with an eyepiece micrometer. Two attempts were made to obtain additional specimens from each of two accessions of *Elytrigia repens* (L.) Beauvois, but colonies grew inadequately to produce sufficient adults.

Host plants for each of the described *Diuraphis* (*Holcaphis*) spp. were obtained including *Calamagrostis* sp., *Agrostis alba* L., *Agrostis palustris* (Hudson) Persoon, *Agrostis tenuis* Sibthorp, *Apera interrupta* (L.) Beauvois (formerly in *Agrostis*), *Holcus lanatus* L., *Bromus inermis* Leys, *Bromus tectorum* L., *Elytrigia repens* (formerly in *Agropyron*), *Agropyron cristatum* (L.) Gaertner, *Thinopyrum ponticum* (Podperae) Barkworth & D. R. Dewey (second time only) and *T. aestivum.*

The plants were started from seed in the autumn of 1987, except for *Calamagrostis* sp., *E. repens, B. inermis* and *B. tectorum,* which were transplanted from the field, trimmed and allowed to regrow new shoots that were solely used. Plants were infested 30 Nov–3 Dec 1987 using three pots of each plant species for each of the three species of aphids, including the Idaho *D. frequens, D. noxia* and *R. padi.* The infestation rate was ten aphids per plant. On 14 Dec 1987, plants were scored for colonization using the following scale: 1—no aphids, 2—a few solitary aphids, 3—small colonies, 4—plant heavily colonized. After the readings, the plants were cut back and sprayed with Bifenthren (Capture 2EC) (1.26 g a.i./liter), if infestations were found.

On 18–19 Jan 1988, the same plants, with exceptions that *A. interrupta* and the Minnesota accession of *B. inermis* were omitted and *T. ponticum* was added, were infested with 20 aphids per pot in the same manner described above. On 3 Feb 1988, readings were taken as before.

In order to quantitatively determine relative colonization ability, the plants were reinfested in 1989. The same plants (by then more than one year old) were used, except the three *Bromus* accessions and *A. cristatum* (omitted because they had died in the interim), an accession of *E. repens* from Moscow, Idaho (added), and the wheat (about six weeks old). We used three pots of each plant species for each of four species of aphids, including the Idaho *D. frequens, D. noxia, R. padi* and *S. graminum.* Plants were infested with 20 adult aphids per plant on 30–31 Jan 1989. On 14–15 Feb 1989, the parts of the plants above ground were clipped and placed in Berlése funnels until they dried completely. Aphids were counted using a dissecting microscope. In the case of the wheat, 10% subsamples were counted.

The data were analyzed using the ANOVA and LSD mean separation procedures (0.05 significance level) in SAS software (SAS Institute 1985). Because plant and aphid species interactions were significant, the species were analyzed separately. The data were analyzed using a transformation to normalize the variance ($Y = \sqrt{\text{count} + 0.5}$).

Results and Discussion

Morphology.—The subgenus *Holcaphis* is distinguished from *Diuraphis* s. str. by lack of a supracaudal process, and currently includes six described species: *Diuraphis tritici* (Gillette)[1] (native to North America), *Diuraphis agrostidis* (Muddathir), *Diuraphis bromicola* (Hille Ris Lambers), *Diuraphis calamagrostis* (Ossiannilsson), *Diuraphis frequens* (Walker) and *Diuraphis holci* (Hille Ris Lambers) (Eastop & Hille Ris Lambers 1976). In addition to *D. tritici,* only two species, *D. frequens* and *D. holci,* have been reported from North America (Smith & Parron 1978). The ultimate rostral segment of the Idaho *D. frequens* is 0.069 mm long, as compared with 0.12 mm for *D. tritici,* thus ruling out the possibility that our aphid is *D. tritici.* Hille Ris Lambers (1939) separates European *D. holci* from *D.*

[1] After this article went to press, Zhang et al. (1991) published a review of *Diuraphis* that treats *D. tritici* as a subspecies of *D. frequens.* We prefer to retain these as distinct species until their change can be confirmed by hybridization experiments. Two new *Diuraphis* from China, which are described by Zhang et al. (1991), are not discussed here.

frequens using relative lengths of antennal segments III and IV + V, and the ratio of the base of antennal segment VI to the process terminalis. The *D. frequens* found in Idaho will key to *D. frequens* in Hille Ris Lambers (1939), using the former character, and to *D. holci,* using the latter; however, the same was true of five specimens of *D. frequens* collected in Enfield, England on 12 Jul 1987, indicating that the antennal segment VI character is not consistently reliable, even in Europe.

The key by Muddathir (1965) separates the two species using siphuncular placement, and presence or absence of intersegmental muscle insertions and sclerites on abdominal segment VI. Most Idaho material will key to *D. frequens* using Muddathir's key, but the siphunculi on some specimens are slightly closer to the sixth than to the seventh abdominal spiracles, a character given there for *D. holci.*

Of the species in the subgenus not yet reported in North America, *Diuraphis bromicola* was described from *Bromus inermis* (Hille Ris Lambers 1959), and can be separated from *D. holci* and *D. frequens* by the absence of sclerotic areas on the abdomen, other than on abdominal segment VIII. The Idaho specimens have an obvious sclerotic bar on abdominal segment VII, which would appear to rule out *D. bromicola. Diuraphis agrostidis* and *D. calamagrostis* have pore-like siphunculi with the siphuncular aperture facing upward, while *D. holci* and *D. frequens* have longer siphunculi, shaped such that the aperture faces posteriorly (Muddathir 1965). *Diuraphis agrostidis* has $2n = 12$ chromosomes and *D. frequens* has $2n = 14$ (Blackman 1980). The specimens from Idaho have siphunculi that fit the description of *D. frequens* better than those of *D. agrostidis* and *D. calamatrostis,* and have $2n = 14$ chromosomes (R. L. Blackman, personal communication).

Occasional specimens of *D. frequens* collected in Idaho have a posteromedial extension on abdominal tergite VIII that suggests a supracaudal process. These specimens can be separated from *Diuraphis* (*Diuraphis*) *nodulus* (Richards) and *Diuraphis* (*Diuraphis*) *mexicana* (Baker) by the position of the siphunculi in relation to the sixth and seventh abdominal spiracles. Siphunculi of *D. frequens* are clearly between the sixth and seventh spiracles (Muddathir 1965), whereas siphunculi of *D. nodulus* and *D. mexicana* are anterior to the sixth pair of spiracles.

Morphological differences among species found in North America can be summarized by the following key:

Key to Species of *Diuraphis* Reported in North America

1. Supracaudal process present on apterous viviparae; siphunculi anterior to sixth pair of abdominal spiracles (Fig. 1; also see Fig. 3) [*Diuraphis* (*Diuraphis*)] 2

1′. Supracaudal process on apterous viviparae absent or barely indicated; siphunculi between sixth and seventh pair of abdominal spiracles (Fig. 2) [*Diuraphis* (*Holcaphis*)] 3

2(1). Process terminalis of viviparae at least 2.0× as long as base of antennal segment VI; supracaudal process on apterous viviparae fingerlike and at least 1.5× as long as width at the middle (Fig. 1) . . . . . *D. noxia*

Figure 1. *Diuraphis* (*Diuraphis*) *noxia* (Mordvilko) apterous vivipara, showing supracaudal process and position of siphunculi with respect to sixth and seventh pairs of abdominal spiracles.

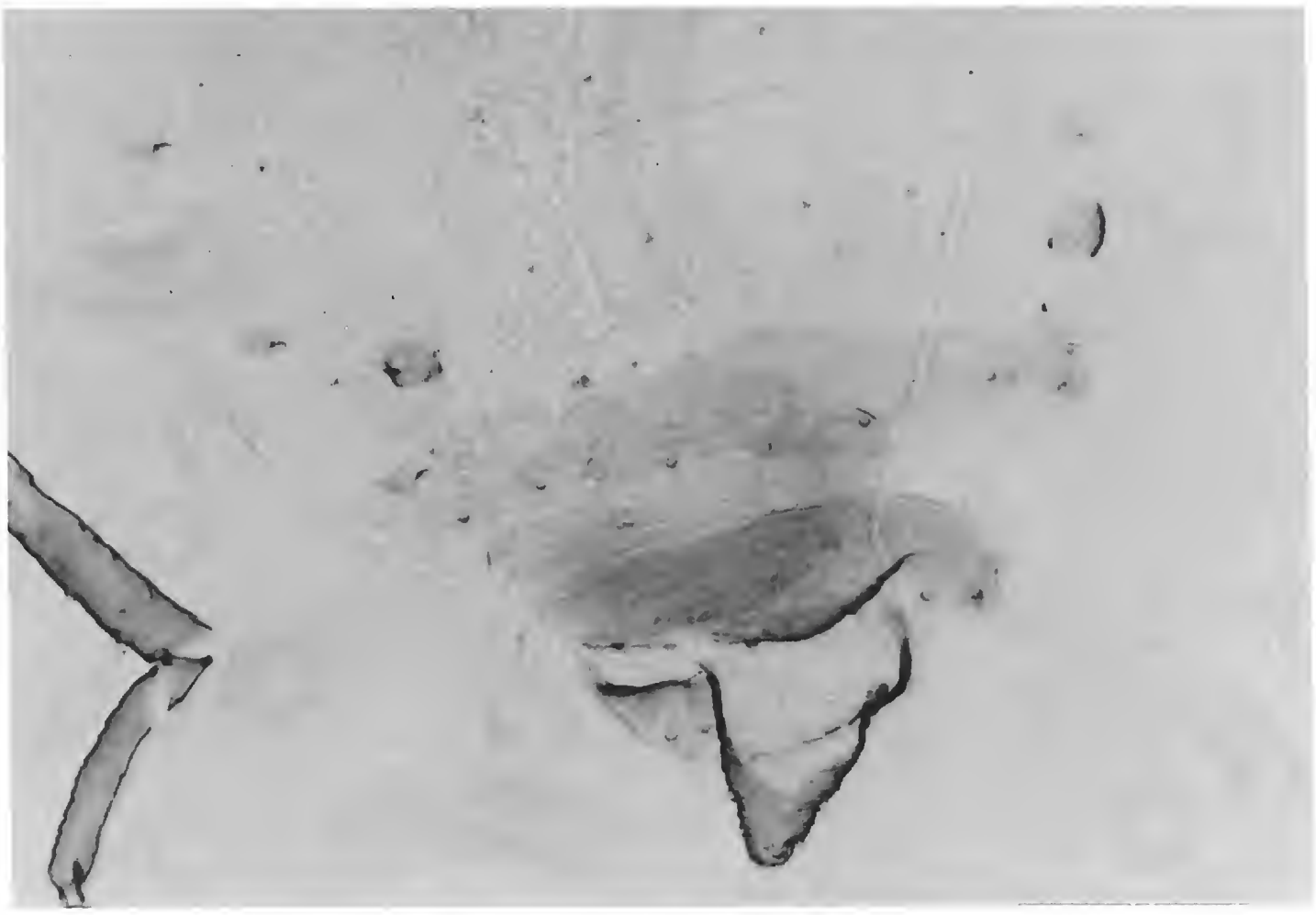

Figure 2. *Diuraphis* (*Holcaphis*) *frequens* (Walker) apterous vivipara, showing supracaudal process and position of siphunculi with respect to sixth and seventh pairs of abdominal spiracles.

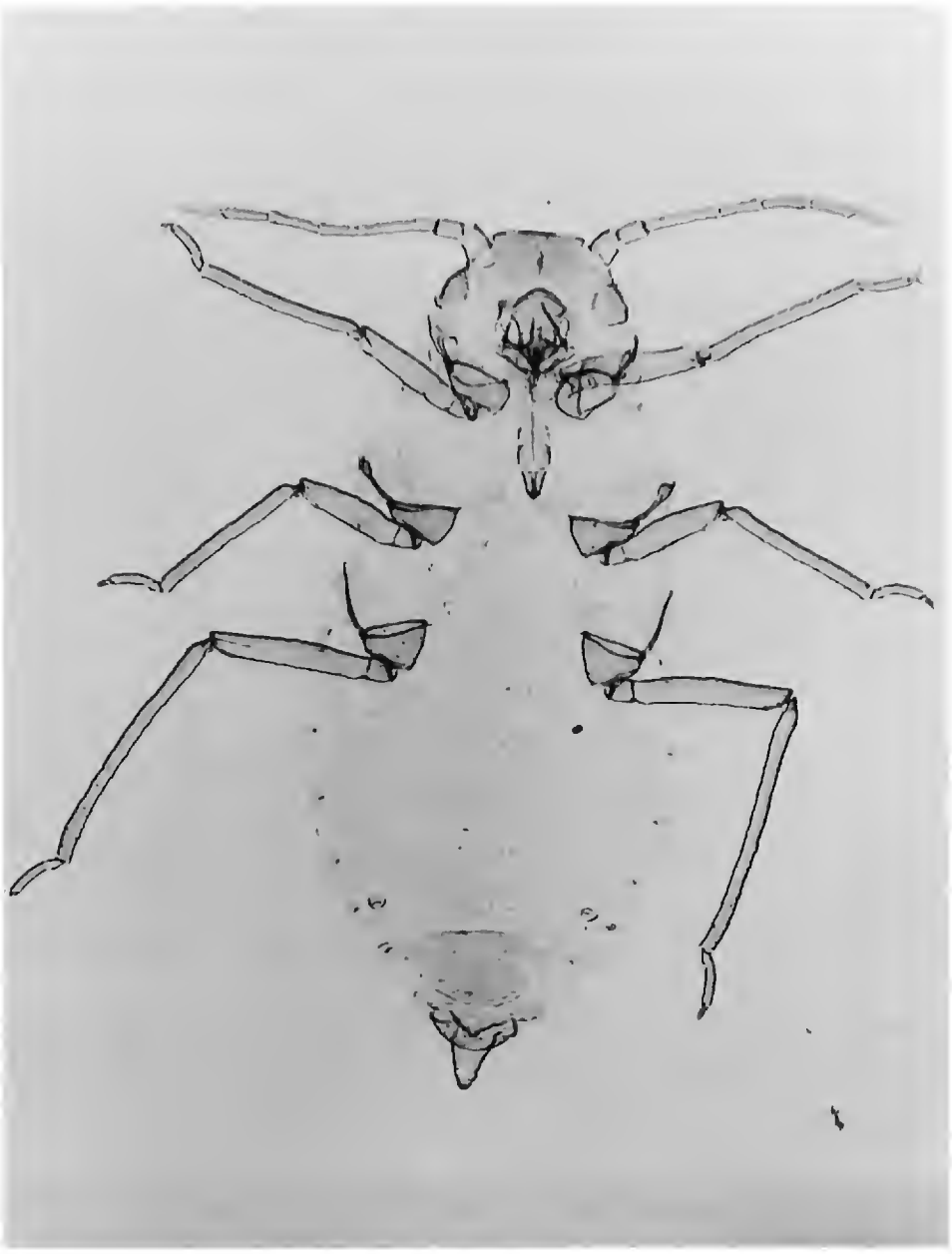

Figure 3. *Diuraphis* (*Diuraphis*) *mexicana* (Baker) apterous vivipara, showing supracaudal process, position of siphunculi and length of process terminalis.

2′. Process terminalis of apterous viviparae less than 1.5× as long as base of antennal segment VI, of alate viviparae less than twice as long as base of VI; supracaudal process on apterous viviparae broad and wider than long, sometimes with a short projection in the center (Fig. 3) .. .. *D. mexicana* and *D. nodulus*[2]

3(1). Ultimate rostral segment of all forms 0.12 mm long and nearly 3.0× as long as wide (Fig. 4) ..... *D. tritici*

3′. Ultimate rostral segment of all forms 0.07 mm long and 2.0× as long as wide (Fig. 5) 4

4(3). Clear markings on abdominal segment VI of all viviparae; antennal segment III on apterous viviparae longer than segments IV and V combined; specific to *Holcus* (Fig. 6) ..... *D. holci*

4′. No markings on abdominal segment VI of viviparae; antennal segment III on apterous viviparae shorter than segments IV and V combined; on *Agropyron, Triticum* and *Elytigia,* but not on *Holcus* (Fig. 7) ... . *D. frequens*

[2] Resolution of *D. nodulus* and *D. mexicana* requires further taxonomic study. A revision of *Diuraphis* is pending (Manya B. Stoetzel, personal communication).

Figure 4. *Diuraphis* (*Holcaphis*) *tritici* (Gillette) apterous vivipara, showing ultimate rostral segment. Scale: 1 cm = 0.05 mm actual size.

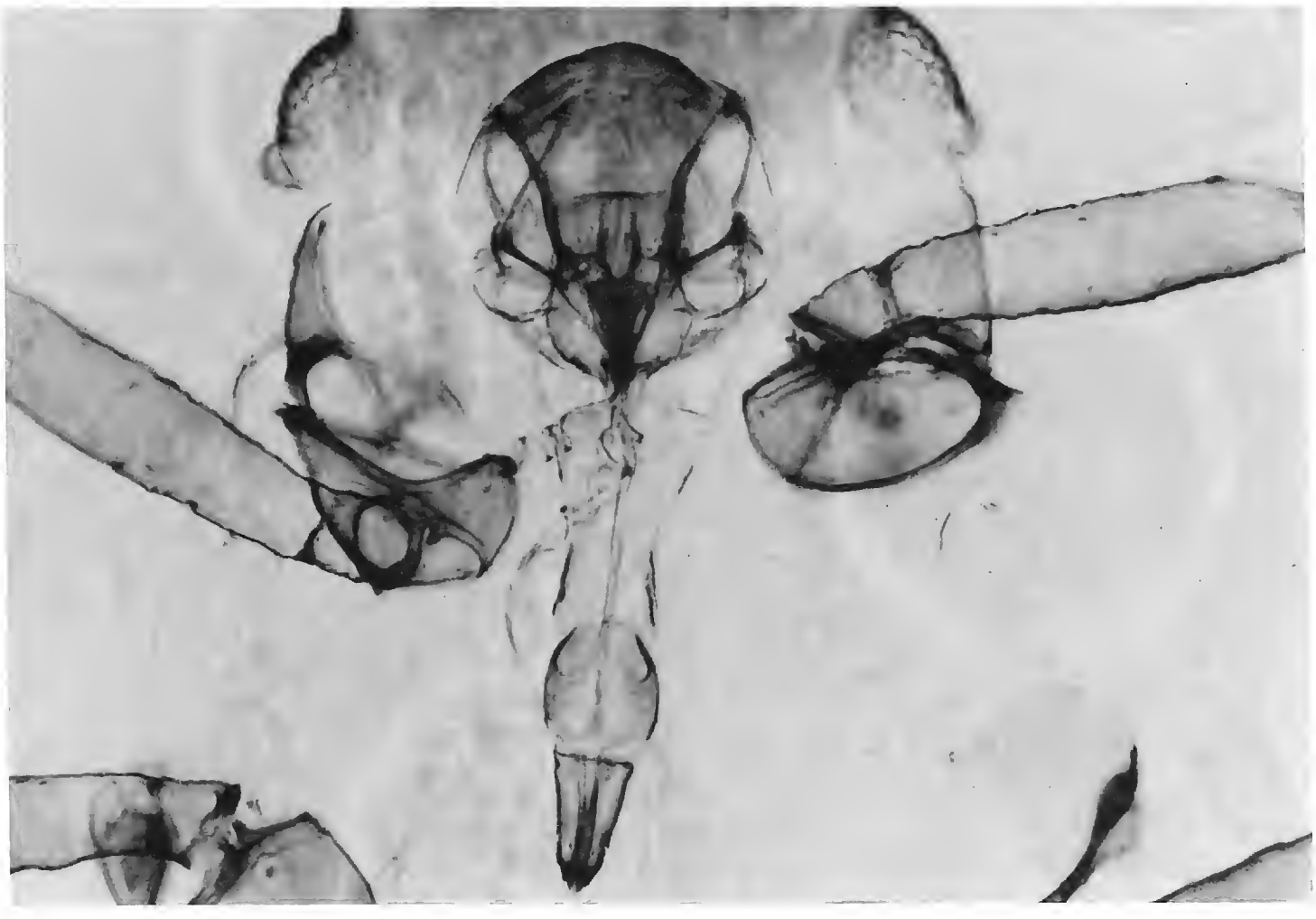

Figure 5. *Diuraphis* (*Holcaphis*) *frequens* (Walker) apterous vivipara, showing ultimate rostral segment. Scale: 1 cm = 0.05 mm actual size.

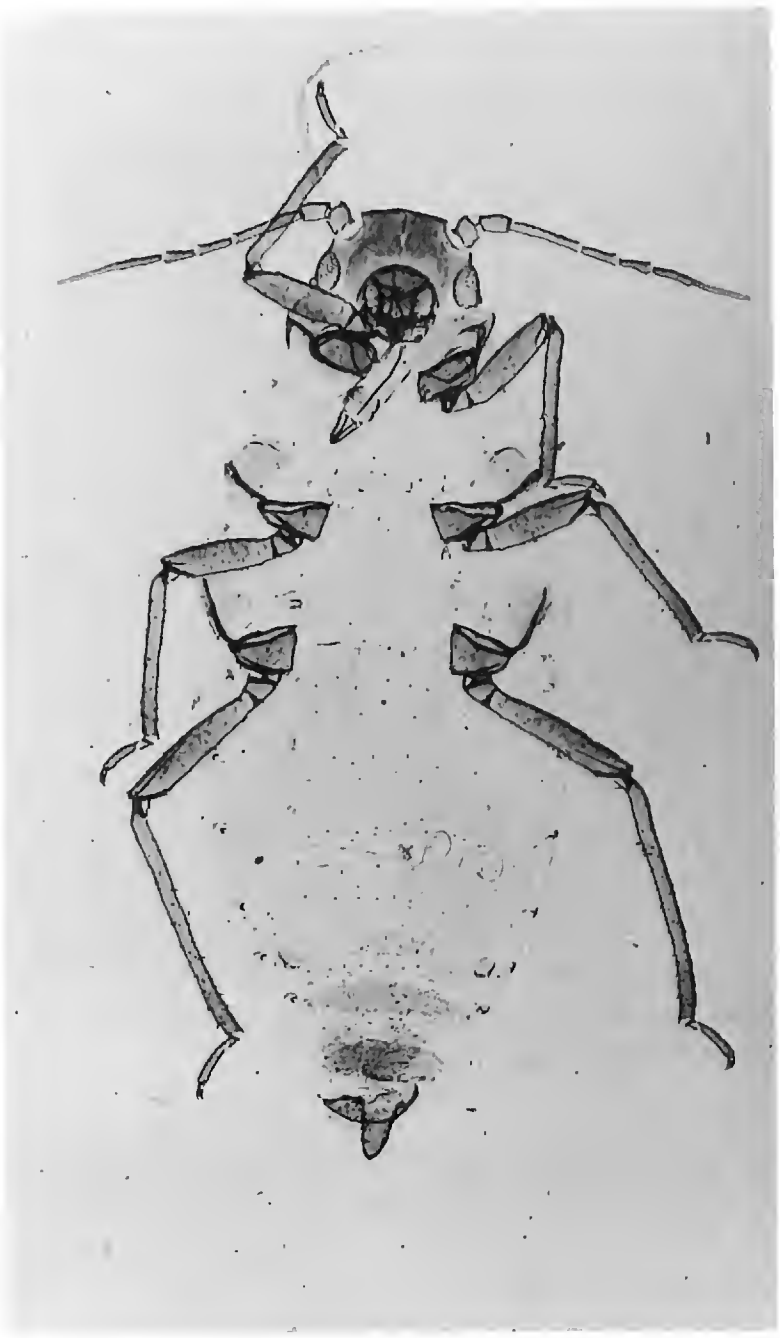

Figure 6. *Diuraphis* (*Holcaphis*) *holci* (Hille Ris Lambers) apterous vivipara, showing markings on abdominal segments VI, VII and VIII and relative lengths of antennal segments.

Host Range.—In the first experiment, the Idaho *D. frequens* colonized only wheat. In the second experiment, it also heavily colonized *T. ponticum* (not included in the first experiment). No colonies were found on *E. repens* in the first two experiments. In the final experiment, there was heavy colonization on wheat, and smaller colonies were found in *A. interrupta, E. repens* and *T. ponticum* (Table 1). This host range fits *D. frequens,* but not *D. holci* or any other *Diuraphis* (*Holcaphis*) sp. except *D. tritici,* which can be ruled out due to its much longer ultimate rostral segment. We observed that Idaho *D. frequens* placed on *Holcus lanatus* exhibited a toxic reaction; within an hour, the aphids fell off the plants and were unable to move in a coordinated manner. We observed no endophytic fungus in our *H. lanatus* leaves when preparations were made according to the procedure by Saha et al. (1988). Thus, *H. lanatus* is not a host of the Idaho *Diuraphis* sp., ruling out any possibility that it is *D. holci.*

It is, in fact, doubtful that *D. holci* occurs in North America in spite of the records cited by Smith & Parron (1978). There are none in the Canadian national collection in 1989 (Robert Foottit, personal communication), nor in the collection at the Illinois State Natural History Survey in 1990 (David Voegtlin, personal communication), nor in the collections at the California Dept. of Food & Agri-

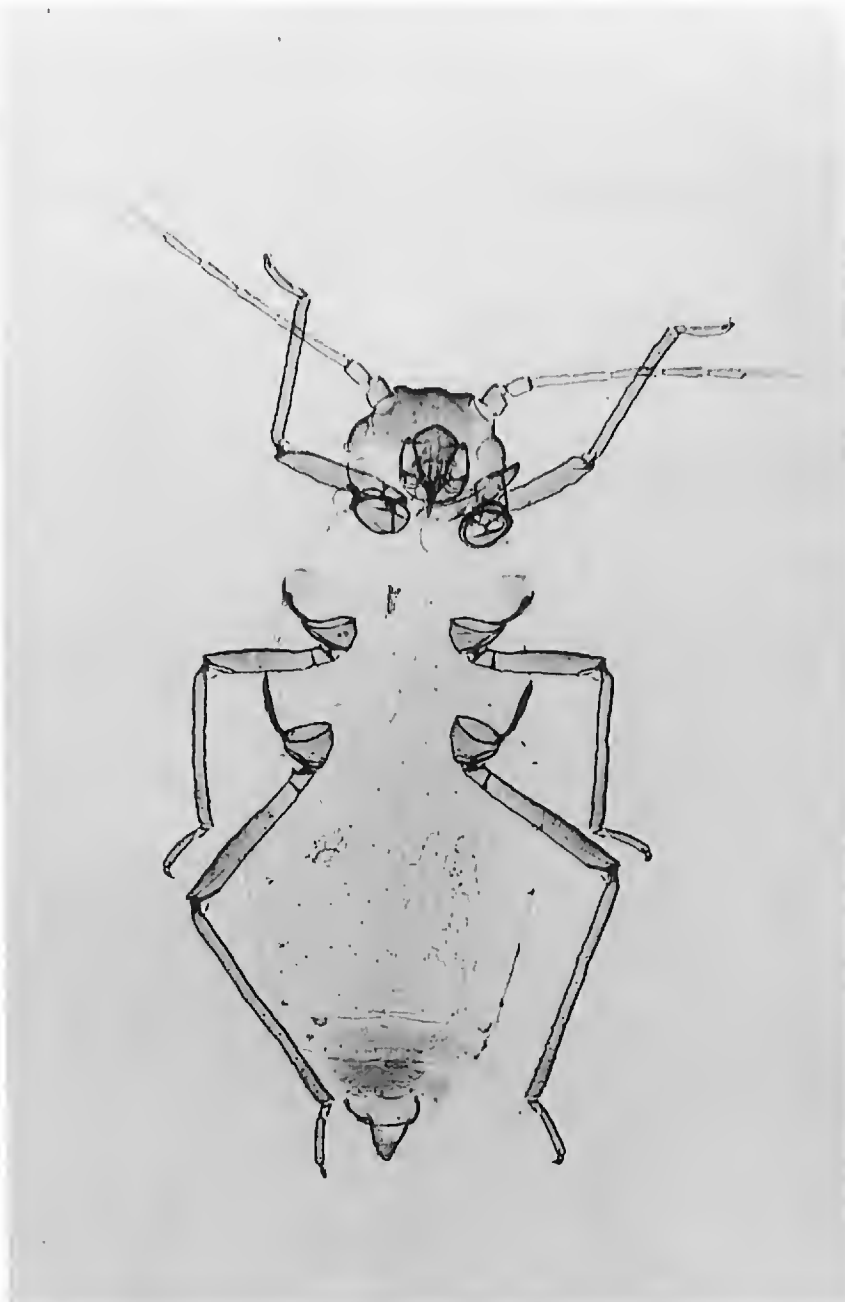

Figure 7. *Diuraphis* (*Holcaphis*) *frequens* (Walker) apterous vivipara, showing pattern of abdominal markings and relative lengths of antennal segments.

culture, Sacramento and the University of California, Berkeley, California in 1990 (John Sorensen, personal communication). Hille Ris Lambers (1939) indicated that *D. holci* is restricted to plants in the genus *Holcus*. None of the North American specimens identified as *D. holci* in collections at the United States National Museum or the Palmer Collection at Colorado State University are specified to have been collected from *Holcus*. About half of the slides have inadequate or no host information, but specified host plants include petunia, quackgrass and *Agropyron glaucum,* all unlikely hosts of *D. holci.* Forbes & Chan (1989) reported an extensive survey of aphids in British Columbia where *Holcus lanatus* is abundant. They report *Hyalopteroides humilis* (Walker) and *Sitobion fragariae* (Walker) on *H. lanatus,* but no *Diuraphis* spp. were found. Thus, we are not aware of evidence that any *Diuraphis* sp. colonizing *Holcus* occurs in North America.

Triticum aestivum was a better host for the Idaho *D. frequens* than any other plant tested, including *E. repens,* the host reported to be preferred by *D. frequens* in Europe (Hille Ris Lambers 1939) (Table 1); however, colonies on wheat were not as large as those produced by the three pest species. We have not found *D. frequens* on *E. repens* in Idaho, although a number of other aphid species have been found, including *Sipha elegans* del Guercio, *D. noxia, Metopolophium dir-*

Table 1. Mean numbers of aphids on various plants after two weeks of colonization, Parma, Idaho, January–February, 1989. Means followed by the same letter (a, b, c) are not significantly different from others in the same column using the LSD method of means separation.

Host	*D. frequens*	*D. noxia*	*S. graminum*	*R. padi*
Triticum aestivum L.	119.0 a	1816.7 a	2793.3 a	1450.0 a
Apera interrupta (L.) Beauvois	31.3 b	42.7 bc	304.3 b	112.3 b
Elytrigia repens (L.) Beauvois (Moscow, Idaho)	6.3 c	94.0 b	57.7 bc	7.3 c
Elytrigia repens (L.) Beauvois (Caldwell, Idaho)	9.0 c	31.0 bc	31.0 bc	36.0 bc
Agrostis alba L.	0 c	0.3 c	12.0 bc	118.7 b
Agrostis tenuis Sibthorp	0 c	0.3 c	38.0 bc	3.0 c
Agrostis palustris (Hudson) Persoon	0 c	0 c	4.3 c	3.7 c
Holcus lanatus L.	0 c	0 c	5.0 c	7.0 c
Thinopyrum ponticum (Podperae) Barkworth & D. R. Dewey	2.3 c	0 c	2.7 c	0 c
Calamagrostis sp.	0 c	0 c	71.7 bc	0 c

hodum (Walker), *Sitobion avenae* (Fabr.), *S. graminum* and *Forda marginata* Koch (Gittins et al. 1976; SEH, unpublished data).

The Idaho *D. frequens, D. noxia* and *R. padi* all colonized *T. ponticum,* a species used in conservation plantings, much more heavily when the plants were young than they did one year later. This observation suggests that some perennial grasses may become less palatable to aphids over time. If so, mature conservation plantings pose fewer problems as reservoirs of aphid pests than young stands. This question should be examined further.

Apera interrupta was usually colonized more heavily than *Agrostis* spp. This supports recent botanical evidence that *A. interrupta* should not be placed in the genus *Agrostis* as it has sometimes been in the past (McNeill 1981, Hitchcock & Cronquist 1973).

Based on morphology and host range analysis, we think the *Diuraphis* sp. found on Idaho wheat is *D. frequens,* although slight differences in morphology and host preference remain to be resolved. These differences could be due to founder effect, because it is likely that very few individuals were originally introduced into North America.

Other species that have been introduced into North America have host ranges that differ from their parent populations. Probably the most famous example is *Therioaphis trifolii* (Monell). According to Blackman (1981), the original North American population fed on *Trifolium.* About 70 years later, *T. trifolii* forma "*maculata*" (Buckton) appeared on alfalfa. This population has several traits that are not typical of the parent population in the Old World. Evidence suggests that the North American alfalfa population resulted from the introduction of a single clone (Blackman 1981).

In the case of *D. frequens,* however, introduction of a single clone from Europe may not explain the marked preference for wheat in Idaho, because wheat is not considered to be a host of *D. frequens* in Europe. Another possible explanation is that Idaho *D. frequens* came from Asia, across the Bering Strait, rather than from Europe, and thus has a host range differing from European populations; however, wheat is not listed as a host in western Siberia (Ivanovskaya 1977).

We have observed wheat plants colonized by this species each year. Infested plants are usually severely damaged, but damage is restricted to isolated plants. We have observed that the most common situation is to find several infested

plants near the edge of a late maturing field of spring wheat. Laboratory cultures of the Idaho *D. frequens* do not produce many alatae in comparison with *D. noxia* and *D. tritici.* If the same is true for field populations, this could explain its restricted distribution. Theoretically, given the right conditions (e.g., when alate production is greatly increased), outbreaks could occur, but it is unlikely that the species will become a serious pest.

Acknowledgment

We thank Roger Blackman of the British Museum of Natural History for determining the chromosome number of our aphids and for loaning specimens. We thank Manya Stoetzel (U.S. National Museum), Robert Foottit (Canadian National Museum), Frank Peairs, B. C. Kondratieff and Robert Hammon (Colorado State University), Paul Brown (British Museum of Natural History), David Voegtlin (Illinois Natural History Survey) and John Sorensen (Calif. Dept. Food & Agriculture) for providing information and/or specimens from collections at their respective institutions. We thank Leslie Boydston and Keith Pike for photographs in Figs. 3, 6 and 7. We thank Richard Old, Edward Northam, Anna Zeigler, Mark Longstroth and Carol Scinocca for providing plants and seeds. We also thank Thomas Mowry and Keith Dorschner for help with statistics, Jane Breen for advice on endophyte analysis and Keith Dorschner for reviewing the manuscript. This is Idaho Agricultural Experiment Station Scientific Paper number 91732.

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Received 22 April 1991; accepted 13 September 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 62–63, (1992)

Scientific Note

NEW HOST, *BAUHINIA VARIEGATA* L., AND NEW LOCALITY RECORDS FOR *CARYEDON SERRATUS* (OLIVIER) IN THE NEW WORLD (COLEOPTERA: BRUCHIDAE: PACHYMERINAE)

The peanut (groundnut) bruchid, *Careydon serratus* (Olivier), is native to the tropics and subtropics of the Old World and attacks seeds of tamarind, *Tamarindus indica* L. and peanut, *Arachis hypogaea* L. (Davey, P. M. 1958. Bull. Entomol. Res., 49: 385–404). This species has been introduced into the New World and may become a serious pest if it becomes well established. In Africa, the species is a serious pest of peanuts (Davey 1958; Prevett, P. F. 1967. J. Stored Prod. Res., 3: 267–268), but in the New World, so far it has been collected only on its primary host, tamarind. However, Vélez Angel, in the article "Tres plagas insectiles recientemente detectadas en Antioquia. 1. El gorgojo del tamarindo, *Caryedon serratus* (Olivier)," (Vélez Angel, R. 1972. Rev. Facultad Nal. de Agronomía, Medellin, Colombia, 27: 71–74) and Johnson reported that this species is already well established in South America and is a potential threat to stored peanuts there (Johnson, C. D. 1986. Coleopt. Bull., 40: 264). Although tamarind is becoming an increasingly important crop for juice production in the tropics, the occurrence of *Caryedon serratus* on this plant is not yet considered serious. Johnson reported *Careydon gonagra* [= *Caryedon serratus*] from Mexico (Johnson, C. D. 1966. Pan-Pacif. Entom., 42: 36), and later (Johnson 1986) reported it from additional localities in Mexico and from Venezuela, but did not give any collection localities for Venezuela. *Caryedon serratus* has been established in Hawaii for a long time (Bridwell, J. C. 1920. Proc. Hawaiian Entomol. Soc., 4: 403–409).

Several new locality records and a new host record, *Bauhinia variegata* L., in Mexico are reported here. It is the first time this species has been collected from a host other than tamarind in the New World, including Hawaii. The new host could be important for the successful dispersal of this introduced seed beetle, and an indication that the species is becoming well established in the New World. It could eventually become a serious pest on both tamarind and peanuts. Because *B. variegata* is a commonly cultivated ornamental plant in the New World tropics, introduced from Asia, this plant could function for dispersal of the insect.

New Host and Locality Records.—(Records from Hawaii are not included, depositories follow in parentheses). MEXICO. *BAJA CALIFORNIA SUR:* La Paz, 4–9 Apr 1967, J. Chemsak & M. Michelbacher (C. D. Johnson). *DURANGO:* 3 km W of El Palmito, 2–3 Oct 1976, E. Giesbert (Nat. Hist. Mus. Los Angeles). *NAYARIT:* San Blas, 14 Jul 1960, R. B. Loomis & J. Maris (LBS). *OAXACA:* 47 km W of Tapanatepec, 27 May 1983, L. O'Brien & G. B. Marshall (CWO). *SAN LUIS POTOSI:* Tamazunchale, ex. seeds of *Bauhinia variegata,* 22 May 1990 (emerged 10 Jul 1990), Jan A. Nilsson (J. A. Nilsson). HAITI. Port-au-Prince, 15–23 Jan 1923 (Am. Mus. Nat. Hist.). ST. CROIX. H. A. Beatty (Mus. Comp. Zool.). VENEZUELA. Puerta Negra, Tocoron, 8 Mar 1978, ex. tamarindo (Univ. Centr. Venez.). *ARAGUA:* Maracay, El Limon, 1 May 1983, ex. tamarindo (Bordón); 14 May 1976,

11 Feb 1977, 6 Feb 1985, G. Yepez, ex. tamarindo (Univ. Centr. Venez.). *CARABOFO:* Maziata, 25 Feb 1965, D. Gonzales, ex. tamarindo (Univ. Centr. Venez.). *ZULIA:* Maracaibo, 28 Jan 1979, B. Tambrano, ex. tamarindo (Univ. Centr. Venez.).

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Received 26 February 1991; accepted 2 June 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 63, (1992)

Scientific Note

HEIMBRA OPACA (ASHMEAD) (HYMENOPTERA: EURYTOMIDAE) DISCOVERED IN WASHINGTON[1]

During 1990, a specimen of *Heimbra opaca* (Ashmead) was collected in southeastern Washington. The site is a grassy slope with scattered forbs and shrubs along the north side of the Snake River. This is the first report of *H. opaca* and, thus, the subfamily Heimbrinae, from Washington. The specimen was identified by the authors using key criteria (Burks, B. D. 1971. Trans. Am. Entomol. Soc., 97: 1–87) and comparison with previously determined specimens.

This species was previously reported from California, Arizona, New Mexico, Utah, Colorado, Kansas, Montana (Burks, B. D. 1979. *In* Krombein, K. V. et al. Cat. Hymen. Am. N. of Mex., Vol. 1: 846), and Idaho (Johnson, J. B. & T. D. Miller. 1987. Pan-Pacif. Entomol. 63: 324). Thus, *H. opaca* is widespread in arid and semi-arid areas of the western U.S. However, it remains rarely collected and biologically virtually unknown. The four collection sites in Idaho and Washington known to the authors are all mixed grasslands, as described above, on sandy or loess soils.

Material Examined.—WASHINGTON. *WHITMAN Co.:* 11.2 km (7 mi) E of Wawawai, 26 Jul 1990, sweeping vegetation, L. M. Wilson collector (specimen deposited: Maurice T. James Collection, Department of Entomology, Washington State University, Pullman, Washington 99164-6432).

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Received 28 February 1991; accepted 8 May 1991.

[1] Published with the approval of the director of the Idaho Agricultural Experiment Station as Research Paper 91714.

PAN-PACIFIC ENTOMOLOGIST
68(1): 64–65, (1992)

Scientific Note

HEMIHYALEA EDWARDSII (PACKARD) (LEPIDOPTERA: ARCTIIDAE) IS THE HOST OF *PARADEJEANIA RUTILIOIDES* (JAENNICKE) (DIPTERA: TACHINIDAE) IN CENTRAL COASTAL CALIFORNIA

Paradejeania rutilioides (Jaennicke) is a widespread species in the western Nearctic, including Mexico. West coast populations, which range from Vancouver Island to southern California, have more extensive black markings on the ochreous abdomen and were designated (Arnaud, P. 1951. Canad. Entomol., 83: 332) as a subspecies, *nigrescens* Arnaud. In California, this race occurs along the coast and Coast Ranges from Humboldt to Monterey Counties, on the west slope of the Sierra Nevada, and in the Transverse and Peninsular Ranges, to elevations of 1900 m; nearly all collection records are from late August to November (Arnaud 1951; University of California, Berkeley, specimens).

Paradejeania rutilioides nigrescens is the largest and most conspicuous tachinid in California, yet its biology is poorly known. General and perhaps presumed host records date back to the early 1900s (Essig, E. O. 1913. Injurious and beneficial insects of California. Calif. State Comm. Hort. Mo. Bull. 2: 261; 1915, ibid, 2nd ed. Suppl. 4: 330), when *Paradejeania* was stated to feed on "caterpillars" and "caterpillars of various species," respectively, without specific taxa given.

Arnaud reported a host of this fly to be an arctiid, *Hemihyalea* sp., based on a specimen from Los Gatos, Santa Clara Co., California, reared by H. P. Allmendiger and R. Maddux (Arnaud, P. 1974. Pan-Pacif. Entomol., 50: 93). Because there is only one species of *Hemihyalea* known in the area, *H. edwardsii* (Packard), this is presumbly Arnaud's host record. The following observations on a rearing lot that produced three examples of the fly and one of the moth agree with this assumption. The only other reared specimen of *P. r. nigrescens* that we have seen is one that emerged from leaf litter collected beneath *Quercus agrifolia* Neé in Golden Gate Park, San Francisco, by P. A. Opler (JAP 67G16). The duff was procured 21 Jul 1967, evidently containing a puparium, and the fly eclosed 6 Sep 1967 (UCB).

During a Lepidoptera survey trip to Big Creek Reserve in coastal Monterery Co., California, 5 Jun 1990, we noticed several large woolybears climing the main trunk of a mature *Q. agrifolia* at dusk. Six were collected from heights of 2.4 to 3.0 m and others could been seen further up. There was a large tree hole in this trunk that contained arctiid exuvia and copious frass. Apparently, the *Hemihyalea* larvae migrate up to the foliage to feed at night and retreat to a shelter during the day. This explains why we have never found larvae of this arctiid on *Q. agrifolia* during diurnal survey for lepidopterous larvae at numerous localities in the region. We also found one larva of *H. edwardsii* at night on *Q. agrifolia* at a higher elevation site at Big Creek in April (JAP 90D64).

The six larvae collected in June were transported to Berkeley for rearing. Five produced cocoons; one larva died prior to, and one following cocoon construction. A large tachinid puparium appeared in each of three of the cocoons in late June and July after emergence of the maggots. Three specimens of *P. rutilioides nigrescens* emerged 12 Jul to 30 Aug and one *H. edwardsii* on 17 Sep.

It is clear that *Hemihylea* serves as a host for *Paradejeania,* and the coincidental autumnal flight periods of the two insects suggest that this moth is the only host in this region, because we do not have any other large fall-flying, univoltine moth in the coastal areas inhabited by *P. rutilioides.* Although we still do not know how this tachinid infects its host, some observations provide clues for a possible answer. Arnaud observed females of this fly that bore dozens of active maggots in uturus, in December, 1966, in San Francisco at the same site where Opler's *Paradejeania* was reared the following September (Arnaud, P. 1968. Pan-Pacif. Entomol., 44: 85). This suggests that this tachinid, at least the females, can survive for a long time, into mid-winter when *H. edwardsii* presumably has entered early larval stages. Considering that the tachinid is larviparous and diurnal and the arctiid larvae are nocturnal, it seems difficult to explain the high parasitism rate of larvae we encountered. *Hemihyalea* larvae likely are widely dispersed during feeding in the expansive canopy of *Q. agrifolia.* The female tachinid produces hundreds, or even thousands, of larvae and the first instars may be distributed generally on the foliage, where they would have to be capable of surviving until arrival of the host caterpillars. Alternatively, *P. rutilioides* may be able to locate resting groups of larvae and larviposit at the retreat either near, or on, the arctiid larvae.

The moths are abundant in late September and October, often 20–30 per black-light trap sample, with a few worn examples persisting into November. The conspicuous fly visits flowers of *Eriogonum, Haplopappus, Aster,* etc. (numerous on introduced ivy, *Hedera,* growing at the Gatehouse), in late October and November. None was observed during late September and early October when adults of the arctiid are most numerous.

Records.—All the following data are from: CALIFORNIA. *MONTEREY Co.:* Big Creek Reserve: *H. edwardsii*: HQ area 0–10 m, coastal scrub, 3–4 Oct 1985, 27–28 Sep 1987, 29 Oct 1989, J. W. Brown, J. A. Powell; Gatehouse, 18 Oct 1988, J. Smiley; Trail to Redwood Camp 80 m, 27 Sep 1987, J. A. Powell; Devils Creek Flat 120 m, 27 Sep 1987, J. W. Brown; South Ridge Rd, 220 m, 7 Nov 1988, 29–30 Oct 1989, and larvae 5 Jun 1990, r.f. *Quercus agrifolia,* emgd. 17 Sep 1990 (JAP 90F12) Y.-F. Hsu, J. A. Powell; South Ridge Rd, 450–500 m, 29–30 Oct 1989; South Highlands, 675 m, larva 27 Apr 1990, r.f. *Q. agrifolia,* emgd. 12 Sep 1990 (JAP 90D64) Y.-F. Hsu.

P. rutilioides nigrescens: HQ area 0–10 m, coastal scrub, 30 Oct 1989; grassland above Brunette Crk, 180–240 m, 31 Oct 1989, J. A. Powell; South Ridge Rd, 220 m, 5 Jun 1990, r.f. *Hemihyalea edwardsii* larvae, emgd. 12 Jul, 20, 31 Aug 1990 (JAP 90F12) Y.-F Hsu, J. A. Powell; South Highlands, 625–750 m, 30 Oct 1989; vic. French Camp, 750–800 m, manzanita-pine-oak woods, 6–8 Nov 1989, J. A. Powell.

Acknowledgment.—We thank John Smiley for cooperation with facilities and field work at the Big Creek Reserve and Paul H. Arnaud, Jr. for comments on the manuscript.

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Received 22 March 1991; accepted 8 May 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 66–68, (1992)

Scientific Note

LOW SUSCEPTIBILITY OF OVERWINTERING MONARCH BUTTERFLIES TO *BACILLUS THURINGIENSIS* BERLINER

The large winter aggregations of the adult monarch butterfly, *Danaus plexippus* L. (Danaidae: Lepidoptera), are spectacular phenomena that occur among selected groves along the California coastline and in the high mountains of Mexico. The overwintering areas in Mexico are periodically infested by larvae of *Evita hyalinaria* (Grossbeck) (Geometridae: Lepidoptera), which defoliate the oyamel fir trees, *Abies religiosa* Lindley, used by the butterflies. Foliage protection can be attained with the use of *Bacillus thuringiensis* Berliner, but the application of this biotic agent may inadvertently affect the monarch butterflies overwintering in the sprayed region. Brower expressed concern over the widespread application of *B. thuringiensis* because of its potential negative effects on the monarch butterflies (Brower, L. 1986. Atala, 14: 17–19). He felt that large scale spraying of this biotic agent should be avoided near an overwintering site unless the procedure could be determined as safe or of minimal risk to the butterflies. Because the susceptibility of adult monarch butterflies to *B. thuringiensis* is unknown, we tested this bacterium against overwintering butterflies under laboratory conditions.

Butterflies were collected from a central coast wintering site located in Oceano, California (Leong, K. L. H. 1990. Ann. Entomol. Soc. Am., 83:906–910) and held in cages without water at room temperature and humidity (21° C ± 0.25 SE, 42% RH ± 1.1 SE) for two days before treatment. The butterflies (10 insects per cage and three cages per treatment) were initially subjected to twice the recommended concentration of commercial *B. thuringiensis* [*kurstaki*] (Javelin®, 1.9 liters/3758 liters of H_2O [16,000 *Spodoptera* units/mg]) or to twice the recommended concentration of dead transgenic *Pseudomonas fluorescens* (Trevisan) Migula containing endotoxin crystals (MVP®, 1.9 liters/3758 liters of H_2O [10,000 Diamondback units/mg]). Control groups were provided water only. Adult monarchs were exposed to *B. thuringiensis* by two ways: (1) spraying an aqueous suspension onto the leaves of *Eucalyptus* sp. (tree species commonly used by overwintering butterflies in California) within the cages until runoff (approximately 16 ml), and (2) placing an aqueous suspension in petri dishes (50 ml) for 24 h.

The adults imbibed the preparation almost immediately after exposure. Five days after exposure, the adults showed a low mortality to both Javelin® and MVP®. The butterflies exposed to Javelin® spray, however, had a significantly higher mortality ($P < 0.05$) than those sprayed with MVP® (20% ± 7 SE for Javelin® vs 3% ± 3 SE for MVP®). The same relationship, but not significantly different, was exhibited between the two groups of butterflies exposed to the inocula in petri dishes (7% ± 5 SE for Javelin® vs 3% ± 3 SE for MVP®). None of the control insects died during the study period. The results suggest that the butterflies were slightly more susceptible to *B. thuringiensis* preparation than to the transgenic *P. fluorescens*.

To confirm the results of the *B. thuringiensis* preparation, another test was conducted with Javelin® at the recommended (0.9 liters/3758 liters of H_2O) and at twice the recommended concentrations by spraying or by placing the aqueous suspension in petri dishes (10 insects per cage, three cages per treatment). The control adults were exposed to water only. The butterflies again exhibited low total mortality rates at both the recommended and twice the recommended concentration rates (7% vs 7% spray; 3% vs 7% petri dishes). The total mortality among the control insects was zero for the spray and 3% for petri dish treatment. *Bacillus thuringiensis* was isolated from the hemocoel of the dead butterflies treated with Javelin, but not from the controls.

The fecal droppings of butterflies treated with twice the recommended concentrations were collected daily and placed in 5 ml of sterile water and agitated. A loopful of the suspension was then streaked onto nutrient agar and incubated at 25° C. *Bacillus thuringiensis* isolates were determined by colony growth characteristics and by microscopic examination (400×). The bacterium was recovered daily throughout the five day holding period. Fewer colonies (based on qualitative observations) of *B. thuringiensis* were isolated after five days than after the first two days. The bacterium was also recovered from the gut contents of the surviving adults after the five-day holding period.

The overwintering butterflies, under laboratory conditions, showed low sensitivity to the *B. thuringiensis* used, both at the recommended and at twice the recommended concentrations for control of lepidopterous larvae. The results suggest that the application of this biotic agent within or near the butterfly's winter habitat presents a minimal threat to their survival. Because a small percentage of the butterflies did succumb to this bacterium or its product (endotoxin), however, the use of *B. thuringiensis* near the butterfly's overwintering site should be minimized.

Assuming that *E. hyalinaria,* the defoliator of fir trees, is equally susceptible to *B. thuringiensis* and transgenic *P. fluorescens,* the latter may be a better choice for controlling this insect. Our data suggest that the butterflies were less susceptible to the endoxotin alone than to a bacterial spore endotoxin mixture. To ensure another level of safety for the roosting butterflies from possible drift of the bioinsecticide, a spray-free buffer zone could be established around the overwintering site. This buffer zone, however, may be subjected to defoliation by *E. hyalinaria,* and could affect the roosting site. The possible threat of introducing the bacterium or its endotoxin into the protected aggregation sites by affected adults (via fecal droppings) exposed to the treated areas is minor due to the dilution effect, the poor survivability of the spores on the leaf surfaces (Leong, K. et al. 1980. Environ. Entomol., 9: 593–599) and the low adult susceptibility to *B. thuringiensis.* Another possible threat is the contamination of the monarch butterfly eggs with *B. thuringiensis* deposited by affected adults (Ali, A. A. & T. F. Watson. 1982. J. Econ. Entomol., 75: 596–598). Presumably, the overwintering butterflies will have eliminated most of the bacterium before egg deposition occurs. The monarch larvae sensitivity to *B. thuringiensis* from adults remains unknown and requires further study.

Although our study suggests that *B. thuringiensis* presents a minimal threat to the adult monarch butterflies, the susceptibility of the populations while in Mexico

still needs to be investigated before wide scale spraying is employed near their winter aggregation site.

Acknowledgment.—Authors thank the Mycogen Corporation, San Diego, California for providing the *Bacillus thuringiensis* materials (Mycogen MVP®) used in this study.

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Received 5 April 1991; accepted 15 June 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 68–69, (1992)

Scientific Note

NEW DISTRIBUTIONAL RECORDS FOR SOME CANDIDATE SPECIES OF *LYTTA* IN CALIFORNIA (COLEOPTERA: MELOIDAE)

Five Californian species of *Lytta* blister beetles (Coleoptera: Meloidae) are candidates for listing as endangered (i.e., a species that is likely to become extinct) by the U.S. Fish and Wildlife Service. These species [*L. hoppingi* Wellman, *L. insperata* (Horn), *L. moesta* (Horn), *L. molesta* (Horn), and *L. morrisoni* (Horn)] have not been listed due to a lack of biological information. Developments in California's central valley and surrounding foothills continue to impact them and their habitat because of three factors: our knowledge of their biology is limited, a lack of adequate survey methods, and the beetles not being fully protected by the Endangered Species Act (1973).

Recently, specimens of four of these candidate species were found in the R. S. Wagner Collection at the Tulare County Agricultural Commissioner's/Sealer's Office, Visalia, California. The specimens represent new distributional records for three species, having been collected in the 1930s but overlooked by researchers. For two of these species, an additional, more recent, distributional record is reported. We present this information (see Records section) to improve and update the distributional data on *Lytta*; to aid federal, state, and county regulatory agencies in their development, management, and protection efforts; and to encourage researchers to utilize the Wagner Collecton and to study the endangered invertebrate fauna. Distributional information on *Lytta* has been summarized (Selander, R. B. 1960. Illinois Biol. Monographs, 28) and recently updated (California Department of Fish and Game. 1991. Natural Diversity Data Base, computer data base of sensitive species. Sacramento, California).

Biological information for the five candidate species of *Lytta* is almost nonexistent. *Lytta molesta* has been collected on *Lupinus* (Leguminosae) feeding on

its flowers and seed pods (personal observations) and on *Erodium cicutarium* (L.) (Geraniaceae) (Selander 1960). Like most meloid beetles, *Lytta* parasitize the nests of wild bees, feeding on provisions or immature stages of the bees (Selander 1960). Bee genera that are parasitized by various other *Lytta* species include: *Anthophora* Latreille, *Diadasia* Patton, *Emphoropsis* Ashmead, *Ptilothrix* Smith (all Hymenoptera: Anthophoridae), *Andrena* subgenus *Onagrandrena* Linsley & MacSwain (Hymenoptera: Andrenidae) and *Colletes* Latreille (Hymenoptera: Colletidae) (Hurd, P. D. Jr. 1979. *In* Krombein et al. (eds.). Cat. of Hymenoptera in America north of Mexico. Vol. II, Smith. Instit. Press, Wash., D.C., pp. 1199–2209; Selander 1960).

The fourth candidate species in the Wagner Collection, *L. molesta,* is represented by three females and five males from a location previously reported by Selander (1960) as Lanes Bridge, Fresno Co., California. These specimens, though not providing new distributional information, have taxonomic value and demonstrate the merit of the Wagner Collection.

Because the candidate *Lytta* are very similar to each other, similar to other *Lytta* species, and more than one species may occur at a site, we urge researchers to collect voucher specimens and have them identified by a taxonomist to validate records. We hope that this information encourages researchers or agencies (state, federal, or private) to study or provide the funding necessary to determine the biological status of these species.

Records.—Lytta hoppingi Wellman. New records: CALIFORNIA. *KERN Co.:* Taft, 29 Apr 1978, W. H. Tyson (California Department of Fish and Game. 1991) [species determined by J. D. Pinto]. *TULARE Co.:* Ducor, 25 Mar 1934, 8 males and 8 females. Historical distribution: CALIFORNIA. *FRESNO Co.:* Coalinga; *TULARE Co.:* Visalia; Delano.

Lytta moesta (Horn).—New records: CALIFORNIA. *KERN Co.:* Arvin, 29 Mar 1931, 2 females. *TULARE Co.:* Springville, 28 May 1933, 1 female; 23 Jun 1936, 1 pair (in copulation). Historical distribution: CALIFORNIA. *FRESNO Co.:* Friant. *KERN Co.:* Edison. *MADERA Co.:* Kismit. *SANTA CRUZ Co.:* Santa Cruz. *STANISLAUS Co.:* Manteca; Modesto; Ripon; Westly. *TULARE Co.:* exact location unknown (county label only); Kaweah; Potwisha, Sequoia National Park.

Lytta morrisoni (Horn).—New records: CALIFORNIA. *FRESNO Co.:* Panoche Road 13.1 km (8.2 miles) W of Interstate 5, 21 May 1978, F. G. Andrews (California Department of Fish and Game. 1991) [species determined by J. D. Pinto]. *TULARE Co.:* Plano, 1 May 1939, 1 male and 1 female. Historical distribution: CALIFORNIA. *FRESNO Co.:* Coalinga. *KERN Co.:* exact location unknown (county label only); Edison. *TULARE Co.:* Kaweah; Tipton; White River (south of). One data locale lists only "southern California."

Acknowledgment.—We thank the Kings River Conservation District for funding this publication, J. D. Pinto (University of California, Riverside) for confirming the identification of *L. moesta*; the former, F. G. Andrews, and W. H. Tyson (both California Department of Food and Agriculture) for providing additional information on the California Department of Fish and Game (1991) records; and D. J. Burdick (California State University, Fresno) and two anonymous reviewers for helpful editorial comments.

Jeffrey A. Halstead and Robert D. Haines, *Kings River Conservation District, 4886 E. Jensen Avenue, Fresno, California 93725 and Tulare County Agricultural Commissioner's/Sealer's Office, County Civic Center, Main and Woodland Drives, Visalia, California 93291, respectively.*

Received 20 February 1991, accepted 3 June 1991.

PAN-PACIFIC ENTOMOLOGIST
68(1): 70–71, (1992)

Scientific Note

RHOPALOSIPHUM RUFIABDOMINALIS (SASAKI) AND *APHIS ARMORACIAE* COWEN (HOMOPTERA: APHIDIDAE) CONFIRMED ON WHEAT IN IDAHO

Two species of aphids were found on wheat in Idaho for the first time during October, 1990. Both were found on winter wheat (*Triticum aestivum* L.) cv. 'Stephens' at the SW Idaho Research & Extension Center at Parma (Canyon County). Neither of these species is likely to become a significant pest as both have been in Idaho for at least five years and are only now being discovered on wheat despite intensive surveys of this crop since 1986. However, these additions to the wheat aphid fauna will further complicate species identifications of aphids found on cultivated cereals by increasing the number of taxa that must be recognized. Additionally, the genus *Rhopalosiphum* includes two common cereal pests, *R. maidis* (Fitch) and *R. padi* (L.), plus *R. insertum* (Walker). Separation of the latter three species requires detailed microscopic examination.

Rhopalosiphum rufiabdominalis (Sasaki) was collected between 16 Oct–19 Nov 1990 on winter wheat roots. *Rhopalosiphum rufiabdominalis* is permanently parthenogenetic on roots of rice and many other species of Gramineae in most parts of the world, though holocyclic populations overwintering on *Prunus* spp. have also been reported. It colonizes the roots of some dicots, especially Solanaceae and can be a serious pest on plants in hydroponic systems (Blackman, R. & V. Eastop. 1984. Aphids on the world's crops: an identification and information guide. John Wiley & Sons, New York; Blackman, R. et al. 1987. World perspectives on barley yellow dwarf. Proc. of intern'l. workshop, 6–11 July 1987, Udine, Italy. Dipartimento Cooperatizione Allo Sviluppol International Maize and Wheat Improvement Center (CIMMYT), pp. 197–214). It is known to vector barley yellow dwarf virus (Jedlinski, H. 1981. Plant disease, 65: 975–978; Johnstone, G. et al. 1987. World perspectives on barley yellow dwarf. Proc. of intern'l. workshop, 6–11 July 1987, Udine, Italy. Dipartimento Cooperatizione Allo Sviluppol International Maize and Wheat Improvement Center (CIMMYT), pp. 228–239; Paliwal, Y. 1980. Can. J. Pl. Path., 2: 90–92).

Rhopalosiphum rufiabdominalis was collected prior to these field collections in suction traps at Parma, Burley, Caldwell and Craigmont. There are no previously published records of collections from host plants in Idaho for *R. rufiabdominalis.* A field survey of cereal aphids between 16 Oct and 5 Dec 1990, on winter wheat showed decreasing numbers of *R. rufiabdominalis* as the season progressed (Table 1). This, along with late season suction trap collections and the presence of alatoid nymphs late in the season indicate the possibility of holocyclic overwintering in Idaho.

Aphis armoraciae Cowen was collected on 12 Oct 1990 from winter wheat using a Berlese funnel, and on 3 Dec 1990 on bluebunch wheatgrass T-2950 (*Agropyron spicatum* (Pursh) Scribner & Smith) at Parma, Idaho. *Aphis armoraciae* infests

Table 1. *Rhopalosiphum rufiabdominalis* (Sasaki) population on winter wheat (*Triticum aestivum* L.) cv. 'Stephens' at Parma, Idaho, 16 Oct–19 Nov 1990.

	Aphid Stage					
Sample date[a]	Nymph 1	Nymph 2–4	Alatoid	Apterae	Alatae	Total
16 Oct	0	48	0	1	0	49
22 Oct	0	12	0	2	0	14
8 Nov	7	4	1	5	0	17
19 Nov	0	1	0	0	0	1
5 Dec	0	0	0	0	0	0

[a] 20 tillers per sample and 10 samples.

roots and sometimes the aerial parts of plants in several families including Compositae, Cruciferae, Umbelliferae, and Gramineae (maize, wheat) (Blackman & Eastop 1984). *Aphis armoraciae* was previously collected from Bear Lake Co. on raspberry, Bingham Co. on potato, Canyon Co. on maize and roots of *Sisymbrium altissimum* L., Caribou Co. on potato, cabbage and radish, Franklin Co. on maize and *Aster* sp., Oneida Co. on *Chrysothamnus nauseosus* (Pallas) Britton and Teton Co. on potato (Gittins, A. et al. 1976. An annotated list of the aphids of Idaho (Homoptera: Aphididae). Rec. Bull., 95. College of Agric. Univ. of Idaho). *Aphis armoraciae* was also collected in suction traps at various areas in Idaho for several years from 1985–1990.

Voucher specimens from our collections from wheat are on deposit at the University of Idaho, SW Idaho Research and Extension Center, Parma, Idaho.

Material Examined.—Rhopalosiphum rufiabdominalis: IDAHO. *CANYON Co.:* Parma, 22 Sep 1985, and 1, 7, 15, 29 Sep 1987, suction trap, 1 specimen on each date; Caldwell, 21 Jul 1990, suction trap, 1 alate. *CASSIA Co.:* Burley, 18 Aug 1986, suction trap, 1 alate. *LEWIS Co.:* Craigmont, 25 Aug 1990, suction trap, 1 alate.

Aphis amoraciae: IDAHO. *CANYON Co.:* Parma, 12 Oct 1990, winterwheat, Berlese funnel, 7 specimens; Parma, 3 Dec 1990, bluebunch wheatgrass T-2950, 2 oviparae; Parma, 16 and 22 Oct, 8 and 19 Nov, 5 Dec 1990, *Triticum aestivum* 'Stephens,' total 81 specimens of various stages (see table).

Acknowledgment.—We thank D. Allison, Washington State University, for providing suction traps data, and J. P. McCaffrey, F. W. Merickel and T. M. Mowry for reviewing the manuscript. Published with the approval of the Director of the Idaho Agricultural Experiment Station as Research Paper 91728.

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Received 12 April 1991; accepted 29 July 1991.

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The PAN-PACIFIC ENTOMOLOGIST

Volume 68 April 1992 Number 2

Published by the PACIFIC COAST ENTOMOLOGICAL SOCIETY
in cooperation with THE CALIFORNIA ACADEMY OF SCIENCES
(ISSN 0031-0603)

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This issue mailed 14 May 1992

The Pan-Pacific Entomologist (ISSN 0031-0603)

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044, U.S.A.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PAN-PACIFIC ENTOMOLOGIST
68(2): 73–96, (1992)

REVISION OF THE SPIDER BEETLE GENUS *NIPTUS* IN NORTH AMERICA, INCLUDING NEW CAVE AND PHOLEOPHILE SPECIES (COLEOPTERA: PTINIDAE)

ROLF L. AALBU AND FRED G. ANDREWS
Insect Taxonomy Laboratory,
California Department of Food and Agriculture,
Sacramento, California 95814

Abstract.—The genus *Niptus* is revised for North America. Four species of *Niptus* Boeildieu (*N. giulianii* NEW SPECIES, *N. neotomae* NEW SPECIES, *N. sleeperi* NEW SPECIES, and *N. arcanus* NEW SPECIES) are described from the Great Basin area, southwestern Arizona, the cape mountain region of Baja California, Mexico, and a California cave, respectively. Notes on the biology of *Niptus* species, as well as *Ptinus clavipes,* are presented. A key is provided to the species of *Niptus* found in North America. Phylogenetic considerations among *Niptus, Pseudeurostus,* and *Eurostus* are discussed. Habitat conservation is stressed for species restricted to single cave localities.

Key Words.—Insecta, Coleoptera, Ptinidae, *Niptus,* southwest United States, Mexico, biology, caves

As a result of improved collecting techniques, such as overnight pitfall traps or longer duration ethylene glycol (antifreeze) traps, and greater accessibility to previously difficult to reach places, numerous specimens of small apterous beetles are now available in collections. Most larval and adult Ptinidae feed on dried plant and animal substances. Others have been recorded from dung. Many are associated with mammals or birds and are often found in caves. Their biology, including rearing methods of economically important species, is adequately covered by Howe (1959).

One species, *Niptus hololeucus* (Faldermann), a stored product pest, is widely distributed in the northern United States. *Niptus kelleri* (Brown) and *N. hilleri* Reitter have previously been placed in the genus *Pseudeurostus.* One of these, *N. hilleri,* is distributed widely, also in stored products (see Brown 1959: 629). *Niptus kelleri,* known only from the type locality, was not examined.

Because all genera of ptinids are flightless (except for certain *Ptinus*), the method found most effective in capturing pholeophilic Ptinidae is the use of numerous dry plastic "punch cup" containers as pit traps, especially near, or at, the entrance to rodent burrows. These traps are set in the late afternoon and collected early the next morning. This permits collection of live adult specimens for rearing and provides additional biological information (substrate type, etc.). Adults are also collected at night with the use of headlamps or lanterns to illuminate surface areas.

In 1978–1979, a year-long trapping survey of the Coleoptera of Mitchell Caverns was conducted using ethylene glycol pitfall traps (Aalbu 1990). Mitchell Caverns are located on the eastern slopes of the Providence Mountains (San Bernardino County), California. A new species of *Niptus* was found to be endemic to one cave.

Abbreviations.—The following abbreviations are used to denote the institutions that loaned material: CASC, California Academy of Sciences, San Francisco,

California; CISC, University of California, Berkeley, California; CNCI, Canadian National Collection, Ottawa, Ontario, Canada; CSLB, California State University, Long Beach; FMNH, Field Museum of Natural History, Chicago, Illinois; KWBC, Kirby W. Brown Collection, Stockton, California; MCZC, Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts; OSUC, The Ohio State University, Columbus, Ohio; SDMC, San Diego Museum of Natural History, California; USNM, United States National Museum, Washington D.C.; UAIC, University of Arizona, Tucson.

Niptus arcanus Aalbu & Andrews, NEW SPECIES
(Figs. 1, 17, 19, 24 and 25)

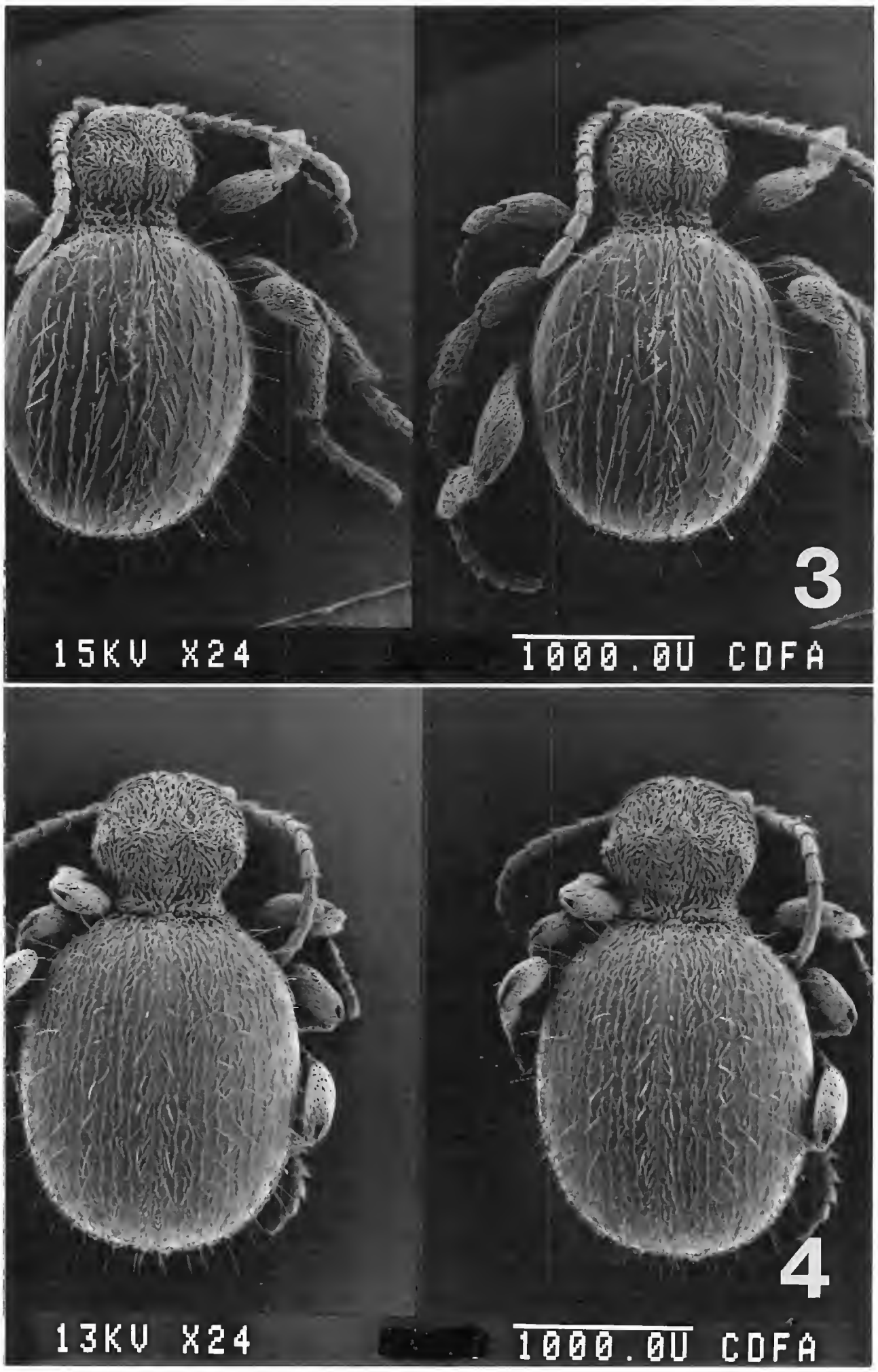
Types.—HOLOTYPE (female) and ALLOTYPE (male): CALIFORNIA. *SAN BERNARDINO Co.:* Providence Mountains State Recreation Area, Mitchell Caverns, el. 1340 m, El Pakiva Cave, 26 Aug–31 Dec 1978, Ethylene glycol pitfall trap near *Neotoma* nest, #6. Type deposited in California Academy of Sciences Collection. PARATYPES: CALIFORNIA. *SAN BERNARDINO Co.:* Providence Mountains State Recreation Area, Mitchell Caverns, el. 1340 m, El Pakiva Cave, 26 Aug 1978 to 31 Dec 1978 trap #6; 17 Mar 1979 to 16 Jun 1979, trap #3 (4); 17 Mar 1979 to 16 Jun 1979, trap #4 (19); 17 Mar 1979 to 16 Jun 1979, trap #6 (34); 17 Mar 1979 to 16 Jun 1979 (1); 27 May 1978 to 26 Jul 1979, trap #5 (28); 31 Dec 1978 to 17 Mar 1979, trap #5 (1); 31 Dec 1978 to 17 Mar 1979, trap #6 (21); 8 May 1981 to 10 Aug 1981 (11), R. L. Aalbu, Ethylene glycol pitfall trap near *Neotoma* nest. Paratypes deposited in USNM, CDFA, CISC, CASC, RLAC, OSUC.

Description.—Female (holotype). Integument red-brown, elytra shiny; length 3.3 mm. HEAD with surface vestiture of closely appressed, spatulate, scale-like setae with few longer fine setae on apical margin of clypeus; antennal fossae with dorsal border not carinate, not laterally elevated; eyes minute, three facets at minimum width, narrowly oval; antenna relatively long, slender, ratio of segment lengths 14:11:10:10:9:9:9:9:10:10:18. PRONOTUM with surface sculpture of rugose, deep punctures posteriorly forming moderately dense, fine tubercles; surface vestiture of one type, stout, arched, recumbent setae; setae dense at anterior margin, at transverse row of four large tufts; tufts equal in size, positioned near midlength. ELYTRA with surface smooth, shiny, strial punctures fine, nearly obsolete; vestiture of two types, nearly equal in length; first consisting of short moderately slender, erect, spatulate setae positioned in rows at regular distances along first to seventh intervals; second arched, recumbent, moderately slender setae positioned in rows at elytral striae and elytral intervals; setae short, dense at elytral margins. VENTRAL SURFACE: Sterna: ratio of segment lengths 17:19:15:5:19; sternal surface vestiture short, golden, closely appressed, spatulate, scale-like setae intermixed with sparse, slightly longer, less spatulate setae; fifth visible abdominal sternite with medial apical area with closely packed postero-directed, semi-erect setae forming a rounded tubercle-like structure. LEGS slender, femora moderately long, capitate, metafemora bent near apex; tibia slender; femoral vestiture of dense, golden, short, appressed, scale-like setae only varying slightly in length; tibiae with similar vestiture except protibiae with dense, slightly longer, slender, golden setae on lower margins, mesotibiae with dense, slightly longer, slender golden setae on lower margins, on apical one-half of outer margins; metatibiae with few sparse, slightly longer, golden setae on lower margins. Ratios of segment lengths: prothoracic legs, 50:49; mesothoracic legs, 54:52; metathoracic legs, 60:65; protarsi, 10:6:6:6:9; mesotarsi, 12:7:6:6:9; metatarsi, 15:8:7:7:10.

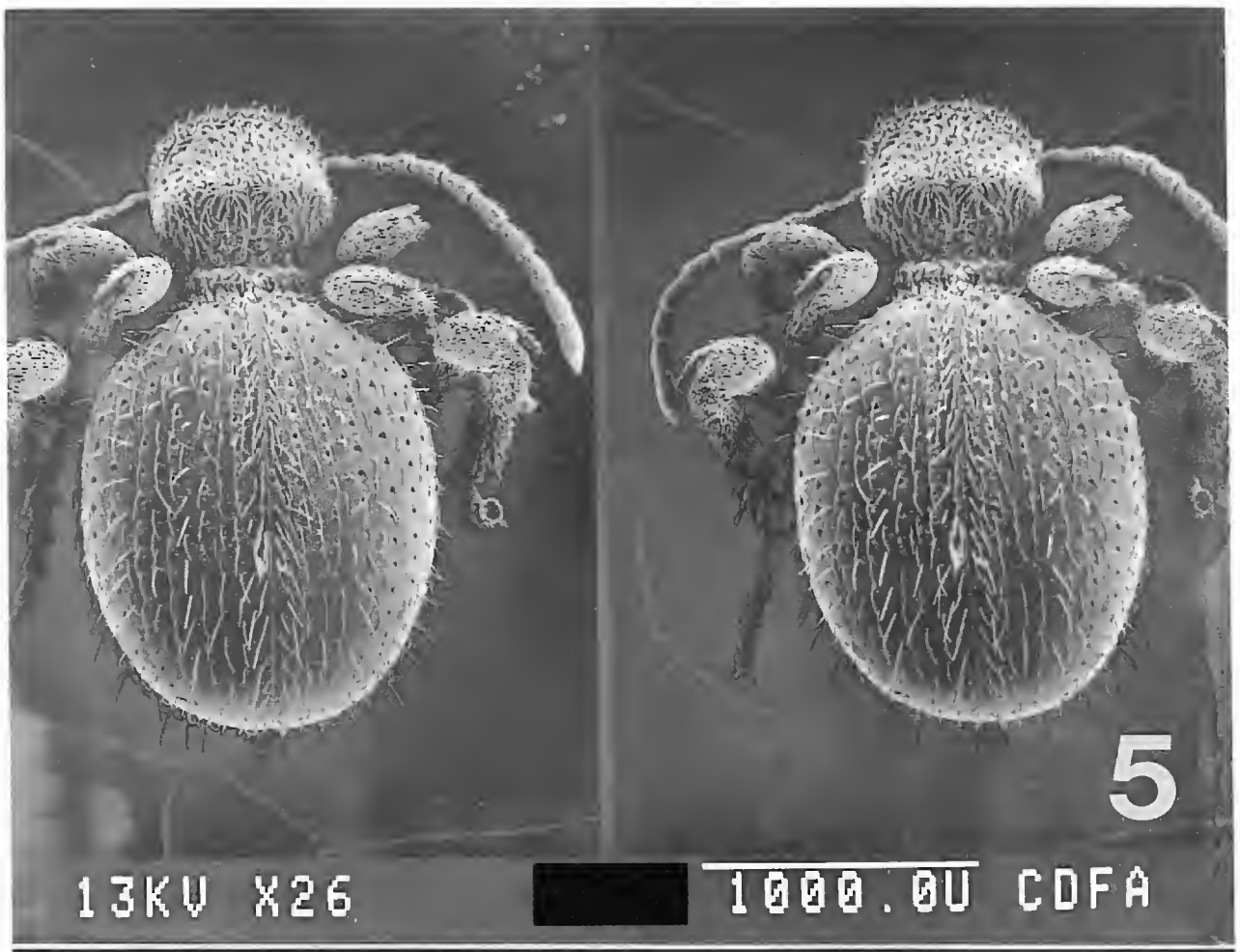
Male (allotype).—Similar to holotype but smaller, approximate length 2.9 mm. Fifth visible abdominal sternite with medial apical area with setae only slightly less appressed, slightly longer than rest of sternal setae; without tubercle-like structure.

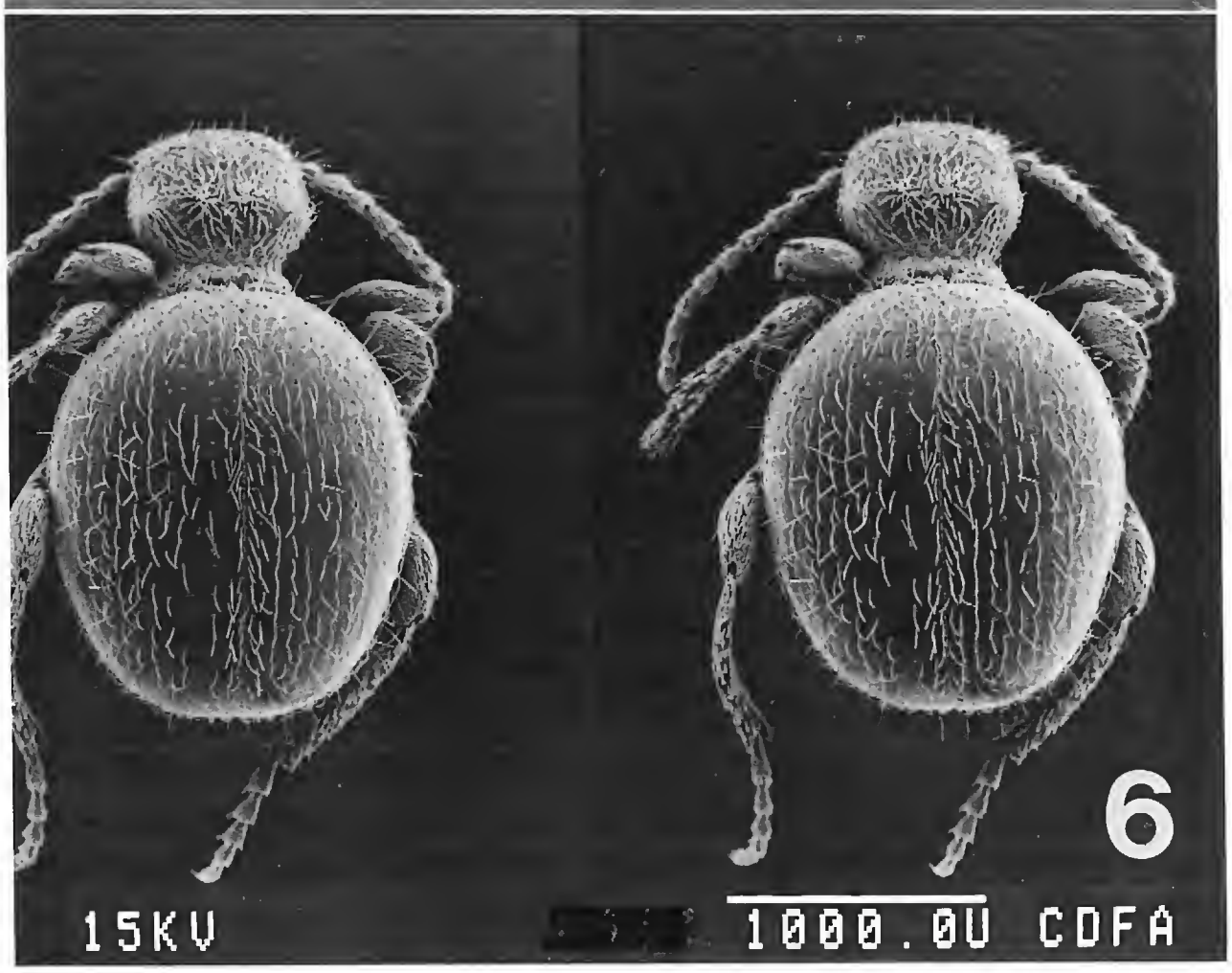
Diagnosis.—The following combination of characters will serve to separate *N. arcanus*: Head with eyes minute (Fig. 24) and antennal fossa with dorsal border

Figures 1–2. Figure 1. *Niptus arcanus,* habitus (stereo pair). Figure 2. *Niptus neotomae,* habitus (stereo pair).

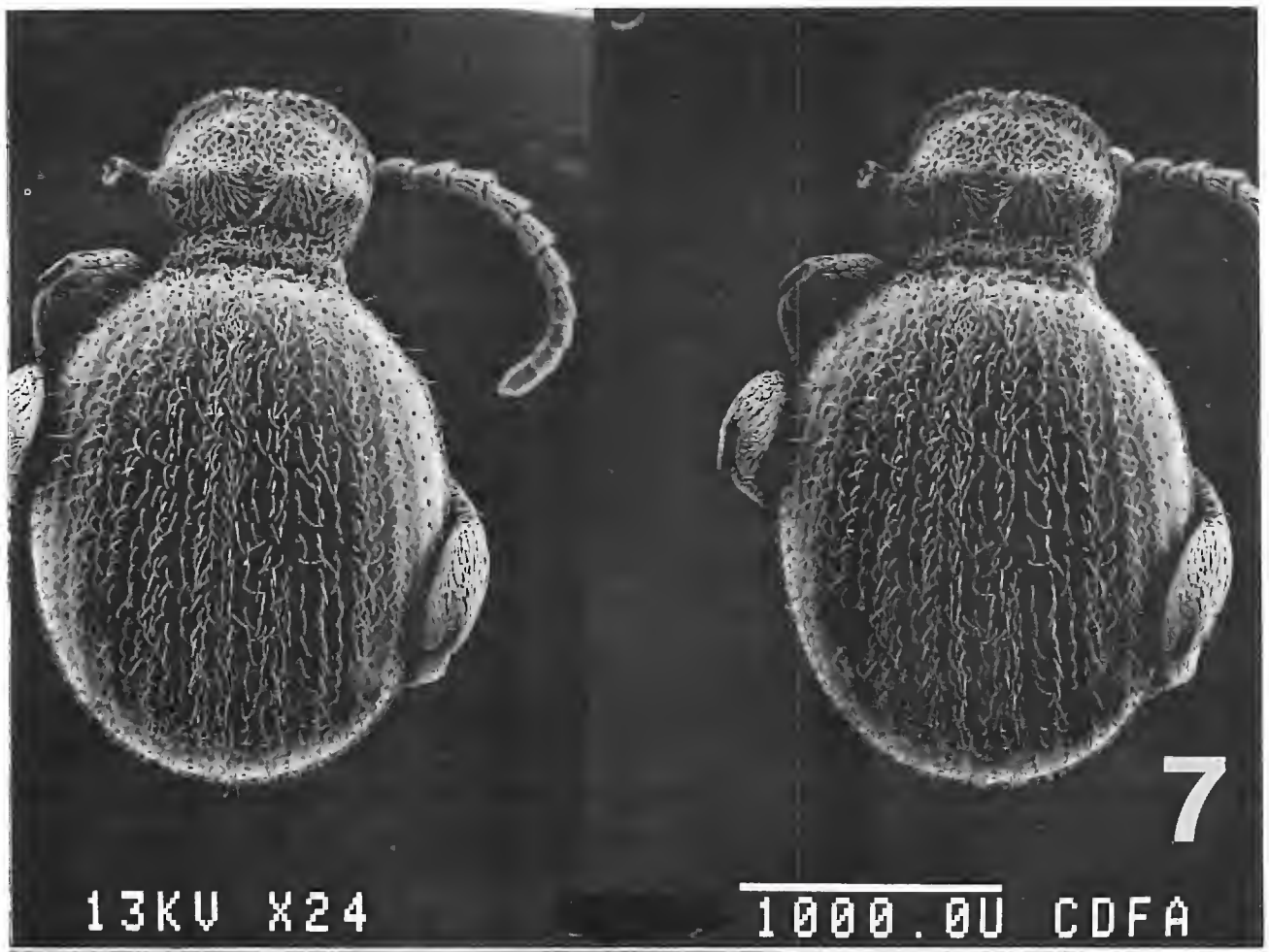


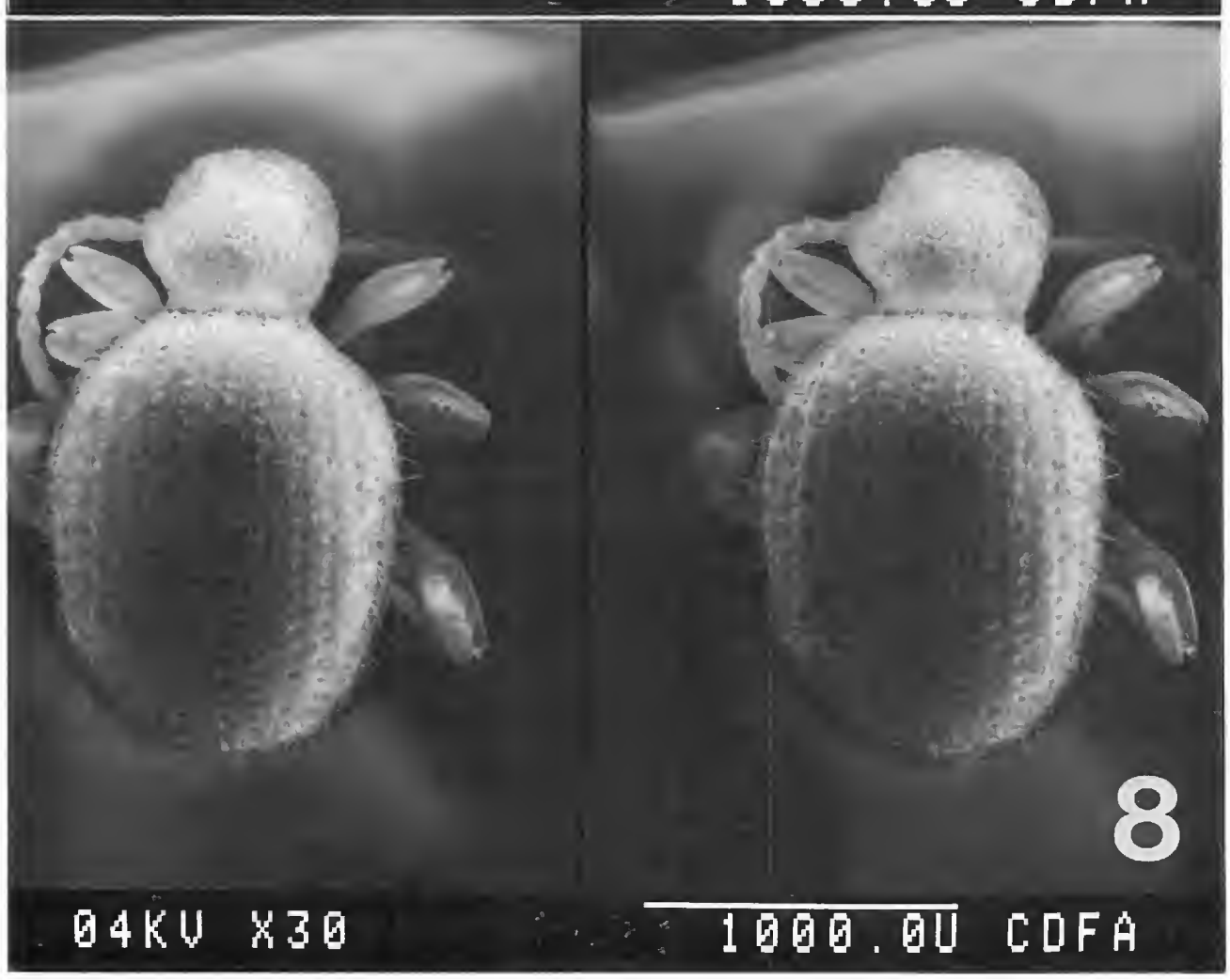
Figures 3–4. Figure 3. *Niptus giulianii,* habitus (stereo pair). Figure 4. *Niptus abditus,* habitus (stereo pair).



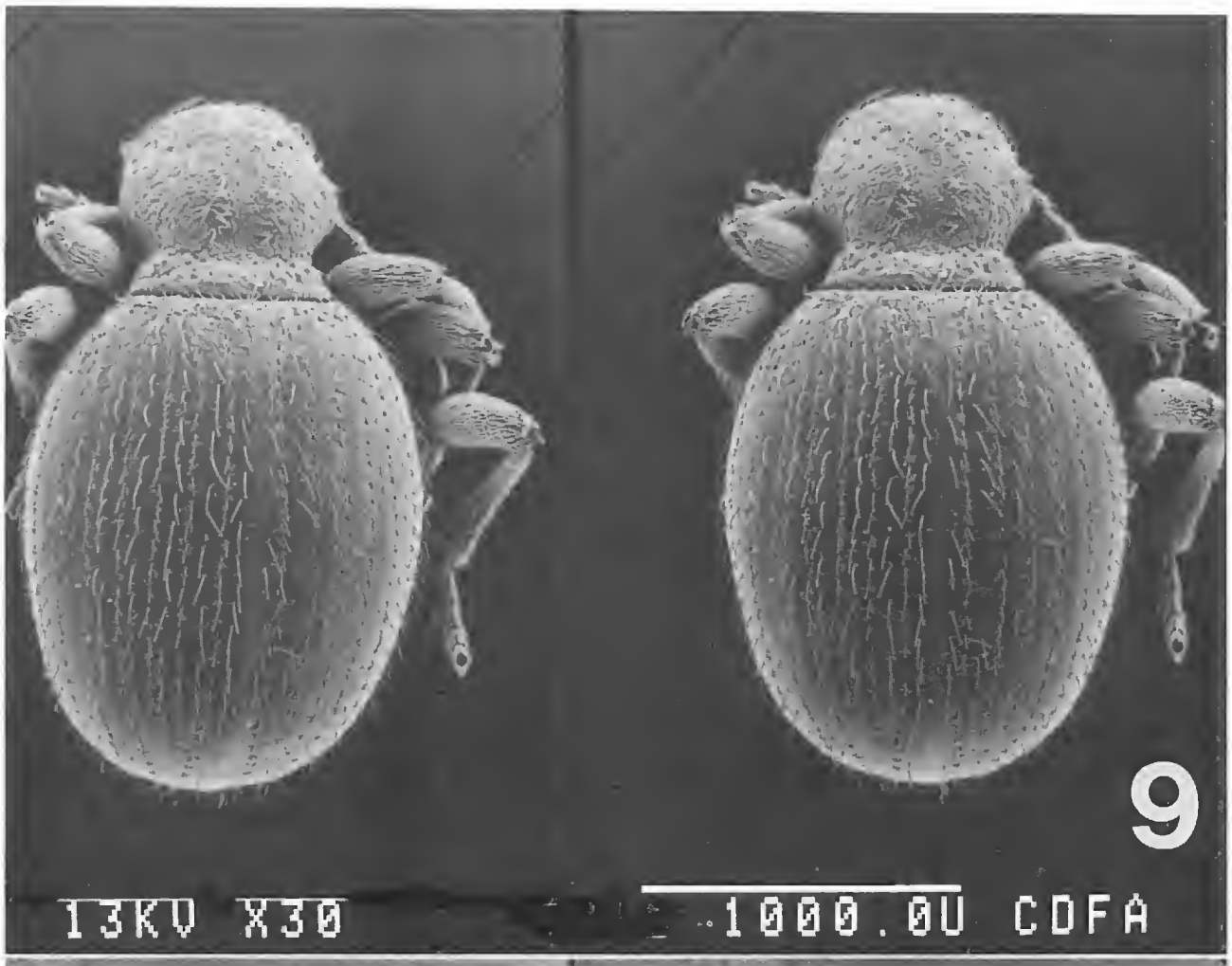


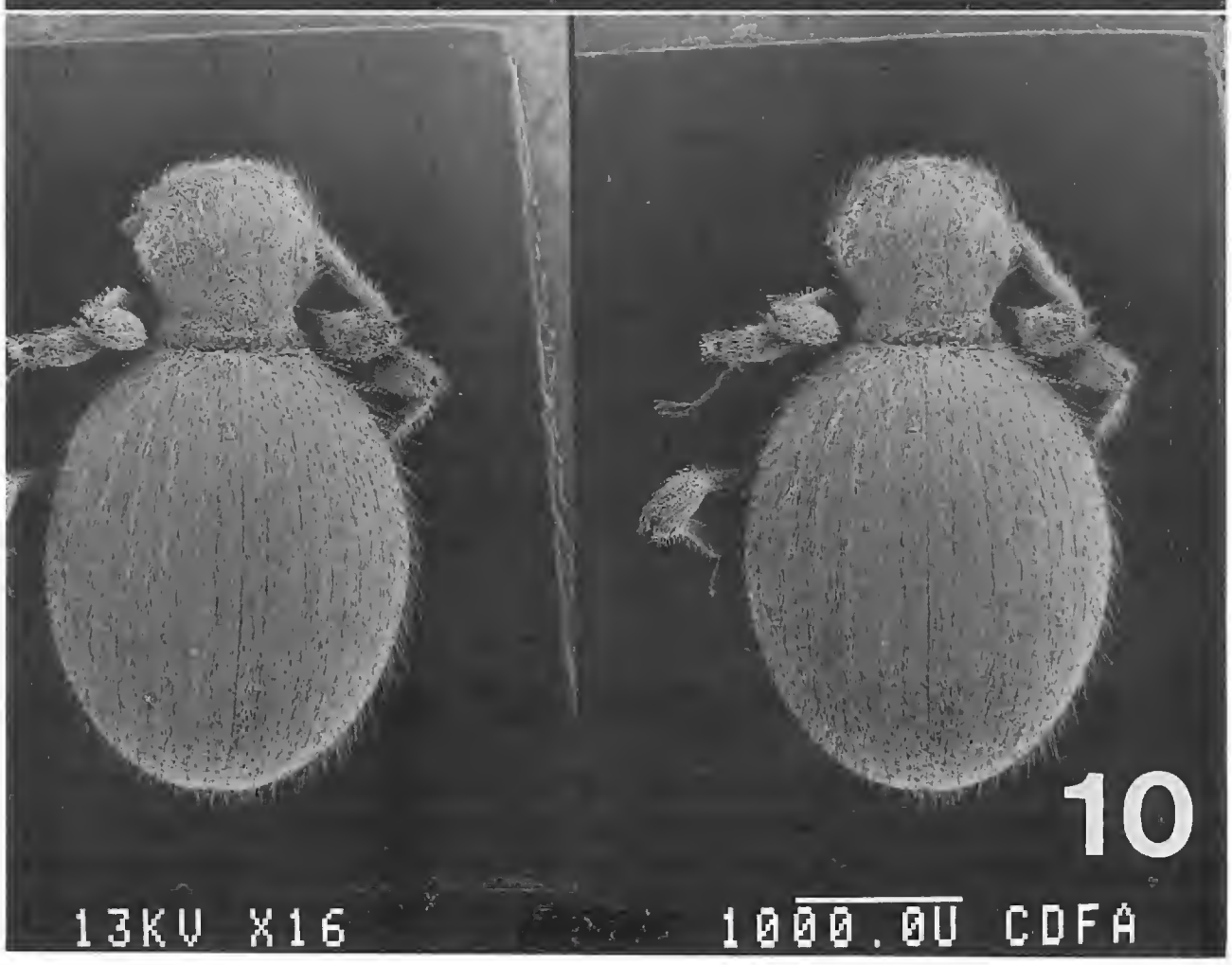
Figures 5–6. Figure 5. *Niptus ventriculus,* habitus (stereo pair). Figure 6. *Niptus abstrusus,* habitus (stereo pair).



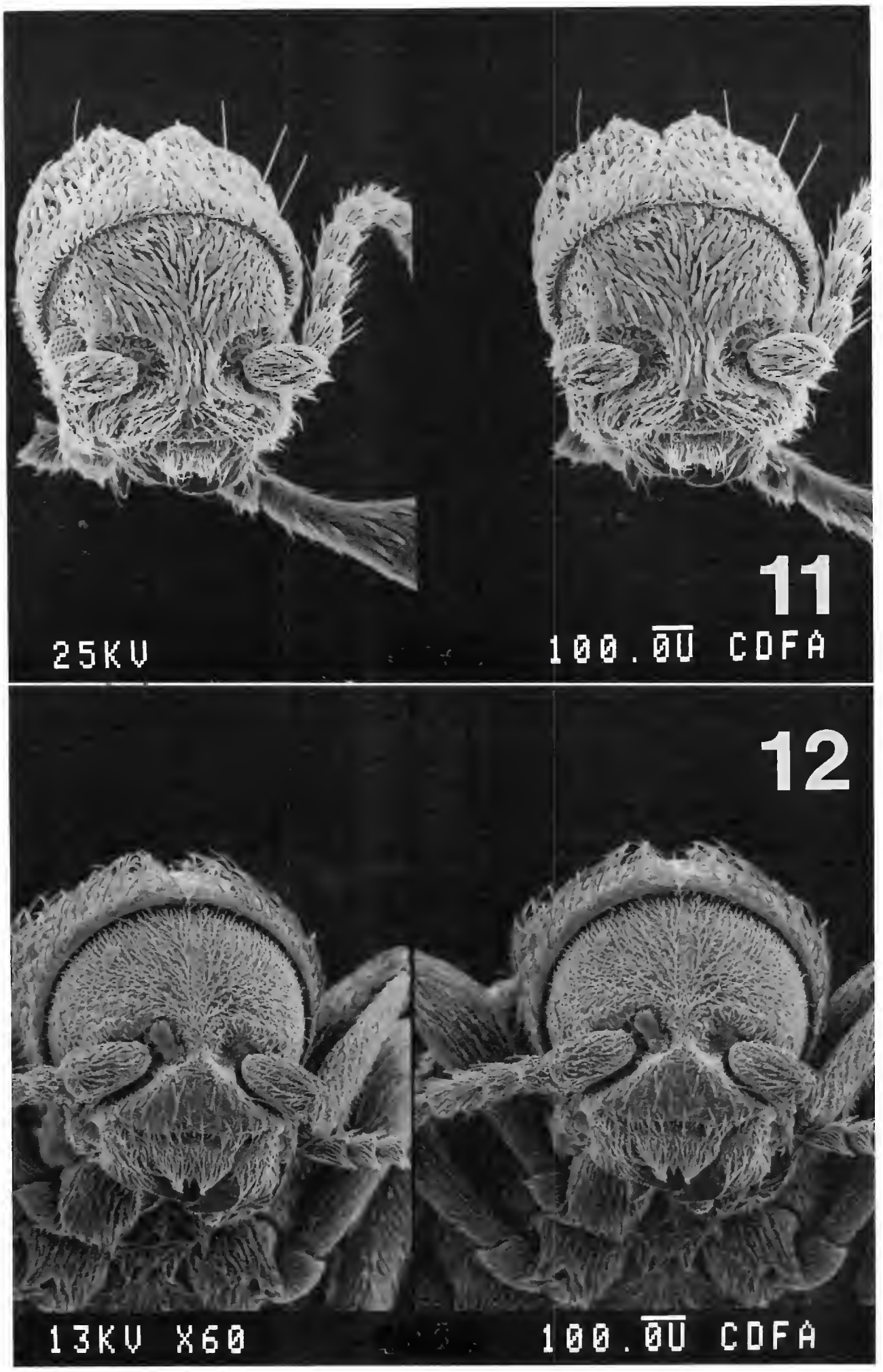


Figures 7–8. Figure 7. *Niptus absconditus,* habitus (stereo pair). Figure 8. *Niptus sleeperi,* habitus (stereo pair).

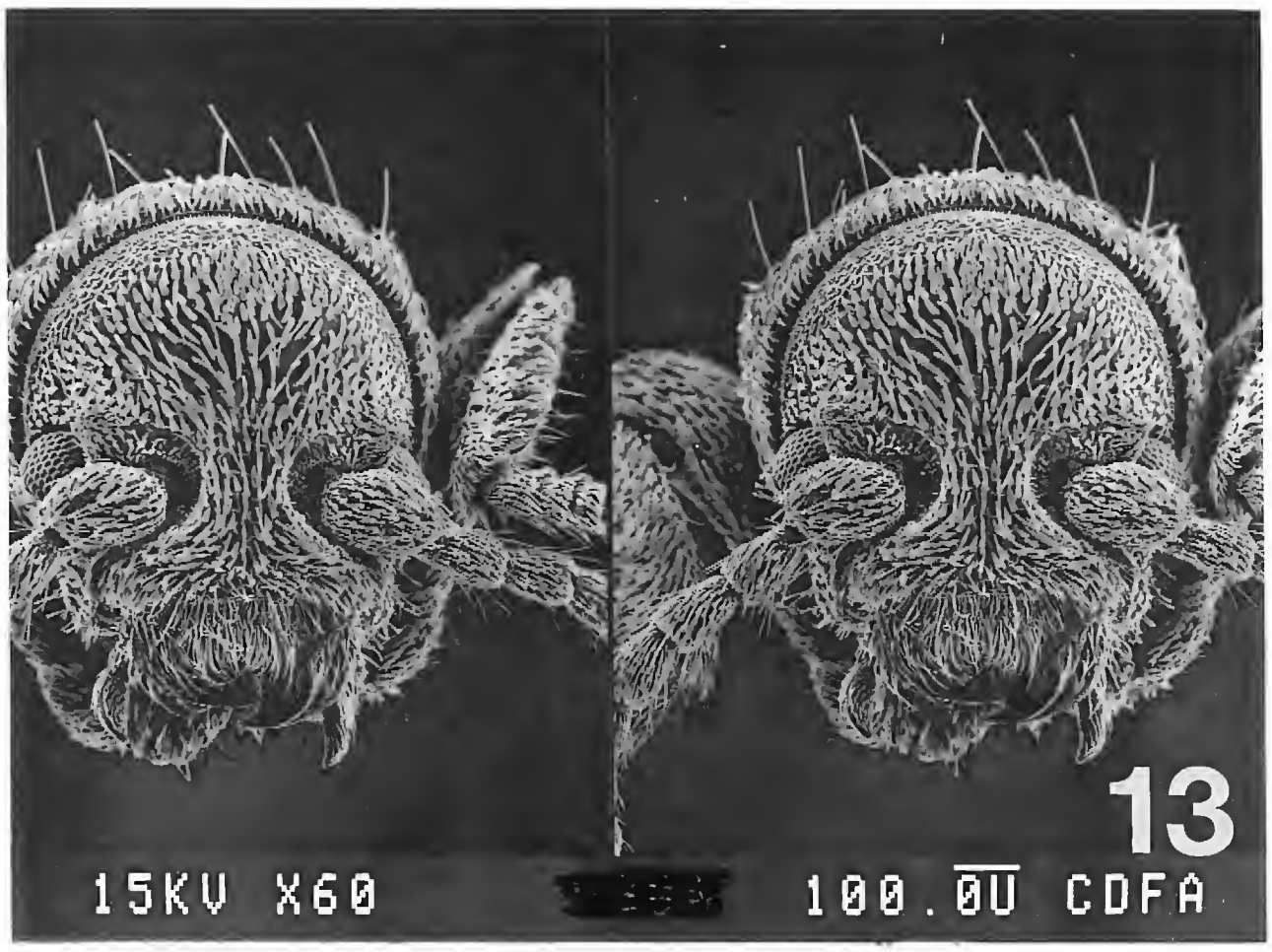




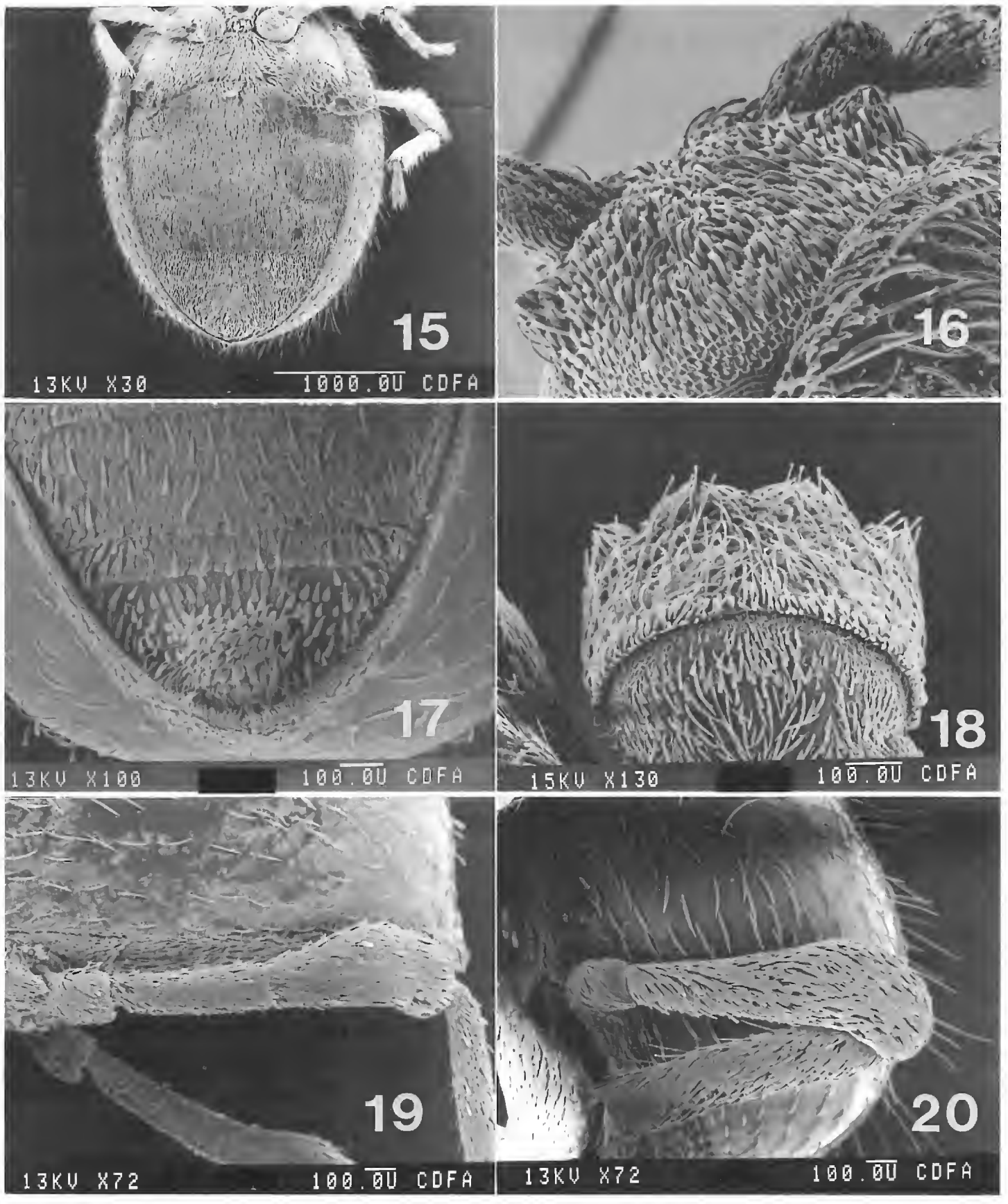
Figures 9–10. Figure 9. *Niptus hilleri,* habitus (stereo pair). Figure 10. *Niptus hololeucus,* habitus (stereo pair).



Figures 11–12. Figure 11. *Niptus giulianii,* anterior aspect of head (stereo pair). Figure 12. *Niptus hilleri,* anterior aspect of head (stereo pair).

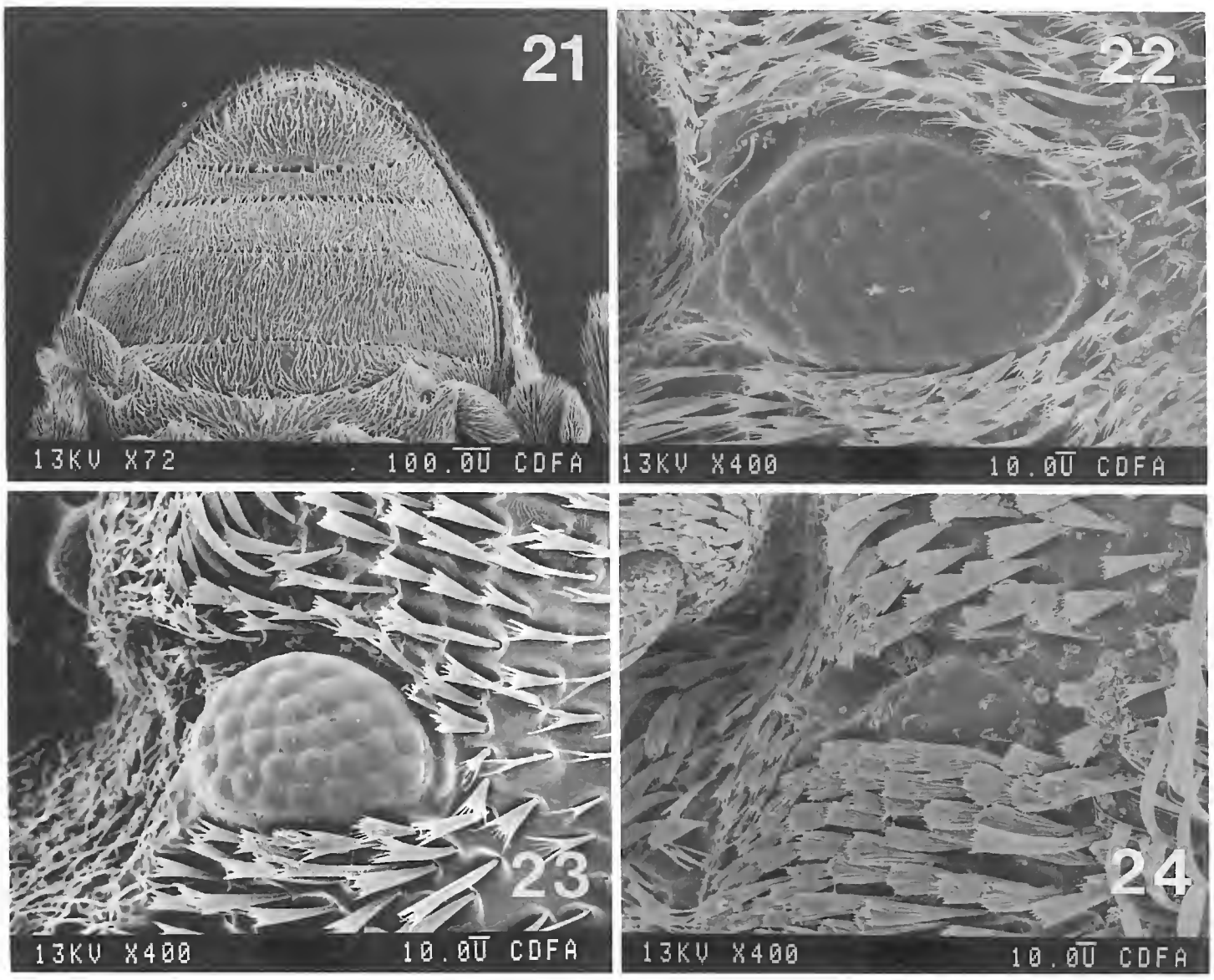


Figures 13–14. Figure 13. *Niptus ventriculus,* anterior aspect of head (stereo pair). Figure 14. Fecal pellets of *Neotoma lepida* Thomas showing feeding damage by *Niptus arcanus.*



Figures 15–20. Figure 15. *Niptus hololeucus,* sterna, ventral view. Figure 16. *Niptus ventriculus,* dorsal-apical aspect of head. Figure 17. *Niptus arcanus,* apical aspect of sterna, ventral view. Figure 18. *Niptus ventriculus,* dorsal-apical aspect of pronotum. Figure 19. *Niptus arcanus,* lateral aspect of metafemur. Figure 20. *Niptus giulianii,* lateral aspect of metafemur.

not carinate or laterally raised. Pronotum with medial and lateral transverse pronotal tufts equal in size; anterior margin of pronotum without long erect setae. Elytra with erect setae on intervals one to five short, spatulate. Legs long, with metafemur capitate, metatibia slender, slightly curved. Sexually dimorphic: female with fifth visible abdominal sternite with medial apical area bearing closely packed patch of postero-directed, semi-erect setae forming a rounded tubercle-like structure.



Figures 21–24. Figure 21. *Niptus hilleri,* sterna, ventral view. Figure 22. *Niptus ventriculus,* lateral aspect of eye. Figure 23. *Niptus absconditus,* lateral aspect of eye. Figure 24. *Niptus arcanus,* lateral aspect of eye.

Niptus arcanus is most closely related to *N. neotomae,* sharing short spatulate elytral setae. These species also lack long erect setae on pronotal margins as well as being sexually dimorphic, characters also shared by *N. abscondidus* Spilman. *Niptus neotomae* differs from *N. arcanus* in having shorter setae both on the pronotum and elytra and in the configuration of the legs. In *N. neotomae,* the legs are short and stout, the metafemora clavate; in *N. arcanus,* the legs are long and slender, the metafemora capitate. *N. arcanus* and *N. abscondidus* Spilman also share strongly reduced eyes.

Distribution.—(Fig. 25) This species is only known from the type locality, El Pakiva Cave, Mitchell Caverns, Providence Mountains, San Bernardino County, California.

Label Biological Notations.—Ethylene glycol pitfall trap near *Neotoma* nest, dry pit traps.

Biological Notes.—There are a number of caves in the Providence Mountains State Recreation Area. Mitchell Caverns, located at about 1340 m, actually refers to two separate limestone caves, believed to be Miocene in origin. Both caves are at about the same level, although one cave, El Pakiva, contains a large secondary, lower chamber at the far south end, which is approximately 18 meters lower. These caves were exploited as a tourist attraction in the 1930s. In 1970, to facilitate

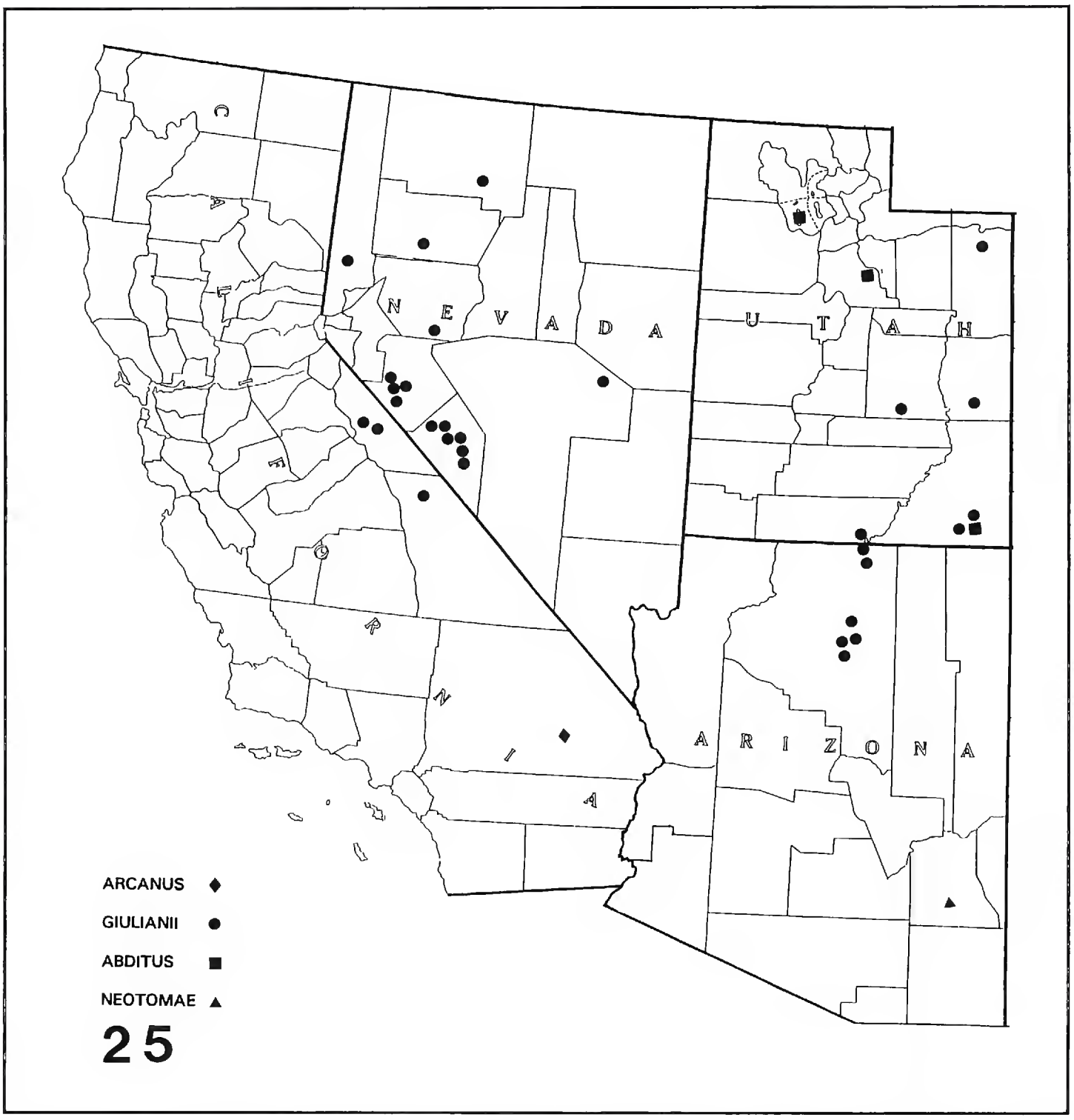


Figure 25. Distribution of *Niptus arcanus* (solid diamond), *Niptus giulianii* (solid circles), *Niptus abditus* (solid squares) and *Niptus neotomae* (solid triangle).

visitor tours, a tunnel was completed connecting the two caves. During the 1979 survey, trapping periods (intended to sample seasonal differences during an entire year) were segregated into four series, averaging approximately three months (see Aalbu 1990).

Although nine years had elapsed since the construction of the tunnel connecting the two caves during the faunal survey, some species of troglophilic Coleoptera were found to remain concentrated or even completely restricted to one cave. *Niptus arcanus* was the best example. Close to 100% (292) of the specimens were found in both the main section and the lower caverns of El Pakiva (one specimen found near an entrance) but was entirely absent from Tecopa, the other connected cave. This is also one of the few species to be found in numbers deep in the lower caverns of El Pakiva. Specimens of *Niptus* were trapped in greater numbers in the fall but were present in large numbers throughout the year. Since this survey,

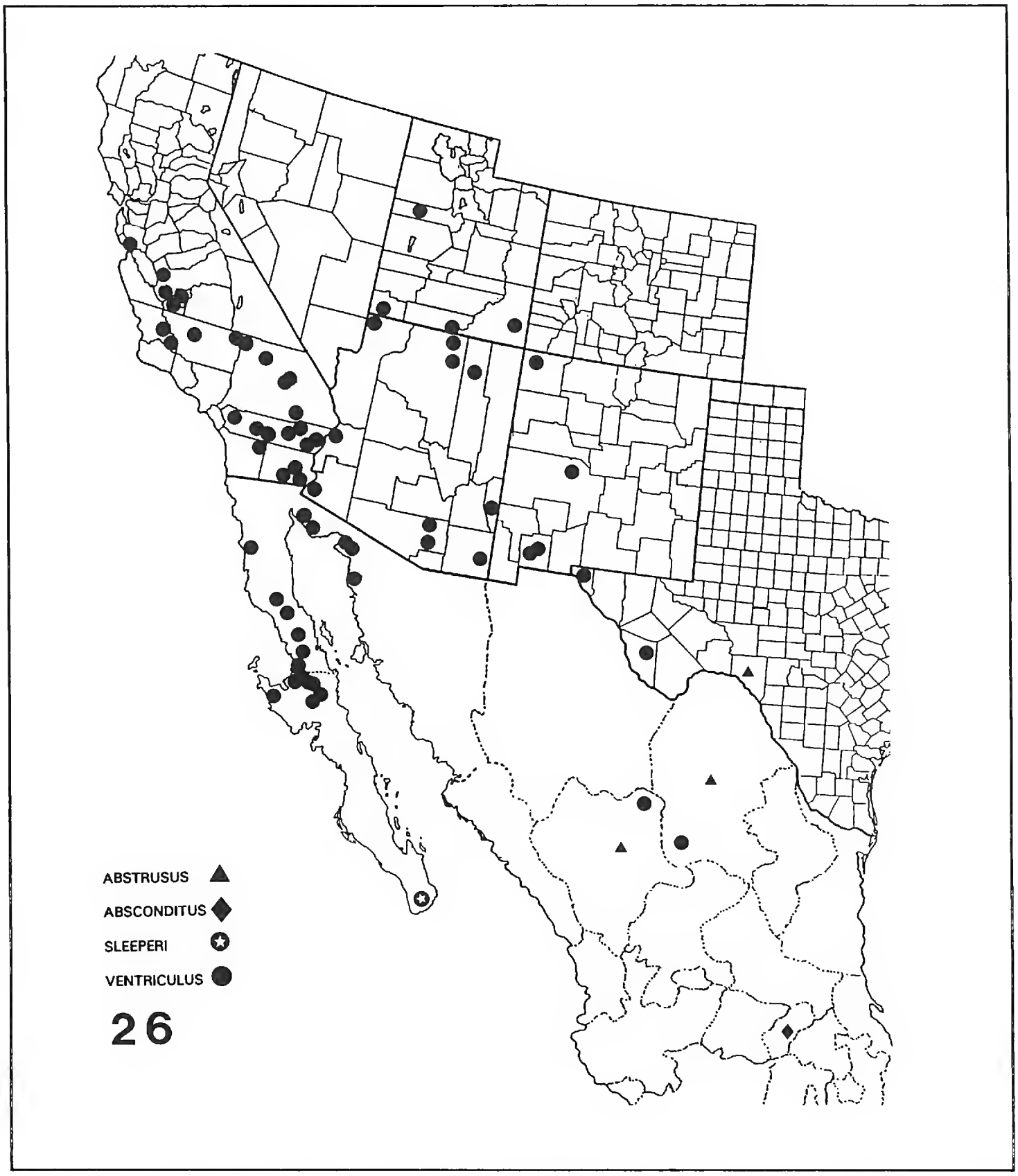


Figure 26. Known geographical distribution of *Niptus abstrusus* (solid triangles), *Niptus absconditus* (solid diamond), *Niptus sleeperi* (star in circle) and *Niptus ventriculus* (solid circles).

other caves (Medicine Cave, Cave of the Winding Stairs) and mines in the area have been surveyed or partially surveyed for insects. *N. arcanus* was not found in any of these.

Most of the food energy in Mitchell Caverns comes in with packrats (*Neotoma lepida* Thomas). The rats bring organic materials, such as twigs, cacti, grass, leaves, etc., collected outside into their nests. The packrats and other rodents, such as mice, also leave fecal pellets, which are found sometimes in great numbers in the caverns. Rodents nesting in the caverns are in most instances not found in the

deeper areas. From data gathered from an analysis of substrate composition near each trap (Aalbu 1990), *Niptus arcanus* was found most abundantly in substrate consisting of mostly fine cave dust, with few calcite and limestone pebbles and rocks, and a small amount of organic matter or in the lower caverns area of very fine, highly organic dust and conglomerate (dust-clay-rocks). *Niptus arcanus* was not abundant in packrat nesting areas. However, it appears there is an association with packrats.

A number of species of ptinids are known to breed in rat dung (Howe 1959), but no larvae were trapped or found in the cave substrate. Close examination of *Neotoma* droppings in the areas of *Niptus* abundance proved interesting. Most of these droppings, although relatively few in numbers compared with packrat nesting areas in other parts of the cave, contained numerous cavities with diameters approximately equal to *Niptus* specimens in size. No other insect in the area is known to create similar cavities. It appears that the larvae, and possibly also the adults, of this species feed on *Neotoma* pellets (Fig. 14). Unfortunately, attempts to rear live adults on the dung were unsuccessful as adults died within a short period of time.

An additional ptinid, *Ptinus feminalis* Fall, was also trapped in the caves. This species has a wide geographical range. It is known to feed on dried vegetable matter and animal substances. *P. feminalis* was found in both caves during the survey. Most were found near the entrances.

Material Examined.—313 specimens (see types), from the type locality distributed as follows: 292 trapped during cave survey (see Aalbu 1990: table 6); 12 from substrate samples and nine collected alive in pitfall traps 6 Jun–20 Jun 1988.

Niptus giulianii Aalbu & Andrews, NEW SPECIES
(Figs. 3, 11, 20 and 25)

Types.—HOLOTYPE (female): ARIZONA. *COCONINO Co.:* 6.3 km SE of Moenkopi, sand dunes/ dry canyon, 31 Jul–1 Aug 1983, Rolf L. Aalbu coll., dry overnight "punch cup" pitfall trap. ALLOTYPE (male): UTAH. *UINTAH Co.:* 16.1 km SSW of Vernal, 28–29 Jul 1983, Rolf L. Aalbu coll., dry overnight "punch cup" pitfall trap. Holotype and allotype deposited in the collection of the California Academy of Sciences. PARATYPES: ARIZONA. *COCONINO Co.:* 3.2 km S of Moenkopi, 3 Jul 1972, F. Andrews & E. A. Kane [CDFA] (49); 1.6 km E of Moenkopi, 31 Jul 1983 to 1 Aug 1983, R. L. Aalbu pitfall near *Neotoma* nest, [RLAC] (9); 6.3 km SE of Moenkopi, sand dunes/dry canyon, 31 Jul 1983 to 1 Aug 1983, R. L. Aalbu, pit traps [RLAC] (161); 3.9 km S of Moenkopi, Moenkopi Dunes, 17 Jul 1975, F. Andrews & A. Hardy, cereal bowl trap [CDFA] (11); Moenkopi sand dunes, Mar 1983 to Sep 1983, D. Giuliani, antifreeze pit trap [CDFA] (21); Waheap, 4.8 km NW of Lake Powell, 1 to 2 Aug 1983, R. L. Aalbu [RLAC] (10); 19.3 km ENE of Tuba City, 31 Jul 1983 to 1 Aug 1983, R. L. Aalbu, sand dunes/dry canyon, [RLAC] (25). CALIFORNIA. *INYO Co.:* Deep Springs Valley Sand Dunes, 17 July 1975, [CDFA] (1); 17 Jun 1978 to 28 Sep 1978, [CDFA] (1); 28 Sep 1979 to 15 Dec 1979, [CDFA] (1); 13 May 1980 to 29 Sep 1980; Deep Springs Valley Sand Dunes, (5000 ft), D. Giuliani, antifreeze pit trap, [CDFA] (2). *MONO Co.:* Mono Lake, sand dunes, 17 Aug 1979 to 21 Nov 1979 [CDFA] (6); same locality, 21 Nov 1979 to 7 Jun 1980 [CDFA] (2); same locality,

7 Jun 1980 to 1 Sep 1980 [CDFA] (17), D. Giuliani, antifreeze pit trap; Mono Lake, NE end, sand dunes, 15 Jun 1979 to 17 Aug 1979, D. Giuliani, antifreeze pit trap, [CDFA] (56); Mono Lake, 1 km E of Sulfur Pond, #17, no date, J. H. Harris, ethylene glycol pit trap [CDFA] (4). *SANTA CRUZ Co.:* Watsonville, May 1936, E. L. Kellogg [CDFA] (1). NEVADA. *CHURCHILL Co.:* Sand Mountain, 19 Jul 1977, D. Giuliani, UV light [CDFA] (1); Sand Mountain dunes, 16 Sep 1974, F. Andrews & A. Hardy [CDFA] (18). *ESMERALDA Co.:* Clayton Valley Sand Dunes, 17 Sep 1974, F. Andrews & A. Hardy [CDFA] (3); Clayton Valley Sand Dunes, 11.3 km S of Silver Peak, 1280 m, 2 May 1974, T. Eichlin & A. Hardy [CDFA] (3); 9.7 km N of Oasis, 3.2 km W of Fish Lake Valley, 1376 m, 24 Feb 1982 to 24 Jun 1982, D. Giuliani, antifreeze pit trap, [CDFA] (3); Fish Lake Valley Sand Dunes, 17 Aug 1976, D. Giuliani, cereal bowl pit trap [CDFA] (1); 11.3 km N of Dyer, sand dunes, 1494 m, 24 Jun 1982 to 30 Sep 1982, D. Giuliani, antifreeze pit trap [CDFA] (2); 16.1 km SE of Dyer, sand dunes, 1494 m, 24 June 1982 to 30 Sep 1982, D. Giuliani, antifreeze pit trap [CDFA] (4); 21 km N, 12.9 km E of Dyer, Fish Lake Valley, 1433 m, Sep 1986 to Sep 1987, D. Giuliani, antifreeze pit trap [CDFA] (11); 4.8 km N of Goldfield, sand dunes, 1676 m, 28 Mar 1982 to 1 Oct 1982, [CDFA] (6); same locality, Mar 1983 to Sep 1983, [CDFA] (4); same locality, Oct 1982 to Mar 1983, D. Giuliani, antifreeze pit trap [CDFA] (1). *HUMBOLDT CO.:* 19.3 km NW of Winnemucca, 18 Jul 1977, D. Giuliani, cereal bowl trap [CDFA] (23). *MINERAL Co.:* Teels Marsh, 17 Feb 1979 to 16 Jul 1979, D. Giuliani, antifreeze pit trap, sand dune association [CDFA] (6); Teels Marsh, sand dunes, 22 May 1976 [CDFA] (25); same locality, 16 Aug 1979 to 22 Nov 1979, [CDFA] (13); 22 Sep 1979 to 30 Jan 1980, [CDFA] (7); 7 Jun 1980 to 31 Aug 1980, D. Giuliani, antifreeze pit trap, [CDFA] (11); 8 km W of Marietta, sand dunes, 1920 m, 6 Jun 1980, D. Giuliani [CDFA] (1); 12.9 km S of Mina, sand dunes, 22 May 1976, D. Giuliani [CDFA] (14); 14.5 km S of Mina, 30 Jun 1965, M. E. Irwin, sand dune association [CDFA] (2); Huntoon Valley Sand Dunes, 16 Aug 1979 to 22 Sep 1979 [CDFA] (3); same locality, 7 Jun 1980 to 31 Aug 1980 [CDFA] (4); same locality, 31 Aug 1980 to 25 May 1981 [CDFA] (1); D. Giuliani, antifreeze pit trap. *NYE Co.:* Current, 14.5 km S, 3.2 km W of Railroad Valley, 1494 m, Sep 1986 to Sep 1987, D. Giuliani, antifreeze pit trap [CDFA] (3). *PERSHING Co.:* Woolsey, 27 Jun 1972, T. R. Haig [CDFA] (1); Woolsey RR Stn., 6 June 1973, T. R. Haig, blacklight [CDFA] (1). *WASHOE Co.:* Pyramid Lake Dunes, 7 Sep 1941, LaRivers [CASC] (3). UTAH. *EMERY Co.:* 27.4 km N of Hanksville, sand dunes nr. Glison Butte Well, 26 Jul 1978, F. Andrews & A. Hardy, cereal bowl trap [CDFA] (22); 20.8 km N, 11.2 km E of Hanksville, sand dunes, Sep 1983 to Mar 1984, D. Giuliani, antifreeze pit trap [CDFA] (9). *GRAND Co.:* Arches Nat. Mon., Devils Garden Campgr., 14 Sep 1983, R. L. Aalbu [RLAC] (19). *KANE Co.:* 8 km SE of Glen Canyon City, sand dunes, 15–17 Jun 1988, R. L. Aalbu, pit traps, sand dune/rodent burrows, [RLAC] (4); Lake Powell, Lone Rock Campgr., 15/17 Jun 1988, R. L. Aalbu, pit traps, sand dune/rodent burrows, [RLAC] (44); Kanab, 16.1 km N of Kanab cyn., 18–19 Jun 1988, R. L. Aalbu, pit trap sandstone overhang *Neotoma* nest, [RLAC] (3). *SAN JUAN Co.:* Bluff Sand Dunes, 8 km W of Bluff, 24 Jul 1978, F. Andrews & A. Hardy, cereal bowl trap [CDFA] (13). *UINTAH Co.:* 16.1 km SSW of Vernal, 13 Sep 1983, R. L. Aalbu [RLAC] (14). Paratypes deposited in USNM, CASC, CISC, CASC, RLAC, OSUC.

Description.—Female (holotype). Integument red-brown, elytra shiny; length approximately 2.9 mm. HEAD with surface vestiture consisting of closely appressed, spatulate, scale-like setae with few longer fine setae on apical margin of clypeus; antennal fossae with dorsal border not carinate, not laterally elevated; eyes large, at least seven facets wide at minimum width, oval; antenna of moderate length, stout, ratio of segment lengths 11:9:8:8:8:8:8:8:8:9:15. PRONOTUM with surface sculpture consisting of rugose, deep punctures posteriorly forming moderately dense, small tubercles; surface vestiture of two types, first of sparse, long setae in a row at anterior margin; second of short, stout, arched, recumbent setae, dense, often subspatulate, forming dense ring at anterior margin; midlength transverse row of four tufts unequal in size, medial tufts prominent, lateral tufts small to nearly obsolete. ELYTRA with surface smooth, shiny, strial punctures obsolete; vestiture of two types: first of long, fine, erect setae sparsely positioned at regular intervals on first, third, fifth, seventh intervals; second of moderately long, stout, arched, recumbent setae, positioned in rows on elytral intervals, more abundant and shorter, around suture, on lateral margins. VENTRAL SURFACE: Sterna: ratio of segment lengths 15:17:15:5:19; sternal surface vestiture of short, dense golden closely appressed, spatulate setae intermixed with less dense, slightly longer, fine setae; fifth visible abdominal sternite with medial apical area with closely packed patch of short appressed, scale-like setae. LEGS stout, with femora short, clavate; tibiae short; metatibia curved proximal-posteriorly; femoral vestiture consisting of dense, golden, short, appressed, scale-like setae only slightly varying in length; tibiae with similar vestiture except protibiae with dense, longer, slender, golden setae on lower margins; mesotibiae with dense, longer, slender, golden setae on lower margins, on apical one-half of outer margins; metatibiae with few sparse, longer, golden setae on lower margins. Ratios of segment lengths: prothoracic legs, 41:40; mesothoracic legs, 46:45; metathoracic legs, 60:59; protarsi, 8:4:4:4:7; mesotarsi, 10:4:4:4:9; metatarsi, 15:7:6:6:11.

Male (allotype).—Similar to holotype but smaller, approximate length 2.6 mm. Fifth visible abdominal sternite with medial apical area with setae similar to rest of sternal area.

Diagnosis.—The following combination of characters will serve to separate *N. giulianii*: Head with eyes large and antennal fossa with dorsal border not carinate or laterally raised. Pronotum with medial transverse pronotal tufts, larger than lateral tufts; anterior margin of pronotum with long erect setae. Elytra with erect setae on intervals three and five long and slender, short on one and absent on two and four. Legs short, with metafemur clavate, metatibia stout, curved proximal-posteriorly. Sexually dimorphic: female with fifth visible abdominal sternite with medial apical area bearing closely packed patch of minute, scale-like setae.

Label Biological Notations.—Dry overnight "punch cup" pitfall trap, ethylene glycol pitfall trap near *Neotoma* nest, pit traps sand dune/rodent burrows, pit traps sandstone overhang *Neotoma* nest.

Distribution.—(Fig. 25) The peculiar east-west distribution of this species probably reflects lack of adequate collections from this middle area instead of a real distributional gap. There is, however, a curious absence of this species from the Eureka Valley sand dunes region, an area that has undergone intensive trapping; whereas, the species is present in Deep Springs Valley sand dunes, only eight miles away.

Biological Notes.—This species is often associated with rodent burrows near or on sand dunes, although it is also found off of the dunes.

Material examined.—See types.

Niptus neotomae Aalbu & Andrews, NEW SPECIES
(Figs. 2 and 25)

Types.—HOLOTYPE (female) and ALLOTYPE (male): ARIZONA. *GRAHAM Co.:* Pinaleno Mountains, Heliograph Peak, 3055 m elevation, 9 Sep 1987, G. E. Haas col. Holotype and allotype deposited in the collection of the California

Academy of Sciences. PARATYPES: 5, same data. Deposited in USNM, CDFA and RLAC.

Description.—Female (holotype). Integument red-brown, elytra shiny; length approximately 2.6 mm. HEAD with surface vestiture consisting of closely appressed, short, spatulate, scale-like setae; antennal fossae with dorsal border not carinate, not laterally elevated; eyes small, five facets at minimum width, oval in shape; antenna of moderate length, ratio of segment lengths 10:8:7:6:6:6:6:6:6:7:13. PRONOTUM with surface sculpture consisting of rugose punctures; surface vestiture of short, stout, recumbent setae; setae dense at anterior margin, at transverse row of four weakly developed tufts; tufts equal in size, positioned near midlength. ELYTRA with surface shiny, sculpture small deep regular punctures; vestiture of two types, nearly equal in length; first of short, moderately slender, erect, strongly spatulate setae positioned in rows at regular distances along first to seventh intervals; second arched, recumbent, moderately slender setae positioned in approximate rows on both elytral striae and elytral intervals; setae short, dense at elytral margins. VENTRAL SURFACE: Sterna: ratio of segment lengths 12:15:14:4:17; sternal surface vestiture consisting of short, closely appressed, spatulate, scale-like setae; fifth visible abdominal sternite with medial apical area with dense patch of apically directed, semi-erect setae. LEGS stout, femora short, clavate, metafemora slightly bent near apex; tibia stout; femoral vestiture consisting of dense, golden, short, appressed, scale-like setae only slightly varying in length; tibiae with similar vestiture except protibiae with dense, slightly longer, slender, golden setae on lower margins, mesotibiae with dense, slightly longer, slender, golden setae on lower margins, on apical one-half of outer margins; metatibiae with few sparse, slightly longer, golden setae on lower margins. Ratio of segment lengths: prothoracic legs, 32:31; mesothoracic legs, 35:33; metathoracic legs, 39:40; protarsi, 5:4:3:4:7; mesotarsi, 5:4:4:4:6; metatarsi, 8:5:4:4:7.

Male (allotype).—Similar to holotype but slightly smaller, approximate length 2.3 mm; eyes slightly smaller than female, four facets in width; fifth visible abdominal sternite with setal pattern unmodified.

Diagnosis.—The following combination of characters will serve to separate *N. neotomae*: Head with eyes small and antennal fossa with dorsal border not carinate or laterally raised. Pronotum with medial, lateral transverse pronotal tufts equal in size, only slightly developed; anterior margin of pronotum without long erect setae. Elytra with erect setae on intervals one to five short, spatulate. Legs short, stout, with metafemur clavate. Sexually dimorphic: female with fifth visible abdominal sternite with medial apical area bearing closely packed apically directed, semi-erect setae forming a rounded patch.

Niptus neotomae is most closely related to *N. arcanus,* sharing short spatulate elytral setae. These species also lack long erect setae on pronotal margins and have sexual dimorphism, characters also shared by *N. abscondidus* Spilman. *Niptus neotomae* differs from *N. arcanus* in having shorter setae both on the pronotum and elytra and in the configuration of the legs: short and stout, metafemora clavate in *N. neotomae*; long and slender, metafemora capitate in *N. arcanus.*

Distribution.—(Fig. 25) This species is only known from the type locality.

Label Biological Notations.—Nest of *Neotoma mexicana* in U.S.F.S. shed.

Biological Notes.—Haas (T. J. Spilman, personal communication) mentions finding the beetles while searching for fleas in a rather dry and dusty nest composed of shredded cloth, newspapers, wrappers, cardboard, and packing material surrounded by cones, bark, sticks and various dried green plant material on the floor of the shed between some storage boxes.

Material Examined.—See types.

Niptus abstrusus Spilman
(Figs. 6 and 26)

Niptus abstrusus Spilman, 1968: 195.

Diagnosis.—The following combination of characters will serve to separate *N. abstrusus*: Head with eyes small and antennal fossa with dorsal border carinate and laterally raised. Pronotum with medial and lateral transverse pronotal tufts equal in length; anterior margin of pronotum with long erect setae. Elytra with erect setae on intervals three and five only slightly longer than those on intervals one, two and four; legs with metafemur clavate, metatibia stout, curved. Not sexually dimorphic.

Distribution.—(Fig. 26) Southwestern Texas and north-central Mexico. Known from caves in Texas (Fern Cave [Val Verde Co.], Bat Cave [Brewster Co.) and Mexico (Pedrigosa Circle Cave, Pedrigosa Pipe Cave, and Cueva de San Vincente [Coahuila]).

Label Biological Notations.—On pineapple, on dry beans, with *Ariocarpus lloydi.*

Biological Notes.—Ashworth (1973) reports finding fragments of individuals of this species in a 12,000 year old fossil *Neotoma* nest in western Texas. Individuals have been reported on raccoon droppings (Reddell 1966) and on bat guano (Reddell 1970).

Material Examined.—Twenty-one from the following seven localities: TEXAS. *VAL VERDE Co.:* Fern Cave, 27.4 km N of Comstock (7); bat room (3). MEXICO. (2) (state unknown) *DURANGO:* Tepehuanes (8). *COAHUILA:* (1).

Niptus absconditus Spilman
(Figs. 7, 23 and 26)

Niptus absconditus Spilman, 1968: 197.

Diagnosis.—The following combination of characters will serve to separate *N. absconditus*: Head with eyes small and antennal fossa with dorsal border not carinate or laterally raised. Pronotum with medial and lateral transverse pronotal tufts equal in size; anterior margin of pronotum without long erect setae. Elytra with erect setae on intervals one to five short; legs long, with metafemur capitate, metatibia stout, almost straight. Sexually dimorphic: female with fifth visible abdominal sternite with medial apical area bearing closely packed patch of dense, short scale-like setae. *Niptus abscondidus* is most closely related to *N. arcanus.* See discussion under *N. arcanus.*

Distribution.—This species is only known from the type locality.

Label Biological Notations.—None.

Material Examined.—Four specimens (PARATYPES) from: MEXICO. HIDALGO: Grutas de Xoxafi, VIII-19-65, J. Reddell, J. Fish & W. Bell cols.

Niptus abditus Brown
(Figs. 4 and 25)

Niptus abditus Brown, 1959: 631.

Diagnosis.—The following combination of characters will serve to separate *N. abditus*: Head with eyes minute and antennal fossa with dorsal border not carinate or laterally raised. Pronotum with lateral transverse pronotal tufts more developed than medial pronotal setal tufts; anterior margin of pronotum without long erect setae. Elytra with erect setae on intervals three and five longer than those on intervals one, two and four; legs with metafemur capitate, metatibia slender,

straight. Sexually dimorphic: female with fifth visible abdominal sternite with medial apical area bearing closely packed patch of postero-directed, semi-erect setae forming a rounded tuberclelike structure.

Distribution.—This species is only known from the three localities mentioned.

Label Biological Notations.—Ex. nest of *Neotoma* sp., ethylene glycol pit trap.

Material Examined.—UTAH. *SAN JUAN Co.:* 12.9 km E of Bluff, 1402 m, September 1984 to March 1985, ethylene glycol pit trap, D. Giuliani col. (2). *TOOELE Co.:* Great Salt Lake, Stansbury Island, floor of Spider Cave, 9.1 m from the entrance, 29 Nov 1952, J. R. Keller col., PARATYPE #6916, [CNCI]. *UTAH Co.:* Rock Canyon near Provo, 15 Jun 1964, V. J. Tipton col., (8).

Niptus sleeperi Aalbu & Andrews, NEW SPECIES
(Figs. 8 and 16)

Type.—Holotype (male). MEXICO. *BAJA CALIFORNIA SUR:* 27.4 air km ENE of Todos Santos, Sierra Laguna, La Laguna, 4–7 Jun 1973, E. L. Sleeper col. Type deposited in California Academy of Sciences Collection.

Description.—Male (holotype). Integument dark red-brown, vestiture golden to yellow; length approximately 2.4 mm. HEAD with surface vestiture consisting of closely appressed, spatulate, scale-like setae with few longer fine setae on apical margin of clypeus; antennal fossae with dorsal border carinate, laterally elevated; eyes small, four facets at minimum width, narrowly oval in shape; antenna short, stout; ratio of segment lengths 10:9:7:6:6:6:6:6:7:13. PRONOTUM with surface sculpture consisting of rugose, deep punctures posteriorly forming moderately dense, small tubercles; surface vestiture of two types, first of few, sparse, moderately long, fine setae (with apical ends occasionally finely spatulate) positioned near anterior margin; second of short, stout, dense, arched, recumbent setae; setae denser, shorter, stouter at anterior margin; denser at midlength transverse row of four tufts; tufts equal in size. ELYTRA with surface sculpture of deeply impressed, large, contiguous strial punctures, equal in size, impression throughout; surface vestiture of two types: first of moderately long, fine, sparse, erect setae (equal in length to erect setae on pronotal margin) positioned at regular intervals along first to seventh elytral intervals; second of shorter, stout, arched, recumbent setae positioned throughout elytral surface, more abundant on intervals. VENTRAL SURFACE: Sterna: ratio of segment lengths 11:12:6:3:15; sternal surface vestiture of short, golden, closely appressed, fine setae; fifth visible abdominal sternite with medial apical area unmodified. LEGS short, stout, with femora clavate; tibiae short; metatibia curved proximoposteriorly; femoral vestiture consisting of dense, golden, short, appressed, scale-like setae slightly varying in length; tibiae with similar vestiture except: protibiae with dense, longer, slender, golden setae on lower margins, mesotibiae with dense, longer, slender golden setae on lower margins, on apical one-half of outer margins; metatibiae with few sparse, longer, golden setae on lower margins. Ratio of segment lengths: prothoracic legs, 28:31; mesothoracic legs, 40:33; metathoracic legs, 37:42; protarsi, 5:3:3:3:6; mesotarsi, 7:3:3:3:7; metatarsi, 9:4:4:4:7.

Female.—Unknown.

Diagnosis.—The following combination of characters will separate *N. sleeperi*: Head with eyes small and antennal fossa with dorsal border carinate, laterally raised. Pronotum with medial and lateral transverse pronotal tufts equally developed; anterior margin of pronotum with long erect setae. Elytra with deeply impressed, large, contiguous strial punctures, equal in size and impression throughout; erect setae on intervals one to five short. Legs with metafemur clavate, stout, metatibia stout, curved. Sexual dimorphism unknown.

Distribution.—(Fig. 26) This species is only known from the type locality.

Label Biological Notations.—Berlesed from oak duff.

Material Examined.—Holotype; only it is known.

Niptus ventriculus LeConte
(Figs. 5, 13, 16, 18, 22, and 26)

Niptus ventriculus LeConte, 1859: 13.

Diagnosis.—The following combination of characters will separate *N. ventriculus*: Head with eyes large and antennal fossa with dorsal border carinate, laterally raised. Pronotum with medial and lateral transverse pronotal tufts equally developed; anterior margin of pronotum with long erect setae. Elytra with erect setae on intervals three and five long; short on intervals one, two and four. Legs with metafemur clavate, metatibia broad, curved. Not sexually dimorphic.

Elytral strial setal length and punctures vary greatly in populations from subequal setal length and completely smooth punctures, except for the ninth interval in specimens from Coahuila, to slight variation in strial setal length and few rows of punctures in specimens from Glamis, California, to strongly punctate with long setae in specimens from near Bakersfield, California.

Label Biological Notations.—UV light; rodent nest; ex mouse nest *Peromyscus eremicus*; kangaroo rats: in burrows of, excavating and sifting burrow of; sifting beach dunes under ambrosia; base of Palo Verde; at night: walking dunes, pitfall; pitfalls: cereal bowl trap, under *Larrea* and *Petelonyx thurberi,* ethylene glycol trap, antifreeze trap on sand dune with creosote and sand verbenas, rye bread trap, dry overnight "punch cup" trap, interdune traps. Spilman (1968) mentions records from nests of *Neotoma,* and the kangaroo rats *Dipdomys deserti* Stephens and *Dipdomys spectabilis* Merriam, pitfall traps in sand dunes, under seaweed and rocks at high tide line, sifting sand on dunes, pit traps sand dune/rodent burrows, antifreeze pit trap on sand dune.

Distribution.—(Fig. 26) Widespread throughout southwest U.S. and Mexico.

Material Examined.—(945 from the following 103 localities). ARIZONA (76 specimens/12 localities). no locality (3). *COCHISE Co.:* 6.4 km E of Portal (1); A.M.S.W.R.S. (7). *COCONINO Co.:* Moenkopi, Moenkopi sand dunes (12); 6.3 km SE of Moenkopi, sand dunes/dry canyon (11); 3.2 km S of Moenkopi (3); 16.1 km S and 8 km W of Page (29). *GREENLEE Co.:* Guthrie (3). *LA PAZ Co.:* 4.8 km SE of Parker (1). *MOHAVE Co.:* Littlefield, 580 m (7). *NAVAJO Co.:* (1). *PIMA Co.:* Santa Rita Mts. (5). *YUMA Co.:* Yuma (4); CALIFORNIA (302 specimens/50 localities). *FRESNO Co.:* Monocline Ridge Sand Dunes (1); 12.9 km NNW of Coalinga, Los Gatos Cyn. (2); 29 km SW of Mendota, Cievo Hills (5). *IMPERIAL Co.:* Holtville (1); 12.9 km ESE of Holtville, East Mesa Geothermal Site (11); Seely (17); Glamis (31); 1.6 km S of Glamis (6); 4.8 km NW of Glamis (1); 22.5 km NW of Glamis (5); 1.6 km N of Glamis (25); 3.2 km N of Glamis (1); 3.2 km NW of Glamis (13); 5.6 km WNW of Glamis (2); 5.6 km NW of Glamis (9); 11.3 km SE of Glamis, Algodones Dunes, 32°55′20″ N, 114°59′14″ W, Site 4 (12); 6.5 km W of Ogilby, 32°48′48″ N, 104°53′51″ W (1); 6.4 km SSW of Ogilby, 32°45′33″ N, 104°51′32″ W, Site 7 (3); Algodones Dunes, 4 km NE of Coachella Bridge No. 1, 32°51′41″ N, 115°4′6″ W, Site 24, (1); Algodones Dunes, 20 km ESE of Holtville, 32°44′34″ N, 115°11′53″ W, Site 30, (1). *INYO Co.:* Chicago Valley Sand Dunes (2). *KERN Co.:* 12.9 km N and 4.8 km W of Ridgecrest (1); 1.6 km E of Bakersfield Hart Peak (1). *KINGS Co.:* no locality (2); 7.7 km W of Kettleman City, 7.7 km W (8) of, and 3.2 km S of Leemoore. *RIVERSIDE Co.:* Hopkins Well (2); Palm Springs (1); Rice Dunes (13); Palen Dunes (16); 11.3 km SE of Freda (2); 4.8 km W of Blythe (7); 1.6 km W of Blythe (10); Indio (1); 8 km E of Indio (2); La Quinta (1); Mule Mts. (3); 3.2 km NW of Gilman Hot Springs, Lamb Canyon (9). *SAN BERNARDINO Co.:* Cadiz Dunes (33); Kelso Dunes (4); 28.2 km SE of Baker; Cronese Valley (2); 14.5 air km S of sand dunes S of Zzyzx (3); 14.5 km N and 16.1 km E of Ridgecrest (3); 16.1 km N and 16.1 km E of Ridgecrest (1); 9.7 km N and 3.2 km W of Ridgecrest (1); 30.6 km N of Ridgecrest, Baby Mt. (7); Amargosa River at st. hwy. 127 (1). *SAN DIEGO Co.:* Borrego (1). *SAN LUIS OBISPO Co.:* 12.1 km W of Simmler (18); 24.9 km NW of Reyes Station (1). *SANTA CRUZ Co.:* (1); Watsonville (1). NEW

MEXICO. (32 specimens/5 localities). Hot Springs (4). *LUNA Co.:* Deming (2); E of Deming at base of Red Mt. on Humocky Rd. (14). *SAN JUAN Co.:* Ship Rock (11). *SOCORRO Co.:* Sevilletta Sand Dunes (1). TEXAS. (4 specimens/2 localities). *EL PASO Co.:* El Paso (3). *PRESIDIO Co.:* Marfa (1). UTAH (55 specimens/5 localities). *JUAB Co.:* Fish Springs Range, 40.2 km SE of Callao, Sand Pass (4). *KANE Co.:* 8 km SE of Glen Canyon City, sand dunes (3); Lake Powell, Lone Rock Campgr. (27). *SAN JUAN Co.:* 3.2 km S and 32.2 km W of Bluff (10). *WASHINGTON Co.:* 17.9 km N of St. George, red sand dunes (1). MEXICO. *BAJA CALIFORNIA* (327 specimens/13 localities): Miller's Landing (84); 16.1 km S of Punta Prieta (2); 12. 4 km NW of Catavina (2); El Crusero (22); 41.4 km SE of Laguna Chapala (15); 19.3 km NW of San Bartolo (1); 9.7 km N of Guerrero Negro (154); 5 km N of Guerrero Negro (8); 11.3 km N of Guerrero Negro (6); 25.7 km E of Rosarito, Rancho San Ignacito (22); 10 km NE of Rosarito (9); 5.0 km SW of Colonet (1); Bahia San Quintin, Santa Maria Beach (1). *BAJA CALIFORNIA SUR* (96 specimens/8 localities): 22.5 km E of Guerrero Negro (1); 55.4 km SE of Guerrero Negro (4); 13.7 km ESE and 8.6 km S of Guerrero Negro (2); 11.3 km SE of Guerrero Negro (27); 20.9 km SW of Guillermo Prieto (43); 19.3 km S of Guillermo Prieto (10); 20.9 km S of Rancho Tablon (8); Tortugus (1). *COAHUILA* (42 specimens/1 locality): 12.9 km N of Viesca, sand dunes at Bilbao (42). *DURANGO* (26 specimens/1 locality): 43.5 km S of Ceballos (26). *SONORA* (12 specimens/7 localities): Puerto Penasco, 0.5 km from coast (1); Desemboque (1); El Golfo (4); 80. 5 km SW of Sonoyta (1); 16.1 km N of C. Sotelo nr. Bahia Adair (1); San Carlos Bay (1); 9.7 km W of San Carlos Bay, Los Algodones (3).

Phylogenetic Considerations

Pseudorostus and *Eurostus* have historically either been separated from *Niptus* (Brown 1940: 119, 1944: 19, 1959: 627; Hinton 1941: 343; Spilman 1968: 193) or included as synonyms of *Niptus* (Papp 1959: 258, 1962: 385; Spilman [North American Beetle Fauna Project] 1975: R62-1). Of these, *Eurostus* has generally been accepted as being congeneric with *Pseudeurostus. Pseudeurostus* has been separated from *Niptus* based on the carinate frons between the antennal fossae in *Pseudeurostus* (Fig. 12), which is not narrowly flat as in *Niptus* (Fig. 11). Clearly, this character is unique and synapomorphic in species of *Pseudeurostus.* However, *P. hilleri* and *P. kelleri* and all species of *Niptus* except *N. hololeucus* (Fig. 15) share a strongly reduced fourth visible abdominal sternite (Figs. 17, 21), another clearly synapomorphic character. Thus, if *Pseudeurostus* is to be generically separated from *Niptus,* then *N. hololeucus,* the type species of *Niptus,* needs also to be separated from both groups, making it necessary for a new generic name for the eight "wild" species of *Niptus.* It is clearly preferable to lump all these under the genus *Niptus* as indicated by Spilman (1975: R62-1).

Key to North American Species of *Niptus*

1. Body large (usually above 3.8 mm in length), golden throughout, color result of scale-like setae that completely conceal integument of entire insect; fourth visible abdominal sternite only slightly shorter than third (Fig. 15); pronotum lacking distinct tufts of setae (Fig. 10) .. .. *hololeucus*

1′. Body smaller (usually under 3.4 mm in length), red-brown above, elytra not completely covered with scale-like setae; fourth visible abdominal sternite less than one-half length of third 2

2(1′). Frons carinate between antennal fossae (Fig. 12); pronotum lacking distinct transverse row of four tufts of setae (*Pseudeurostus* group) 3

2′. Frons narrow but flat between antennal fossae (Figs. 11, 13); pronotum with distinct transverse row of four tufts of setae (Fig. 18) 4

3(2). Elytral intervals with closely placed, recumbent setae as well as single row of semi-erect setae ..... *kelleri*

3′. Elytral intervals with single row of semi-erect setae, lacking closely placed, recumbent setae (Fig. 12) ..... *hilleri*

4(2′). Antennal fossa with dorsal border distinctly carinate and laterally strongly elevated (Figs. 13, 16) 5

4′. Antennal fossa with dorsal border not distinctly carinate and laterally not strongly elevated (Fig. 11). 7

5(4). Elytra with strial punctures deeply impressed, large, contiguous, equal in size and impression throughout; erect setae on intervals one to five short; legs with metafemur clavate, very stout; eyes small (Fig. 8) ..... *sleeperi*

5′. Elytra with strial punctures unevenly impressed, always fine to minute at apex and lateral margins; erect setae on intervals three and five long to moderately long; legs with metafemur clavate; eyes variable 6

6(5′). Elytra with erect setae on intervals three and five long; short on intervals one, two and four; strial punctures often large and deeply impressed on disc; eyes large (Figs. 5, 22) ..... *ventriculus*

6′. Elytra with erect setae on intervals three and five only slightly longer than those on intervals one, two and four, strial fine to minute; eyes smaller (Fig. 6) ..... *abstrusus*

7(4′). Elytra with length of erect setae on intervals three and five greater than width of one interval; pronotal tufts not equal in size; eyes variable 8

7′. Elytra with length of erect setae on intervals three and five less than width of one interval; pronotal tufts equal in size; eyes very small 9

8(7). Pronotum with medial transverse pronotal setal tufts more developed than lateral pronotal setal tufts; anterior margin of pronotum with long erect setae; elytra with erect setae absent on intervals on two and four; legs with metafemur clavate, metatibia stout, strongly curved; eyes large; sternites sexually dimorphic (Fig. 3) ..... *giulianii*

8′. Pronotum with lateral transverse tufts more developed than medial pronotal setal tufts; anterior margin of pronotum lacking long erect setae; elytra with erect setae short but present on two and four; legs with metafemur capitate, metatibia slender, straight; eyes small; sternites not sexually dimorphic (Fig. 4) ..... *abditus*

9(7′). Erect setae on elytra spatulate at tip (Figs. 1, 2); width of metatibiae variable 10

9′. Erect setae on elytra unmodified, pointed at tip; width of metatibiae at apex equal to widths of eighth and ninth intervals combined (Fig. 7) ..... *absconditus*

10(9). Erect spatulate setae on elytra very short; legs short, stout, metafemora clavate (as in Fig. 20), width of metatibia at apex equal to widths of eighth and ninth intervals combined (Fig. 2) ..... *neotomae*

10′. Erect spatulate setae on elytra short (Fig. 1); legs long, slender, metafemora capitate (Fig. 19), width of metatibia at apex subequal to widths of eighth and ninth intervals combined ..... *arcanus*

Biology

North American species of *Niptus* not associated with stored products seem to be distributed in two seemingly different habitats: caves and sand dune areas. These two habitats do share one important aspect of the microhabitat in which *Niptus* species are found. This is a fine to very fine substrate (in the form of fine sand or cave dust) with a varying amount of organic debris due to rodent activity. All species seem to be associated with various desert rodents especially species of packrats (*Neotoma*), but also mice (*Peromyscus*), and kangaroo rats (*Dipdomys*).

Niptus arcanus, N. abstrusus, N. absconditus, and *N. kelleri* are found in caves. These reveal to varying degrees, morphological characteristics typically associated with cave coleoptera (see Aalbu 1990). Of these *N. arcanus, N. Kelleri* and *N. absconditus* are restricted to single cave habitats. *Niptus arcanus* is considered to be a true troglobite (Aalbu 1990) a relative rarity in Northwestern American beetles. It is possible that upon further study, other species will also be classified as troglobites rather than troglophiles. We can only stress the importance of conserving these unique cave habitats, especially in caves where considerable environmental impact is present due to high visitor traffic (such as in Mitchell Caverns). This would entail assuring species survival by providing for long term microhabitat protection in terms of the least amount of habitat disturbance possible.

Acknowledgment

The following individuals and institutions are gratefully acknowledged for loan of their material: David Kavanaugh, California Academy of Sciences, San Francisco, California; John T. Doyen, University of California, Berkeley, California; Ives Bousket, Canadian National Collection, Ottawa, Ontario, Canada; E. L. Sleeper, California State University, Long Beach, California; Al Newton, Field Museum of Natural History, Chicago, Illinois; Kirby W. Brown, Stockton, California; Scott Shaw, Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts; Charles A. Triplehorn, The Ohio State University, Columbus, Ohio; Dave Faulkner, San Diego Museum of Natural History, San Diego, California; Ted J. Spilman, United States National Museum, Washington D.C.; Carl A. Olson, University of Arizona, Tucson, Arizona. The following individuals deserve special mention: Ives Bousket of The Canadian National Collection for loan of paratype of *N. abditus*; Phillips L. Claud, Jim Hart, Bill Wisehart and John Kelso-Shelton of the California Department of Parks and Recreation, for granting collection permits and aiding in collections of *N. arcanus.*

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Received 1 May 1990; accepted 15 July 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 97–99, (1992)

THE SOLITARY BEE *MELISSODES THELYPODII THELYPODII* COCKERELL (HYMENOPTERA: ANTHOPHORIDAE) COLLECTS POLLEN FROM WIND-POLLINATED *AMARANTHUS PALMERI* WATSON

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Abstract.—The native solitary bee *Melissodes thelypodii thelypodii* Cockerell was observed to harvest pollen from panicles of the anemophilous plant *Amaranthus palmeri* Watson in southeastern Arizona. Pure *Amaranthus* pollen loads were removed by females foraging at this plant, suggesting floral fidelity and this bee's potential value for commercial pollination of the related grain amaranths.

Key Words.—Insecta, pollination, anemophily, *Melissodes, Amaranthus,* pollen-foraging, bees

Foragers of social bees will sometimes collect pollen from flowering plants that rely upon wind to transport pollen to receptive pistils (Faegri & van der Pijl 1978). Honey bees (*Apis mellifera* L.) and sometimes stingless bees (*Trigona* s.l.) collect pollen from diverse anemophilous (wind-pollinated) plants (Sharma 1970; O'Neal & Waller 1984; C. D. Michener, unpublished data). Less commonly, bumble bees (*Bombus* sp.) may collect pollen from anemophilous plants, such as bahia grass, *Paspalum notatum* var. *saurae* Parodi (JHC, unpublished data).

In contrast, nonsocial or solitary bees have rarely been reported to gather pollen from anemophilous plants. The pollen of oaks (*Quercus*), which are considered anemophilous, may be gathered by solitary bees when their preferred pollen hosts are not available (*Andrena erythronii* Robertson [Michener & Rettenmeyer 1956]; *Osmia rufa* [Raw 1974]; *Habropoda laboriosa* (Fabr.) [Cane & Payne 1988]). Several British *Andrena* reportedly collect pollen periodically from several anemophilous trees, such as oak and chestnut (Chambers 1945). Nomiine bees of the Old World genus *Rhopalomelissa* collect and may depend on grass pollen for larval provisions (C. D. Michener, unpublished data). The sweat bee *Dialictus illinoiensis* (Robertson) avidly harvests pollen from dallis grass, *Paspalum dilatatum* Poiret, augmenting the seed set of this grass (Adams et al. 1981).

Careless-weed (*Amaranthus palmeri* Watson) is a weedy, dioecious amaranth occurring through much of the central and western United States and Mexico (Munz 1959). The species exhibits several characteristics that typify anemophilous plants. It produces copious pollen that bears little of the oily pollenkitt typical of pollen usually collected by bees. Its small (24–26 μm diam) periporate "chenoam" (Chenopodiaceae–Amaranthaceae) type pollen grains are commonly implicated in human hayfever allergies (Wodehouse 1971). Bees have not been reported to visit this anemophilous plant.

We observed female *Melissodes thelypodii thelypodii* Cockerell working the spike-like panicles of male plants of *A. palmeri* for pollen during mornings of August, 1990, along the edge of a cotton field in the San Simon Valley of southeastern Arizona (Cochise Co.). In this vicinity, we previously noted this bee species sonicating flowers of *Solanum elaeagnifolium* Cavanilles and *S. rostratum* Dunal (Solanaceae) for pollen. Bees of other species that worked nearby *Solanum* flowers were never seen at *Amaranthus* (*Protoxaea gloriosa* (Fox), *Protandrena mexicanorum* (Cockerell), *Bombus sonorus* Say, and *Caupolicana yarrowi* (Cresson)).

The first female *M. thelypodii thelypodii* to visit a given inflorescence frequently released a visible cloud of pollen upon alighting. Females walked along the spikes gathering pollen, proceeding distally from mid-base along those spikes that were upright. They would then fly to a neighboring spike to continue collecting pollen. Some females accumulated a full load of *Amaranthus* pollen from five to seven spikes in as few as six minutes. A microscopic survey of the taxonomic constitution of their pollen loads revealed good floral fidelity. Pure loads of *Amaranthus* pollen were carried by five of six females collected at *Amaranthus*. The remaining female bore 11% cotton pollen and 89% *Amaranthus* pollen. We have found only one other reference to species of *Melissodes* gathering pollen from anemophilous plants. Adams et al. (1981) reported *M. bimaculata* (Lepeletier) to occasionally collect pollen from dallis grass.

The role, if any, of bees in the pollination of dioecious anemophilous plants has been debated in the pollination literature. Usually, solitary or social bees that harvest anemophilous pollen are considered mere pollen thieves, removing pollen from male plants but never subsequently visiting the nectarless female plants. Their contribution to pollination can not be discounted, however. Foragers may mistakenly visit female flowers upon occasion. Even if they only visit male flowers, wing and leg movements during pollen collection may dislodge prodigious quantities of pollen which, once airborne, can travel to female flowers.

The relative contributions of wind and insects, specifically bees, to the pollination of wild and cultivated amaranths also remains equivocal. Several weedy species have been implicated in human respiratory allergies, including *A. palmeri* (Wodehouse 1971). Unlike many anemophilous pollens, such as conifer pollen, the pollen of *A. palmeri* seems to be moderately nutritious for bees, containing 3.5% nitrogen, or 18.38% crude protein by micro-Kjeldahl analysis (SLB, unpublished data). Bee activity varies greatly at amaranths. Kaufman (1979) reported an absence of bees at cultivated grain amaranth. In contrast, Singh (1961) sometimes observed abundant bees at grain amaranth in India, and O'Neal & Waller (1984) found *Amaranthus* pollen to constitute 6% of the average annual pollen intake of honey bee colonies in the Sonoran desert, near Tucson, Arizona. Using pollen traps on honey bee colonies, one of us (SLB) found that cheno-am pollen constituted from 2–8% of the annual colony pollen harvest near Tucson during the years 1981–1989. The solitary bee *Hylaeus bisinuatus* Forster has been recorded visiting members of the Amaranthaceae (Krombein et al. 1979). We conclude that amaranth pollen is not a mere scopal contaminant in these cases. Bees will actively collect amaranth pollen, perhaps reflecting the ease with which quantities of this pollen can be harvested relative to other competing floral species.

For *Amaranthus retroflexus* L., Murphy (1978) demonstrated that insects alone could provide cross-pollination. Further, Hauptli & Jain (1985) found wide dis-

parities in outcrossing rates for their field experiments with cultivated *Amaranthus cruentus*. They attributed this result to variable densities of pollen-foraging honey bees in their plots.

Our observations demonstrate that females of the solitary bee *M. t. thelypodii* avidly visit staminate flowers of amaranth for pollen, exhibiting good species fidelity on a given foraging trip. For at least hermaphroditic species of commercial amaranth, the visitations of pollen-foraging bees have promise to improve outcrossing rates for the enhancement of genetic variation and perhaps even seed set of desirable cultivars.

Acknowledgment

Voucher bees are deposited with the Illinois Natural History Survey. This article is contribution number 17-912991P of the Alabama Agricultural Experiment Station, which partly supported this research (H-803).

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Received 17 May 1991; accepted 13 August 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 100–104, (1992)

SPHERICAL HYPHAL BODIES OF *PANDORA NEOAPHIDIS* (REMAUDIÈRE & HENNEBERT) HUMBER (ZYGOMYCETES: ENTOMOPHTHORALES) ON *ACYRTHOSIPHON PISUM* (HARRIS) (HOMOPTERA: APHIDIDAE): A POTENTIAL OVERWINTERING FORM

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Abstract.—Cadavers of the pea aphid, *Acyrthosiphon pisum* (Harris), occurred abundantly on commercial alfalfa in Kennewick, Washington, during late autumn of 1990. An aphid-specific fungal pathogen, *Pandora neoaphidis* (Remaudière & Hennebert) Humber, was responsible for the death. Numerous hyphal bodies of the fungus inside the cadavers were spherical and averaged 11.5 (9.3–15.0) μm in diameter (n = 100). Such spherical hyphal bodies apparently developed from regular hyphal bodies forming septa, which has never been recorded for *P. neoaphidis*. Over 300 cadavers collected in the field on 15 Oct were randomly sorted into three batches and then maintained under different environmental conditions for studying the overwintering potential of the fungus. Cadavers maintained in a dark refrigerator at approximately 4° C or placed within nylon-chiffon mesh bags (ca. 5 × 5 mm) and secured to the branches of shrubs (approximately 0.5 m above the ground in Bozeman, Montana) were capable of producing conidia and infecting aphids in monthly observations from November to April with consistently visible snow cover. In contrast, cadavers placed in polypropylene microcentrifuge tubes (38 × 13 mm), corked with sterile cotton and then buried in the field soil (approximately 6 cm deep), were found to have exhausted all their sporulation potential and infective capability in the first observation of late November. The results indicate that *P. neoaphidis* may survive winter months in the form of hyphal bodies on plant substrates above the ground rather than in the soil.

Key Words.—Insecta, *Acyrthosiphon pisum,* Entomophthorales, *Pandora neoaphidis,* aphid-specific fungal pathogen, overwintering

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A mycosis of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), was observed in a commercial alfalfa field in Kennewick, Washington, during late September through mid-October, 1990. Alfalfa stems were heavily infested with aphids (100% of the plants infested and more than 100 aphids per alfalfa stem). Aphid cadavers, resulting from fungal infection, were observed in abundance. Approximately 10% of the axillary shoots on alfalfa stems contained at least one cadaver, and some of the shoots contained 10 or more.

Aphid cadavers collected on 27 Sep, 1 Oct and 9 Oct (the last date coinciding with alfalfa harvest) were shipped via overnight mail to MGF in Bozeman, Montana, for identification of pathogens involved. The aphid-specific fungus, *Pandora neoaphidis* (Remaudière & Hennebert) Humber (Zygomycetes, Entomophthora-

les), was found to be the only pathogen responsible for the mycosis observed. This was based on microscopic examination of nearly 200 cadavers individually mounted on slides with aceto-orcein following maintenance in a moist chamber at approximately 25° C for 20 h. No secondary infection by other entomophthoralean fungi was detected.

Morphological features including conidiophores, conidia (Fig. 1a) and hyphal bodies (Fig. 1b) coincided well with those previously documented for *P. neoaphidis* (e.g., Feng et al. 1990). Measurements of 100 primary conidia randomly taken from 20 slides (cadavers) averaged 22.0 (17.5–27.5) × 11.3 (9.25–14.3) μm, falling within the previously defined range of *P. neoaphidis* (Waterhouse & Brady 1982).

Spherical hyphal bodies (SHB) (Figs. 1c, 1d, 1h), not previously documented for *P. neoaphidis,* appeared with primary conidia and regular hyphal bodies (RHB) in all the cadavers examined. The relative abundance of these unusual hyphal bodies seemed to be negatively correlated with the abundance of primary conidia and RHBs. Some of the cadavers were nearly filled with SHBs. The frequency of cadavers containing SHBs tended to increase with each successive collection date.

The SHBs measured 11.5 (9.3–15.0) μm in diameter (n = 100), and were nearly equal to the diameter (width) of primary conidia (Fig. 1a) and RHBs (Fig. 1b). Like uninucleate primary conidia of *P. neoaphidis,* most SHBs contained only a single large nucleus (Fig. 1c). Some SHBs were found to have two or more nuclei (Fig. 1d). SHBs with multiple nuclei were usually larger in size than those with only one nucleus.

The SHBs apparently developed from RHBs, as shown in Figs. 1e–1h. A septum sometimes appeared in the hyphal body, preceding the formation of a SHB (Figs. 1e–1g). Septa are usually absent from the vegetative cells in the Entomophthoraceae (Humber 1989) and have never been recorded for *P. neoaphidis.* Subsequently, the single cell separated by a septum became spherical, often at the end of the hyphal body (Fig. 1g). Eventually, the remainder of the hyphal body gradually disappeared as its contents (protoplasts) entered the new SHBs (Fig. 1h).

The appearance of SHBs late in the season suggests that SHBs may function as an overwintering form in the life cycle of *P. neoaphidis.* This hypothesis was tested by tracing the infectivity of cadavers collected from the field, then exposed to different environments during winter months. Over 300 cadavers were collected from uncut alfalfa plants on the border strips of the field in Kennewick on 15 Oct and carried back to the laboratory in Bozeman. These cadavers were then separated into 3 batches and about 15 from each batch were placed into polypropylene microcentrifuge tubes (38 × 13 mm) corked with sterile cotton for two batches or nylon-chiffon mesh bags (approximately 5 × 5 cm; four threads per mm) for the third batch. The two batches of tubes were maintained in a dark refrigerator of about 4° C and buried in the field soil (approximately 6 cm deep) on the Montana State University campus, respectively. Mesh bags of the third batch were secured to the branches of outdoor shrubs approximately 0.5 m above the ground on the university campus. Thereafter, one tube or bag of cadavers was randomly taken from each batch every month and used to inoculate aphids reared in the laboratory by suspending the cadavers over the aphids for a spore shower. It was found that cadavers hung in bushes or maintained in the refrigerator were capable of producing conidia and infecting aphids throughout the cold winter with consistently visible snow cover from November to April. However, cadavers in the tubes

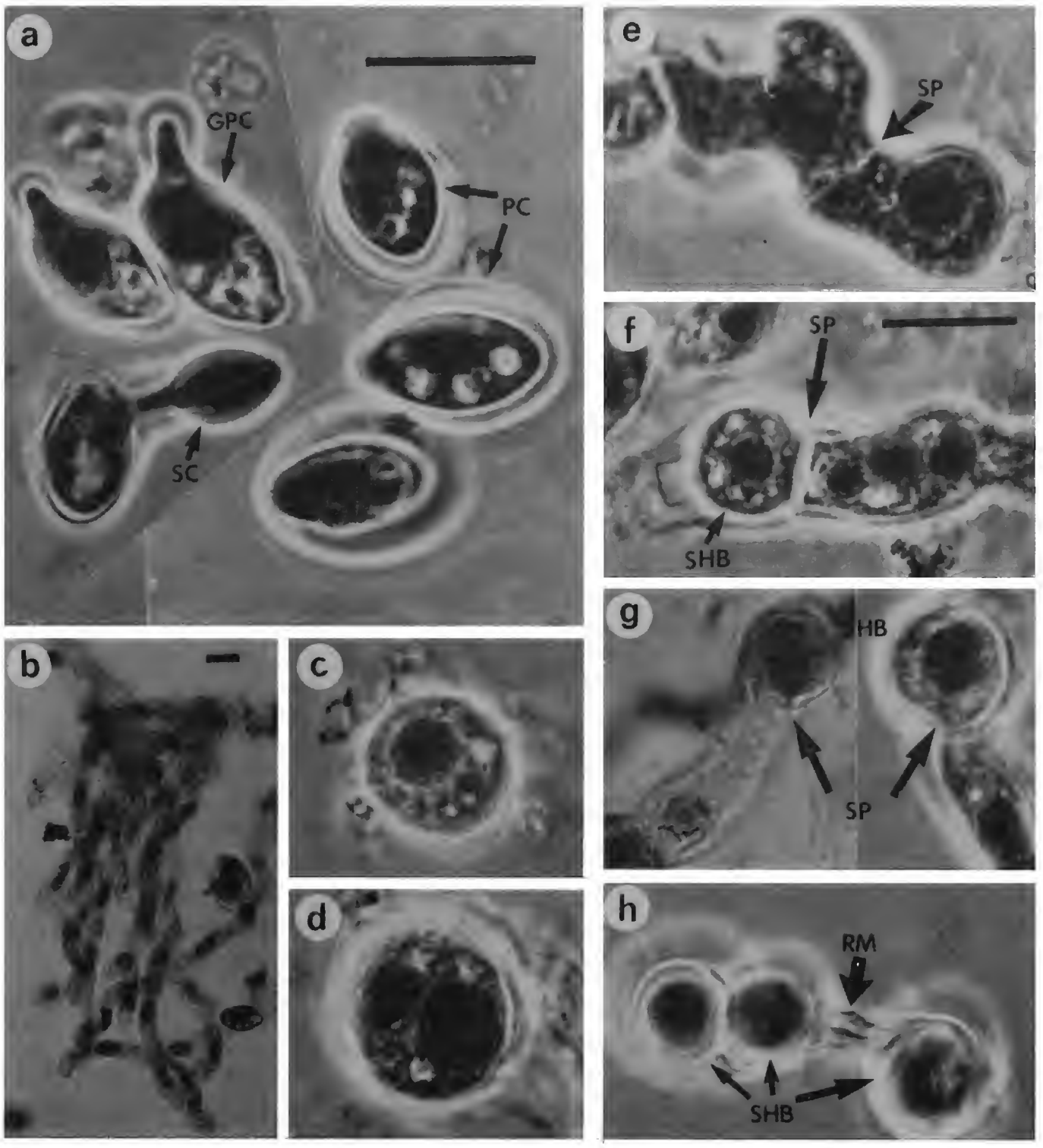

Figure 1. Common morphological characteristics (a, b) and unusual spherical hyphal bodies [SHB] (c–h) of *P. neoaphidis* associated with cadavers of *A. pisum* on alfalfa in Kennewick, Washington, in autumn. (a) Primary conidia [PC], germinating PC [GPC] and secondary conidium [SC] formed from PC. (b) Regular hyphal bodies [RHB]. (c) SHB uninucleate. (d) SHB binucleate. (e, f) Well-defined septum [SP], at arrow, seen in RHB. (g) SHB forming at the end of RHB. (h) Newly-formed SHB and remains [RM] of RHB. Scale bars: 20 μm; the bar for (a) also applies to (c–e) and (g, h).

buried in the soil were found to have exhausted all their sporulation potential in the first observation on 30 Nov. A layer of conidia were then visible on the inside wall of the tube and the cadavers became indistinguishable from one to another. As a result, the cadavers in the soil could not infect aphids at that time. This appeared to be attributable to the high humidity in the soil under snow cover during the relatively mild November.

Therefore, our observations indicate that the *P. neoaphidis* hyphal bodies in aphid cadavers can survive winter months only in relatively dry environments

(e.g., on plant substrates above the ground) rather than in the moist soil, as postulated by some authors (e.g., Latteur & Godefroid 1983). This is similar to a report that hyphal bodies of *P. neoaphidis* may maintain infectivity in cadavers for up to 32 weeks at regimes of 0° C and ≤50% relative humidity (Wilding 1973). In contrast, other entomophthoralean fungi generally overwinter as resting spores, as seen in *Conidiobolus obscurus* (Hall & Dunn) Remaudière & Keller (Latgé et al. 1978) and *Zoophthora radicans* (Brefeld) Batko (Perry & Régnière 1986). Although it was claimed that resting spores of *P. neoaphidis* had been obtained in vitro (Uziel & Kenneth 1986), resting spores have never been observed from aphids infected by *P. neoaphidis* in the field. The SHBs observed in this study are unlikely to be resting spores (zygospores or azygospores) because they are thin-walled and too small for resting spores typically reported for the Entomophthorales (R. A. Humber, personal communication). Resting spores have been observed in the field for another entomophthoralean species, *Entomophthora planchoniana* Cornu, but the primary overwintering form of this latter fungus is hyphal bodies that are distinct from those usually found for the same species (Keller 1987). SHBs in the pea aphids infected by *P. neoaphidis* late in the season seem to be analogous to the hyphal bodies of *E. planchoniana.*

It remains unknown what environmental stimuli may induce the information of septa in the hyphal bodies, thus forming the SHBs. During the period from 16 Sep to 15 Oct, 1990, local day length decreased from about 12.5 h to 11 h, while the daily minimum temperature was 9.3 (range: 1.1–16.1)° C, daily maximum 22.4 (10.6–30.6)° C, and daily mean 15.7 (7.8–22.8)° C. Whether these environmental conditions (short day and low temperature) may be conducive to physiological changes in the aphid hosts, which in turn may influence fungal development, is unclear.

Finally, *P. neoaphidis* may require a variety of host species from different crops or non-crop plants to complete the life cycle. Plant hosts that remain in the field through late autumn or are perennial (e.g., alfalfa) may provide a source of inoculum to initiate infections in aphid populations that infest spring and summer crops the following year (e.g., small grains). This hypothesis warrants further studies.

Acknowledgment

We thank R. A. Humber, S. A. Woods and D. A. Streett for their critical review of this manuscript. This article is published as Journal Series No. J-2587 from the Agricultural Experiment Station, Montana State University, Bozeman, Montana.

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Received 25 June 1991; accepted 13 August 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 105–121, (1992)

RECENT COLONIZATION OF THE SAN FRANCISCO BAY AREA, CALIFORNIA, BY EXOTIC MOTHS (LEPIDOPTERA: TINEOIDEA, GELECHIOIDEA, TORTRICOIDEA, PYRALOIDEA)

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Abstract.—Records are given documenting the establishment of seven species of moths in the San Francisco Bay area, California, during 1955–1988: *Opogona omoscopa* (Meyrick) (Tineidae), *Oegoconia quadripuncta* (Haworth) (Blastobasidae), *Mirificarma eburnella* (Denis & Schiffermüller) (Gelechiidae), *Crocidosema plebiana* Zeller (Tortricidae), and three pyraloids, *Uresiphita reversalis* (Guenée), *Parapediasia teterrella* (Zincken), and *Achroia grisella* (Fabr.). Ten additional Microlepidoptera that have colonized this region in the past 50 years are tabulated with literature sources. Most of these species spread to the San Francisco area after establishment in southern California, often following long periods (17–60 years) of naturalization there.

Key Words.—Insecta, Lepidoptera, Tineoidea, Gelechioidea, Tortricoidea, Pyraloidea, colonization

Insects make up an important part of the alien fauna that has been transported by humans to colonize different parts of the world. By 1982, 1700 such immigrants had become established in the 48 contiguous U.S. states, including 134 Lepidoptera (Sailer 1983). Although Sailer calculated that Lepidoptera are poorly represented, relative to their species numbers, as contrasted to Coleoptera, Hymenoptera and particularly Homoptera, some Microlepidoptera and Pyraloidea have become frequent travelers via their association with human activities.

California is an adopted home to more than 60 species of these smaller moths, including many of our most notorious insects, in households (clothes moths, stored foods moths), gardens (e.g., azalea leafminer, buddleia budworm, cotoneaster webworm), and agricultural situations (codling moth, Oriental fruit moth, pink bollworm, etc.). Other species are detritivores, scavengers, or fungus feeders and seldom attract attention. For example, *Opogona omoscopa* (Meyrick), *Nemapogon granellus* (L.), *Oinophila v-flavum* (Haworth), *Batia lunaris* (Haworth), *Endrosis sarcitrella* (L.), and *Oegoconia quadripuncta* (Haworth) are all common members of the urban insect community in California but are seldom noticed except by lepidopterists. A few adventive colonists are even encouraged for possible weed suppression, such as *Agonopteryx alstroemeriana* (Clerck), a specialist on poison hemlock, and *A. nervosa* (Haworth) and *Uresiphita reversalis* (Guenée), which feed on genista and other brooms, although the last species sometimes eats other ornamental legumes or native lupines and causes mixed emotions, varying with circumstances.

Many of these lepidopterous colonists became established in California so early in the immigration of European and Oriental humans that a history of their introduction and spread cannot be reconstructed. There is essentially no record

of the Microlepidoptera fauna of the Pacific coast of North America prior to the remarkable expedition in 1871–1872 in northern California and Oregon by Lord Walsingham, during which he collected and later described many of our native species (see Essig 1941, Powell 1964a: 5). More extensive collections in urban and agricultural situations were made by Koebele and Coquillett during the 1880s and 1890s, primarily in Alameda and Los Angeles counties. Otherwise, there are few records of Microlepidoptera in California prior to the turn of the century, and any other record that may have existed of the fauna in the San Francisco Bay area during the 19th century was lost in the 1906 fire that destroyed the collections of the California Academy of Sciences.

Despite federal and state efforts at quarantine against imported insects, as the human population has increased and ease of transportation improved, the parade of incoming insects has continued. California's population increased an appalling 25%, and that of the S. F. Bay area 16%, during the 1980s alone. Hence, it is not surprising that at least 17 species of small moths have taken up residence in this area during the past half century (Table 1). Included are six species that appear to have colonized during the 1980s. The occurrence of two of these is documented elsewhere: *Athrips rancidella* (Powell 1985) (Fig. 4) and *Agonopteryx alstroemeriana* (Powell & Passoa in press). Here, I give data for the remaining five, and for three species that have been established for longer periods, but apparently not documented in detail in the literature.

Methods.—I recovered data from specimens in the major California collections through 1990, by searching the unidentified accessions and confirming identifications in the determined material. Voucher specimens in collections are indicated in the text by the following abbreviations:

CAS, California Academy of Sciences, San Francisco; CDFA, California Department of Food & Agriculture, Sacramento; EME, Essig Museum of Entomology, University of California, Berkeley; FAC, Fresno County Agricultural Commissioner's Office, Fresno; LACM, Los Angeles County Museum of Natural History; SDNH, San Diego Natural History Museum; SJAC, San Joaquin County Agricultural Commissioner's Office, Stockton; SJS, San Jose State University, Department of Entomology; UCD, University of California, Davis, Bohart Entomological Museum; USNM, U.S. National Museum of Natural History, Washington, D.C. In addition, card- and computer-file records at CDFA were made available. Most of these are not represented by voucher specimens. Data from the identified material in the USNM were recorded, but not from unidentified accessions, through 1977 (*Opogona, Oegoconia, Achroia*) and 1988 (*Crocidosema*).

I made blacklight trap collections in suburban sites at Walnut Creek, Contra Costa Co., from 1961 to 1973 (EME). In the first six years, samples were made most nights I was in residence, near the foot of Shell Ridge, while those during August, 1966, to 1973 were sporadic, at a site near San Ramon Creek. The two localities are respectively about 2.75 airline km NW and 2.5 km SW of the Highway 24-680 interchange. I recorded moths in urban Berkeley on nearly all dates I was residence from May 1978 through 1990. During 1978–June, 1984, I sampled at a site 3.0 airline km NNW of the University of California west gate and during July 1984 through 1990, at a second locality 0.33 airline km north of the 1978–1984 site. This area has been residential since 1915–1920.

Table 1. Exotic Microlepidoptera and Pyraloidea that became established in the San Francisco Bay area during 1939–1988. (l = local colonization; w = widespread occurrence in S. F. Bay area; u = uncertain status.)

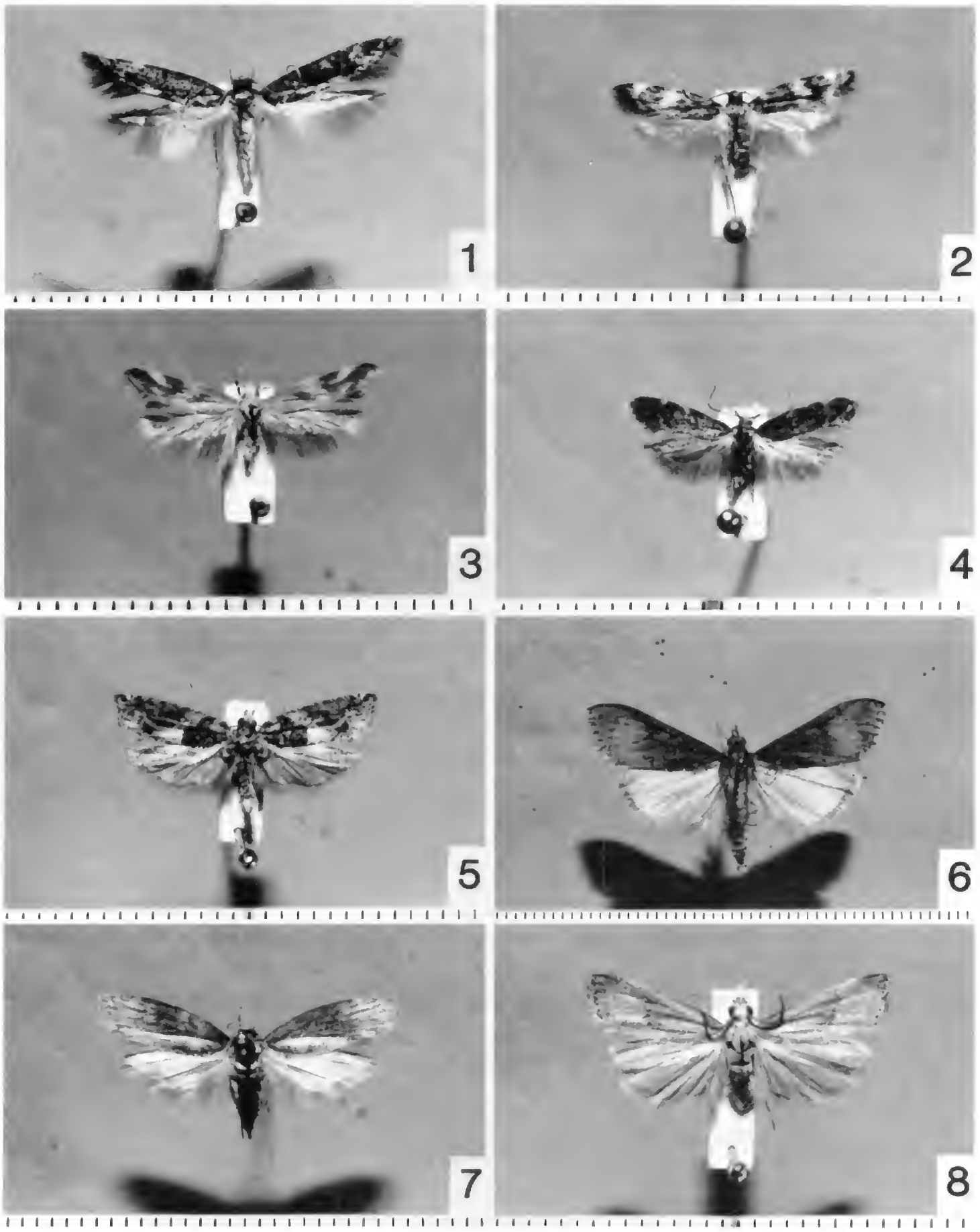
Taxa	Earliest record	Present status	Source
Tineidae:			
Oiophila v-flavum (Haworth)	1947, Stanford	w	Tilden 1951, Powell 1964b
Opogona omoscopa (Meyrick)	1972, Berkeley	w	CDFA, Davis 1978
Oecophoridae:			
Agonopteryx alstroemeriana (Clerck)	1983, Berkeley	w	Powell & Passoa, in press
Batia lunaris (Haworth)	1956, Marin	w	Powell 1964c
Esperia sulphurella (Fabr.)	1966, El Cerrito	l	Powell 1968
Pyramidobela angelarum Keifer	1942, San Jose, San Mateo	w	Keifer 1942
Blastobasidae:			
Oegoconia quadripuncta (Haworth)	1959, Redwood City, 1976, Berkeley	w	present data
Symmoca signatella (Herrich-Schaeffer)	1959, Redwood City	w	Powell 1960
Gelechiidae:			
Athrips rancidella (Herrich-Schaeffer)	1983, Berkeley	l	Powell 1985
Mirificarma eburnella (Denis & Schiffermüller)	1985, Morgan Hill	u	present data
Tortricidae:			
Crocidosema plebiana Zeller	1988, Berkeley	l	present data
Spilonota ocellana (Denis & Schiffermüller)	1939, San Jose	w	Keifer 1939
Cnephasia longana (Haworth)	1947, San Mateo	w	Keifer 1948, Powell 1964a
Platynota stultana (Walsingham)	1967, Antioch, Albany	w	Powell 1983
Pyralidae:			
Uresiphita reversalis (Guenée)	(1966, Stevens Cr.), 1980, San Jose	w	present data
Parapediasia teterrella (Zincken)	1988, Berkeley	l	present data
Achroia grisella (Fabr.)	1955, San Jose	w	present data

Tineidae

Opogona omoscopa (Meyrick)

(Fig. 1)

Opogona omoscopa was originally described from Australia in 1893 and since has been found widely distributed in pan-global warm regions, probably in large part the result of man's activities. The larvae feed in decaying, often damp plant



Figures 1–8. Figure 1. *Opogona omoscopa*; Berkeley, October 1978. Figure 2. *Oegoconia quadripuncta*; Berkeley, June 1988. Figure 3. *Mirificarma eburnella*; Nevada Co., May 1980. Figure 4. *Athrips rancidella*; Berkeley, May 1983. Figure 5. *Crocidosema plebiana* Zeller; Berkeley, November 1990. Figure 6. *Uresiphita reversalis*; Berkeley, December 1983. Figure 7. *Achroia grisella*; Berkeley, August 1983. Figure 8. *Parapediasia teterrella*; Berkeley, May 1989.

material, including wood, bark and dead leaves (Davis 1978) and evidently are easily transported with roots and other plant material. This species has been known in Hawaii since 1905, where it is widespread and abundant (Zimmerman 1978), a likely source for introduction into California.

The earliest Pacific coast record is at Goleta, Santa Barbara Co., California, in May, 1969 (CDFA and Davis 1978), which probably was soon after establishment, because the adults come to lights readily, and I collected at Goleta for five weeks during June and July, 1965, without finding *O. omoscopa.* The moths were taken at nearby Santa Barbara and Summerland in June and July, 1969 (USNM). In fall, 1970, C. Nagano collected a series at Santa Monica, Los Angeles Co. (LACM), and by summer, 1971, *O. omoscopa* was widespread in southern California, having been detected in Gardena (LACM), Los Angeles (USNM) and Rancho Santa Fe, San Diego Co. (EME).

The first records in the S. F. Bay area were two larval collections on ginger roots in a market in Berkeley, in May, 1972, and May, 1973 (CDFA). Ginger roots sold in this area are normally imported from Hawaii. Hence, it is possible that a separate introduction from overseas, rather than from southern California, initiated the S. F. Bay area population. There also were larval collections from Corte Madera, Marin Co. in January, 1974, and Fremont and Livermore, Alameda Co. in 1976 (CDFA), but we do not have documented records of colonies outside of buildings until adults began appearing at lights in the 'east bay' in 1978 (EME). The species has been common in Berkeley since that time, having been recorded on 15–30 dates each year. The moths are seen in every month but are most prevalent in September–November (50% of all records during 1985–1990: JAP, unpublished data).

The peculiar, widely divergent labial palpi, flattened, smooth front and elongate, plicate maxillary palpi make *O. omoscopa* easily recognizable among all California Lepidoptera.

Blastobasidae
Oegoconia quadripuncta (Haworth)
(Fig. 2)

This Palaearctic species is distinctive in the urban fauna of California, having black forewings spotted with yellow. In Europe the larvae are reported to feed on decaying vegetable matter, and we reared *O. quadripuncta* from leaf litter beneath *Quercus* by P. Rude (EME). In England there is a single annual generation, with adults active in July and August, occurring in habitats such as hedge-bottoms (Emmet 1979).

Oegoconia quadripuncta was introduced into the Atlantic states long ago; it was redescribed as *novimundi* Busck, a synonym, in 1915, and it was established in Pennsylvania and New jersey by 1920 (USNM). The adventive range had reached Washington, D.C. by 1927, Martha's Vineyard, Massachusetts by 1941 and Illinois by 1956 (USNM).

There does not seem to be a published report of this species' occurrence in California, such as during Keifer's summaries of introductions during 1935–1955 (Powell 1991). However, *O. quadripuncta* evidently was introduced into southern California, presumably from the eastern U.S., more than 50 years ago. There are specimens from South Pasadena, L. A. Co., collected in August, 1938, and June, 1940 by C. Henne (USNM), and the range extended to Ventura Co. (Ojai) by 1961 (EME) and Orange Co. by 1962 (CDFA). The species had become common in Los Angeles by the time Donahue began sampling there in the early 1970s (LACM).

The first record I have seen in the S. F. Bay area is August, 1959, at Redwood City, San Mateo Co. (EME), but *O. quadripuncta* was not known east of the bay until adults appeared at lights in Berkeley in 1976. The species seems to be becoming more prevalent at Berkeley; it was observed on two or three dates per season until 1986, then five dates in 1987 and 1988, six in 1989, and nine in 1990 (despite 44 nights absence from sampling during summer), when the flight period extended from early June to mid September.

Oegoconia evidently colonized the Central Valley about a decade later than the S. F. Bay area. I did not find the species in Davis when I sampled there in 1956, but there are more than a dozen collections records from Sacramento (1967–1968), Davis (1969–1971) and Fresno (1970–1971) (CDFA, UCD).

Gelechiidae

Mirificarma eburnella (Denis & Schiffermüller)

(Fig. 3)

This moth was reported in North America under the names *M. formosella* (Hübner) (Anonymous 1969, Dowell & Gill 1989) and *M. flamella* (Hübner) (Hodges 1983), which are considered to be synonyms of *M. eburnella* (Pitkin 1984). The species is widespread in Europe and the Mediterranean region, where it feeds on *Medicago,* including alfalfa, and other legumes (Pitkin 1984).

This gelechiid is distinctive in the California fauna, having rust-orange and yellow patterned forewings. It was first recognized in North America when larvae were found defoliating Ladino clover, *Trifolium repens* L., in the Sacramento Valley in Sutter, Placer and Sacramento counties, in April, 1969. Identifications at the time revealed that I had collected specimens near Georgetown, El Dorado Co., in June, 1967 (Anonymous 1969; CDFA, unpublished report). The species was already widely established, however, as evidenced by specimens determined later that had been taken by A. Keuter and G. Keuter in May, 1965, and May–June, 1967, at Citrus Heights, Sacramento Co. (CAS). There are also two specimens labelled 12 Oct 1967, in the Keuter material, suggesting a bivoltine life cycle.

Berkeley students and I found *M. eburnella* at additional localities in El Dorado Co. (Greenville, Somerset) during May and June, 1967 and 1978, and at several sites around the Sierra Foothill Field Station (near Smartville), Yuba Co. and Rough and Ready, Nevada Co., in May, 1980. The species appeared at La Grange, Stanislaus Co. in 1971 (CDFA), at a site that has been sampled for many years by R. P. Allen. The 1971–1980 localities are 55 km NW to 134 km SE of a line between Citrus Heights and Georgetown, along the foothills of the Sierra Nevada.

During a census of Lepidoptera of serpentine grasslands in Santa Clara Co., D. D. Murphy and I collected two specimens of *M. eburnella* at Kirby Canyon Ridge (approx. 6 airline km NE of Morgan Hill), on 29 Apr 1985. This suggested that populations of this gelechiid had spread across the Central Valley and inner Coast Range into the Santa Clara Valley. However, more intensive survey on numerous dates at this locality and serpentine grasslands at a dozen other sites in Santa Clara, San Mateo and Marin counties during March through May, 1986–1987 and 1990 failed to recover *M. eburnella.* Possibly the four year drought following 1985 suppressed the clover or other hostplants severely, limiting or eradicating

the immigrant moth population from this habitat. Hence, the residency status of *M. eburnella* in the S. F. Bay area is uncertain.

TORTRICIDAE
Crocidosema plebiana Zeller
(Fig. 5)

This species was originally described from Sicily in 1847, but its native distribution is unknown. It occurs pan-globally in warmer regions, probably having been transported by man since early times. *Crocidosema plebiana* was reported from Hawaii by several early authors, but Zimmerman (1978) regards the Hawaiian *Crocidosema* as three distinct, endemic species. Differentiation of Pacific island populations also is discussed by Clarke (1971, 1986). The evidence suggests that *C. plebiana* (sens. lat.) occupied a broad range, and that North American populations probably originated from the Mediterranean. The larvae of *C. plebiana* feed in flowers and fruit of various Malvaceae, including *Hibiscus,* and have been taken on cotton several times in California.

Heinrich (1923) reported *C. plebiana* in the U.S. from California and Texas. In addition, the species has been collected widely in the south, in Louisiana (1916), Florida (1918 onwards) and South Carolina (1944) (USNM; Kimball 1965). The species has long been established and abundant in southern California; the earliest available record is June, 1911 at San Diego, collected by W. S. Wright (USNM). In 1917–1918, it was collected at Chula Vista, San Diego Co. (CAS). By about 1920 it occurred in the San Bernardino area (Barnes collection: USNM), at Riverside by 1932, and on Santa Catalina Island by 1931 (CDFA, LACM). By that time probably it was established throughout much of the Los Angeles basin and Orange Co., where its colonization was documented in the 1940s during the statewide Oriental fruit moth survey by dimalt bait traps (CDFA). Specimens were reared from *Hibiscus* buds at Exposition Park, Los Angeles in 1942 (LACM). The distribution also extended to the coast in the Ventura (1943) and Santa Barbara (1936) areas (CDFA, LACM), and San Luis Obispo Co. (Pismo Beach) by 1959 (EME). *Crocidosema plebiana* was found in the San Joaquin Valley in Kern Co. in 1968 (CDFA).

I had not seen any subsequent records north of a line between Pismo and Bakersfield until *C. plebiana* appeared in Berkeley recently. In late September and October, 1988, two males came to a blacklight, but none was observed in 1989, suggesting that the moths captured in 1988 did not represent an established population. In 1990, however, *C. plebiana* reappeared, with males attracted to blacklight on 9, 12 Jul and on 10 dates between 11 Sep and 17 Oct, confirming the colonization.

PYRALIDAE
Uresiphita reversalis (Guenée)
(Fig. 6)

This large pyraustine, which is known as "the genista caterpillar," has bright rust-brown forewings and ochreous-yellow hindwings. The moths are primarily nocturnal and come to lights but are easily flushed into activity during the daytime. The larvae are aposematic in color and behavior; they are orange and black spotted, live exposed, without a shelter, and are rendered distasteful by sequestered

alkaloids (Bernays & Montllor 1989). They often occur in defoliating numbers. Hence, populations are easily seen in the field, and this species is not likely to colonize unnoticed for long.

Although its relatives are Old World species, *Uresiphita reversalis* is believed to be a native Nearctic species, having been described originally in 1854 from "North America" without a specified locality. The natural distribution is unknown, but it may have encompassed parts of the southeastern U.S. and Mexico. The present range is reported to be "southern Canada to southern Florida and west to California" (Munroe 1976), but it is likely sustained in northern areas by migrations, not continuously resident populations. In California, moreover, populations are dependent upon introduced plants, particularly *Genista,* grown as ornamentals or in weedy situations, and there are no known records prior to 1930, so *U. reversalis* is assumed to be an introduced or adventive exotic.

In the west there are records as early as 1912 in the Davis Mountains, Texas (LACM) and 1927 in the mountains of southern Arizona (CAS), and there are scattered collections from the Mexican plateau and coastal Sinaloa (EME, UCD), suggesting that native populations may have lived in these areas.

The earliest known record in California is a series collected in Los Angeles in September, 1930, by J. A. Comstock (LACM). By late 1931, *U. reversalis* occurred widely in urban Los Angeles, Orange, San Diego and Ventura counties and had been reared from "Genista and other brooms" at several localities (Keifer 1931). There are records at Riverside and San Bernardino by September, 1932, and Santa Barbara in 1933 (CDFA, CAS, LACM). McKenzie (1933), who described the early stages and recorded hostplants, stated that the initial appearance of this insect in California had been noted only recently.

Populations seemed to stabilize in cismontane southern California during the following 30 years, and there are collection records for nearly every year, indicating that residency was continuous.

The earliest known collection of *U. reversalis* in the San Francisco Bay area is August, 1966, at Stevens Creek [5 km SW of Cupertino], Santa Clara Co., by R. Denno (UCD). This record is puzzling because one would expect this species to have appeared first in an urban area, rather than a forested canyon in the foothills, and because if the collection sampled an established population, it is surprising that no other colonies were detected in the south bay area during the subsequent 13 years. Continuous residency is documented beginning in 1980. Larvae were collected from *Laburnum* in Fremont in July, 1980 (CDFA) and on *Genista* at San Jose at least three times between September, 1980, and September, 1981 (CDFA, EME, SJS), the first by F. Iltis (W. E. Ferguson, personal communication); and the species rapidly colonized northward in the S. F. Bay area during the next 10 years. In 1983, larvae of *U. reversalis* were found in Oakland by P. Neyland (EME), and adults began appearing at localities that R. L. Langston, W. W. Middlekauff or I had been sampling regularly: Antioch, Contra Costa Co. (August), Berkeley (November), San Bruno Mts., San Mateo Co. (December), in Contra Costa Co. at El Cerrito the following year, and Fish Ranch Canyon and Kensington by 1985 (CAS, EME).

Uresiphita reversalis was widely established north of San Francisco Bay by the late 1980s, in Marin (1986) (including Angel Island and Marin Island, 1989), Napa (1988) and Solano (1987) counties (CDFA, EME).

It is likely that *U. reversalis* also spread through the Central Valley and Sierra Nevada foothills during or preceding the 1980s. By 1968, when records were suspended in a card file system at CDFA[1], there were no listings of this pyralid from counties north of the Transverse Ranges; also, there are no voucher specimens for records during the following 11 years. Larvae were collected at Tracy, San Joaquin Co. in late 1982 (SJAC), and at Bakersfield, Kern Co. and near Fresno, Fresno Co. a year later (CDFA, FAC). By 1987, when computerization came on line at CDFA, *U. reversalis* was found in Kern, Tulare, Merced, Placer, and Sacramento counties; by 1988 in Yolo Co. (January) and in the northern Sacramento Valley, in Sutter and Butte (October), and Shasta (1989) counties (CDFA) (Fig. 9). Simultaneously, *Uresiphita* colonized the foothills of the Sierra Nevada in Amador, Nevada, and Tuolumne counties, to elevations of 550–800 m at Sonora and Grass Valley (CDFA).

The genista caterpillar feeds on a variety of legumes, particularly those of the tribe Genisteae (Fabaceae) including *Genista, Cytisus,* and *Lupinus,* as well as on *Baptisia* and *Sophora* (Dyar 1901, McKenzie 1933, Kimball 1965, Munroe 1976, Bernays & Montllor 1989). In California, the adventive populations evidently are dependent primarily on *Genista* (= *Cytisus*) *monspessulana* (L.) (French broom) and horticultural hybrids. *Cytisus scoparius* (L.) (Scotch broom) has been recorded as the larval host on several occasions, but at least some of these evidently originate from plant misidentifications or equating the common names "genista," "broom" and "Scotch broom" as applied to various *Genista* species. For example, there are records from "Scotch broom" in San Diego County in 1931 (CDFA) and 1967 (EME), but *Cytisus scoparius* was not established anyplace south of Monterey County by 1978 (Mountjoy 1979).

There are numerous records of larvae having been collected on nonleguminous plants, including *Buddleia* (Loganiaceae) (McKenzie 1933; CDFA [1964]), asparagus fern (Liliaceae), *Taxus* (Taxaceae), *Gardenia* (Rubiaceae) (CDFA), and "chamise" (SDNH). Such records, along with other evidence ("pupating in doorway," "barbeque cover," etc. [CDFA]), probably reflect a propensity of late instar larvae to wander. Particularly when colony densities are high and *Genista* is defoliated, larvae of *U. reversalis* are liable to be found on various other plants in the vicinity.

In the S. F. Bay area, larvae of *U. reversalis* feed on native *Lupinus,* including *L. chamissonis* Eschscholtz when growing in proximity to *Genista monspessulana* (Pt. Molate, JAP 87G4, EME), and on *L. arboreus* Sims according to Bernays & Montllor (1989). In no-choice feeding tests in the laboratory, Bernays and Montllor found that larvae did not feed and soon died when offered certain legumes, including *Medicago, Trifolium, Vicia,* and *Pickeringia.* They fed successfully on

[1] *Uresiphita reversalis* is rated "C" in pest status by CDFA (a native or established species, against which no agricultural quarantine action may be needed). Most "C" and "D" (beneficial or non-phytophagous non-economic) rated insects ceased to be routinely entered in the CDFA card system in 1968, due to system size restrictions; those rated "Q" [old "X"] (unassessed exotic), "A" (quarantine action mandated) or "B" (county level quarantine), however, continued to be automatically entered in the post-1968 card database. Individual instances of "C" or "D" rated insects also could have been entered, if requested by a CDFA taxonomic specialist for the group; their post-1968 absence on cards does not necessarily mean that no CDFA identification was done. In 1987, the CDFA data system was computerized, and all data from CDFA identifications was once again routinely entered.—(Ed.)

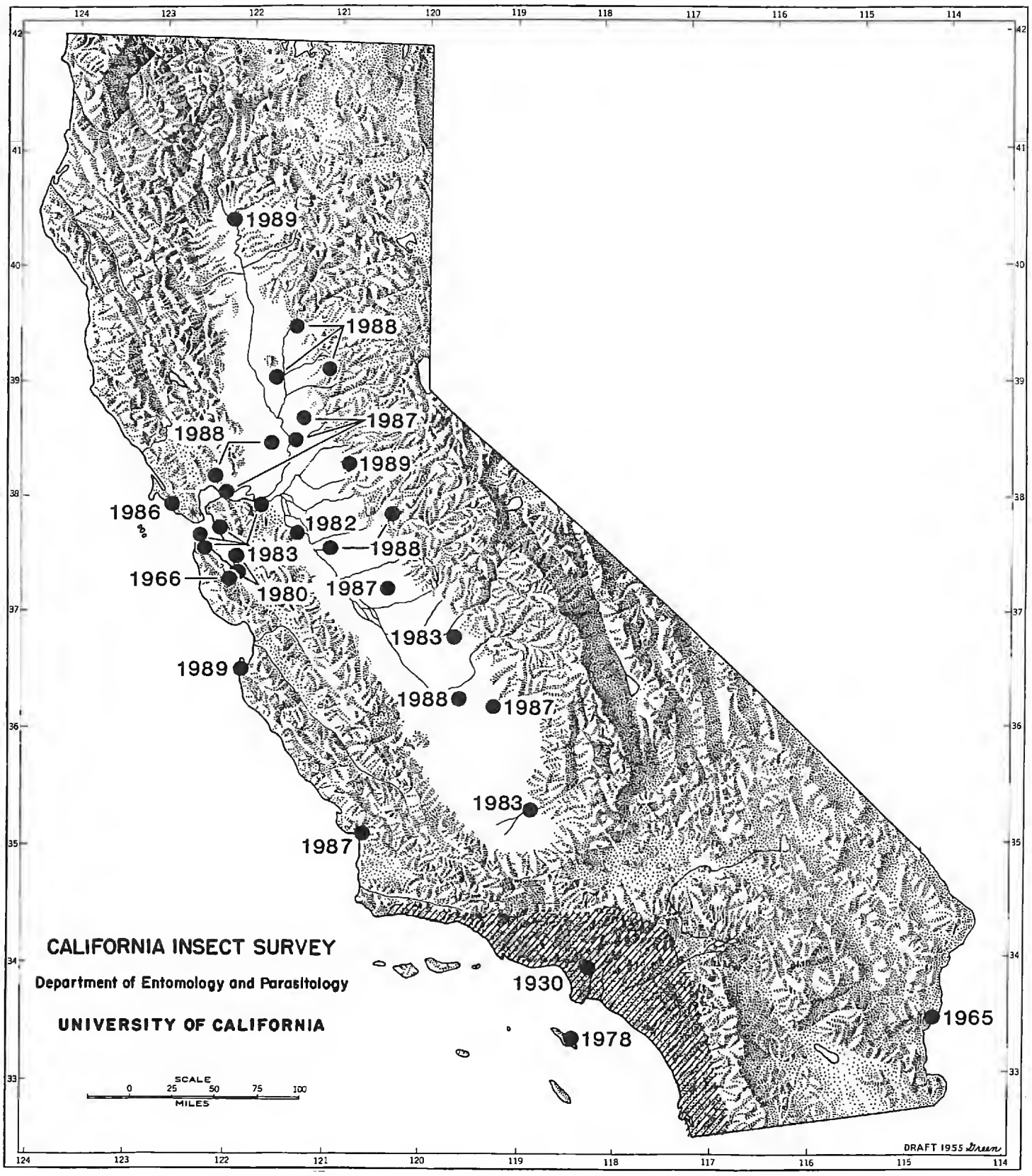


Figure 9. Geographical distribution of *Uresiphita reversalis* in California: by 1931 (shaded area); later dated localities refer to first records in peripheral areas of southern California and first records in counties north of the Transverse Ranges.

Lupinus arboreus, Cytisus striatus (Hill), *G. monspessulana,* and *Cytisus scoparius,* and late instar larvae significantly preferred *Lupinus* over *G. monspessulana,* when given the choice.

Bernays & Montllor (1989) believed that the data indicate that the main hosts of *U. reversalis* in California are species of *Lupinus.* However, I have not seen any evidence that populations inhabit less disturbed plant communities where they would be sustained solely by native plants. Moreover, there are no specimen voucher records of larvae on native plants outside of urban situations after more than half a century residency in southern California and none in more northern areas (CAS, CDFA, EME, LACM, SDNH, SJS, UCD). The CDFA has records

of larval collections from "*Lupinus* sp." from Castro Valley, Alameda Co. (1988), Redding, Shasta Co. (1989) and Santa Maria, Santa Barbara Co. (1988) in garden, park, and nursery settings. Some exotic ornamental legumes also serve as hosts, including *Laburnum* at El Cerrito (JAP 84K1) (EME) and *Piptanthus* at the Strybing Arboretum, San Francisco (CAS).

Parapediasia teterrella (Zincken)
(Fig. 7)

Described in 1821 from Georgia, this was one of the first pyralids known in North America. It is widespread in the eastern U.S. and is often extremely abundant at lights in urban areas, such as around Washington, D.C. The original geographical distribution no doubt was modified by human colonization of North America; by the late 1800s it encompassed the Atlantic and midwestern states. Murtfeldt (1893) reported that *P. teterrella* had become more abundant during the past two or three years around Kirkwood, Missouri, than all other crambids combined.

There are records in the southwest as early as half century ago: Tulsa, Oklahoma (1940); Albuquerque, New Mexico (1944); Tucson (1935) and Madera Canyon (1947), Arizona (LACM). Hence, *P. teterrella* may have spread into that region with urbanization during the early 1900s.

The earliest known occurrence in California is August, 1954, at South Gate, Los Angeles Co. (LACM). Records from other parts of southern California and the Central Valley indicate that this lawn moth had colonized in the early 1950s, then spread southward and northward within a few years (Fig. 10). I collected the urban lawn moths, *Crambus sperryellus* Klots and *Tehama bonifatella* (Hulst) and did not find *Parapediasia teterrella* in San Diego during 1953–1956; but in 1957–1959, light trapping by A. A. Lee and R. A. Mackie produced *P. teterrella* at widely separated inland localities: Escondido and Otay, San Diego Co. and at several coastal sites in 1958–1959 (SDNM, EME). The colonization reached Bakersfield, Kern Co., by July, 1959, then quickly spread through the Central Valley, recorded at Madera (1960), Sacramento (1967), and Davis, Yolo Co. (1969) (CDFA). I did not find *P. teterrella* in urban Davis when I sampled there during the summer of 1956.

The adventive populations appear to have extended through the delta region to S. F. Bay, having been recorded at the Antioch National Wildlife Refuge in August, 1981, and at Berkeley beginning in 1988 (EME), when two adults came to blacklight in October. The following season I recorded *P. teterrella* on 16 dates between 19 May and 17 Oct; in 1990 the species became more abundant and seasonally extensive, flying from 9 Apr to 24 Oct (34 dates recorded), often with 5–10 individuals observed. At Berkeley this species has become the most prevalent lawn moth, while *Tehama bonifatella* (Hulst) appears to have declined in numbers (eight and 13 dates in 1989 and 1990, down from 19–29 dates in 1985–1988), although its adult activity was more prolonged than that of *P. teterrella* in 1990 (25 Mar to 12 Nov). The data suggest that competitive displacement is occurring at this site.

Parapediasia teterrella may be better adapted to inland than coastal areas in California, as I have not seen records of its occurrence in urban areas of the coastal counties, from Ventura to San Francisco.

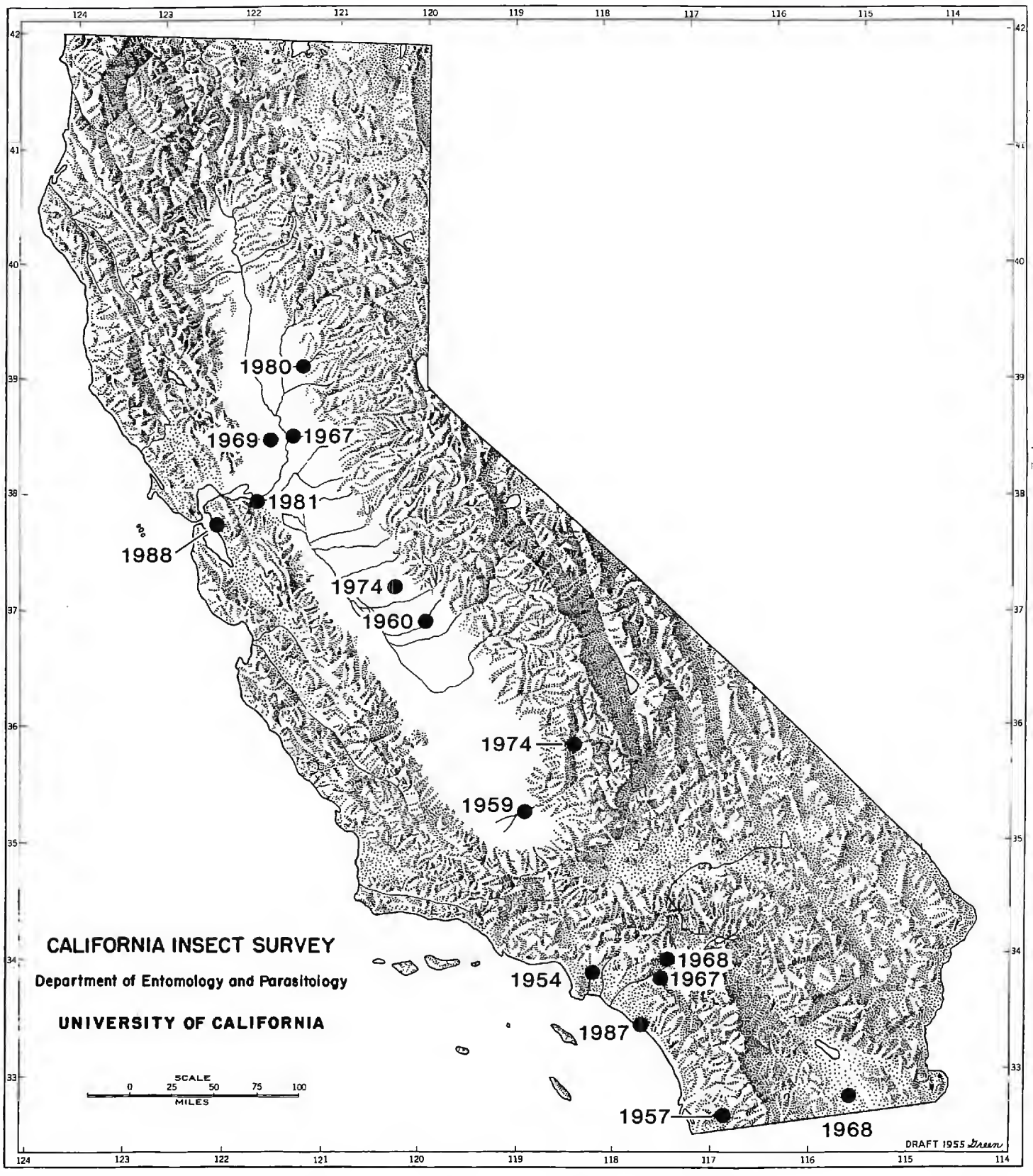


Figure 10. Geographical distribution of *Parapediasia teterrella* in California: dated localities refer to first record in each country.

Achroia grisella (Fabr.)
(Fig. 8)

The lesser wax moth is described in the stored products and general entomological literature as a cosmopolitan insect, but evidently it has not been formally reported in California. *Achroia grisella* is not mentioned by Essig (1926), nor by Keifer during 1927–1954 (Powell 1991); and there were no records from the Pacific states in the USNM in 1977. Larvae of this moth, which is uniformly mouse gray with a contrasting pale yellow head, typically live in old honeycombs but also are said to feed on dried fruit and "apparently" on dried insects (Forbes 1923). The species was originally described from Europe but has been widely established in the Atlantic states at least since the 1890s (USNM).

There are records of *Achroia grisella* in southern California dating back to the early 1900s, but apparently the adults are not readily attracted to lights, and populations likely have been more prevalent and widespread than records indicate. A series was collected by W. S. Wright in San Diego on at least six dates between 1908 and 1915 (SDNH); there are two specimens from the E. Piazza collection, probably from San Diego, taken in 1921, and *A. grisella* was taken at Del Mar, San Diego Co. in 1934–1942 (CDFA, LACM).

Circumstantial evidence suggests that the lesser wax moth colonized central parts of California at a much later date; there are at least 20 collection records from the San Francisco Bay area and Sacramento Valley in the past 40 years but none before that. The earliest vouchered record that I have seen is September, 1952, at Courtland, Sacramento Co. (CDFA); but probably *A. grisella* was widespread in central California by that time, as there are specimens from San Jose, Santa Clara Co. taken in 1955 by J. W. Tilden (SJS) and from Prunedale and Soledad, Monterey Co., in 1956 (CDFA). In the east bay, I took one specimen in 13 years sampling at Walnut Creek, Contra Costa Co. (June, 1964), and adults have been collected sporadically in Berkeley since 1968 (EME). A long series of *A. grisella* was reared by P. A. Rude from larvae in the honeycombs of an abandoned beehive in Kensington in 1978 (EME), but only four individuals, taken on four dates in 1983, 1987 and 1989, have been observed during the past 12 years sampling in Berkeley.

Discussion

Collection records indicate that at least 17 species of exotic Microlepidoptera and pyraloid moths have colonized the San Francisco Bay area during the past half century, including six during the most recent 10 years (Table 1). Five of these evidently were introduced independently from other populations in California, either directly from the Old World (*Batia lunaris, Esperia sulphurella*), or from the Pacific northwest or eastern U.S. (*Agonopteryx alstroemeriana, Athrips rancidella, Cnephasia longana*). The others colonized secondarily from southern California, by local introduction or gradual spread by adventive populations.

Among species that have reached the S. F. Bay area via southern California, several underwent a sequence of introduction-establishment then a long period of naturalization, followed by rapid range extension northward (e.g., Fig. 9) (or colonization via secondary introduction in the bay area). This pattern parallels that shown by other introduced insects, for example the passion vine-feeding butterfly, *Agraulis vanillae* (L.) (Powell 1961), the Old World earwig, *Euborellia annulipes* (Lucas) (Langston & Powell 1975) in California, and the European hesperiid, *Thymelicus lineola* (Ochsenheimer) in midwestern and northeastern U.S. and adjacent Canada (Powell 1983). Such delayed ecogeographical expansions by introduced insects may involve genetic adaptation to environmental situations to which the founder or even source populations were not adapted. The delay cannot always be documented because of incomplete records of adventive populations while they are at low levels, but gaps appear to have been as much as 17 years for *Symmoca signatella,* at least 40 years for *Platynota stultana,* 50 for *Uresiphita reversalis,* and 60 for *Crocidosema plebiana,* following widespread establishment in southern California.

By contrast, a few species have colonized in southern California and then apparently began expanding their range without appreciable delay during natu-

ralization. *Parapediasia teterrella* (Fig. 10) colonized the Sacramento Valley within 6–13 years after detection in the Los Angeles basin (but 21 more years passed before establishment in the east bay); *Pyramidobela angelarum* was established in Santa Clara and San Mateo counties eight years after its discovery in Los Angeles (Keifer 1942), and *Opogona omoscopa* reached the bay area within three years of first notice at Santa Barbara, although this may have been via independent introduction, and was widely established after two (San Diego Co.) to nine years (S. F. Bay area).

The data are too fragmentary to document the history of *Oinophila v-flavum* (Powell 1964b) and *Achroia grisella* in California. It would not be surprising to discover that such species have been established in the S. F. Bay area for a half century or more, as was the case for the urban tortricids, *Acleris variegana* (Schiffermüller) (Powell 1964a) in the bay area and *Clepsis unifasciana* (Hübner) in the Pacific northwest (Powell 1988).

Dowell & Gill (1989) compiled a list of 208 invertebrates that they classified as exotic and believed had been discovered in California between 1955 and 1988, based on several USDA and CDFA publications. They include 24 species of Lepidoptera, of which 16 are Microlepidoptera and Pyraloidea. The list is neither complete nor restricted to exotic species. Included are at least four species that likely are native insects:

Bucculatrix tridenticola Braun (erroneously given as Brown), which was originally described in 1963 from southern and eastern Oregon, eastern Washington, Colorado, Utah, and Nevada, occurs in association with *Artemisia tridentata* Nuttall in natural communities in Modoc County, California (several records in 1960s: Hall 1965; EME) and probably throughout the Great Basin. The probable origin inexplicably was given by Dowell and Gill as eastern U.S.

Periploca nigra Hodges was described originally from Sacramento in 1962 and was found to be widely established in the S. F. Bay area on ornamental junipers (Koehler & Tauber 1964). This may be an introduced species, but it is reported to range from New York to Louisiana "then west to Sacramento and San Diego, California" (Hodges 1978). The natural hostplants and geographical distribution in the west are unknown.

Choristoneura conflictana (Walker) is widespread across boreal America in association with *Populus tremuloides* Michaux and was reported from several sites in native aspen forests of the Warner Mountains, Cascades and Sierra Nevada, having been collected in California from 1922–1962 (Powell 1964a).

Eumysia mysiella (Dyar) is a widespread native insect of the Great Basin and southwest. It was described from Stockton, Utah, in 1905 and by the 1960s was recorded in Arizona, New Mexico, and Nevada (Heinrich 1956) (EME). Probably its natural range included California, east of the Sierra Nevada. The larval host is unrecorded, but the closely related *E. idahoensis* Mackie feeds on several species of *Atriplex* (Chenopodiaceae) (Mackie 1958).

Dowell and Gill's list omits several species that were first detected in California between 1955–1988, including *Opogona omoscopa,* discussed above; *Batia lunaris,* which was established on both sides of S. F. Bay by 1962 (Powell 1964c); *Esperia sulphurella,* an early spring, diurnal moth that was discovered at El Cerrito and Berkeley in 1966 and 1967 (Powell 1968) and has been recorded many times during the subsequent two decades (CAS, EME); and *Agonopteryx alstroemeriana,*

which was widely established in the bay area by 1984 (CAS, EME; Powell & Passoa in press) (Table 1).

Combining species validly listed by Dowell and Gill and those for which data are given here, yields a total of at least 27 species of exotic Microlepidoptera and Pyraloidea that have been discovered in California during the half century after 1940. The residency status of several of those included by Dowell and Gill is unknown; populations have been subject to eradication procedures, and/or we lack subsequent collections to confirm colonization and spread (e.g., *Homadaula anisocentra* (Meyrick) and *Endothenia albolineana* (Kearfott)).

Acknowledgment

I thank all the collectors who have made the special efforts needed to acquire study specimens of Microlepidoptera that have enabled us to document the fauna in California during the past 35 years. Particular acknowledgment is due those who sampled in urban areas, including J. P. Donahue (Los Angeles), R. L. Langston (Kensington), R. H. Leuschner (Gardena, Manhattan Beach), C. D. MacNeill (Richmond, El Cerrito), R. A. Mackie (San Diego Co.), W. W. Middlekauff (El Cerrito), D. C. Rentz (San Francisco, Albany), and P. A. Rude (Oakland). Rosemary Leen provided records of *Uresiphita* from her search of 1980–1987 archive files at CDFA, gave me information on the hostplant nomenclature of *U. reversalis,* and offered critical comments on the ms. *Crocidosema* data at San Diego Natural History Museum and the U.S. National Museum of Natural History were compiled by J. W. Brown. Records from computer and card files at the California Dept. of Food & Agriculture were provided by T. D. Eichlin and R. Somerby; and K. W. Brown and N. J. Smith provided records from the San Joaquin and Fresno County Agricultural Commissioner's Offices, respectively. Cooperation by the following enabled me to use the collections in their care: V. Lee and N. D. Penny (California Academy of Sciences), J. P. Donahue (Los Angeles County Museum of Natural History), D. K. Faulkner (San Diego Natural History Museum), R. Stecker (San Jose State University, Department of Entomology), the late R. O. Schuster (University of California, Davis, Bohart Entomological Museum), and D. R. Davis and R. W. Hodges (U.S. National Museum of Natural History, Washington, D.C.).

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Received 1 July 1991; accepted 18 August 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 122–132, (1992)

REVISION OF THE GENUS *TACHYCOLPURA* BREDDIN (HEMIPTERA: HETEROPTERA: COREIDAE: COLPURINI)

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Abstract.—The genus *Tachycolpura* Breddin (Coreidae: Colpurini) is revised to include *T. luteola* NEW SPECIES, from Borneo, and *T. sumatrana* NEW SPECIES, from Sumatra. *Xenocolpura* Blöte NEW SYNONYM, is synonymized within *Tachycolpura* with the binomial *T. elongata* (Blöte) NEW COMBINATION. The dorsal habitus, pronotum, and female genital plate of each species, and the male genital capsule and parameres of the new species, are illustrated. A key to species is provided.

Key Words.—Insecta, Heteroptera, Coreidae, Colpurini, *Tachycolpura,* NEW SPECIES, Sumatra, Borneo.

The tribe Colpurini contains about 16 genera (*Hygia* with nine subgenera) and 134 species, with several genera and many species awaiting description. Members of the tribe are distributed from Fiji and Australia to India and the eastern Palaearctic region, reaching their greatest diversity in Malaysia, Indonesia and Papua New Guinea (Dolling 1987). The species are usually black or dark colored, with a striking diversity of structure in the male genital capsule and in the female genital plate (Brailovsky 1990).

Breddin (1900) described the genus *Tachycolpura* to include *Lybas penicillatus* Walker, 1871 as the type. Distant (1901) and Bergroth (1913) cited this species only superficially, without adding new morphological or distributional data. Blöte (1936) described and illustrated the new genus and species *Xenocolpura elongata* Blöte, from Sumatra. Within his generic treatment, Blöte does not allude to the affinities that this genus might have with other Colpurini, but only emphasizes, as diagnostic characters, the reduced wings and the conical projections of the humeral angles of the pronotum.

During this revision, we had no doubt in recognizing the close relationship between both genera. In this paper we synonymize *Xenocolpura* with *Tachycolpura,* and create a new binomial, *Tachycolpura elongata.* Two new species, collected in Sumatra and Borneo, are also described.

Tachycolpura is the only genus of Colpurini in which the humeral angles of the pronotum are projected as a conical tooth of variable length, width and trajectory. The tylus, jugae, and the antenniferous tubercles are unarmed and the femora are armed with a double row of spines and granules that decorate their ventral side. The shape of the posterior edge of the genital capsule, the length and width of the gonocoxae I and of paratergite IX, the development of the wings, and the color of the hemelytral membrane, the corium and the tibiae, all characterize the genus.

The following abbreviations identify the institutions where types are deposited, and specimens were loaned: Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); The Natural History Museum, London (BMNH); Colección Entomológica del

Instituto de Biología, Universidad Nacional Autonoma de México (IBUNAM); Museum d'Histoire Naturelle, Geneva, Switzerland (MGHN); Rijksmuseum van Naturlijke Histoire, Leiden, Netherlands (RNHL); Zoologisches Musem, Universiteit Van Amsterdam, Netherlands (ZMUA).

Tachycolpura Breddin

Tachycolpura Breddin, 1900. Rev. d'Entomol. 19: 215.
Tachycolpura: Bergroth, 1913. Mem. Soc. Entomol. Belg. 22: 142.
Xenocolpura Blöte, 1936. Zool. Meded. 19: 44, NEW SYNONYM.

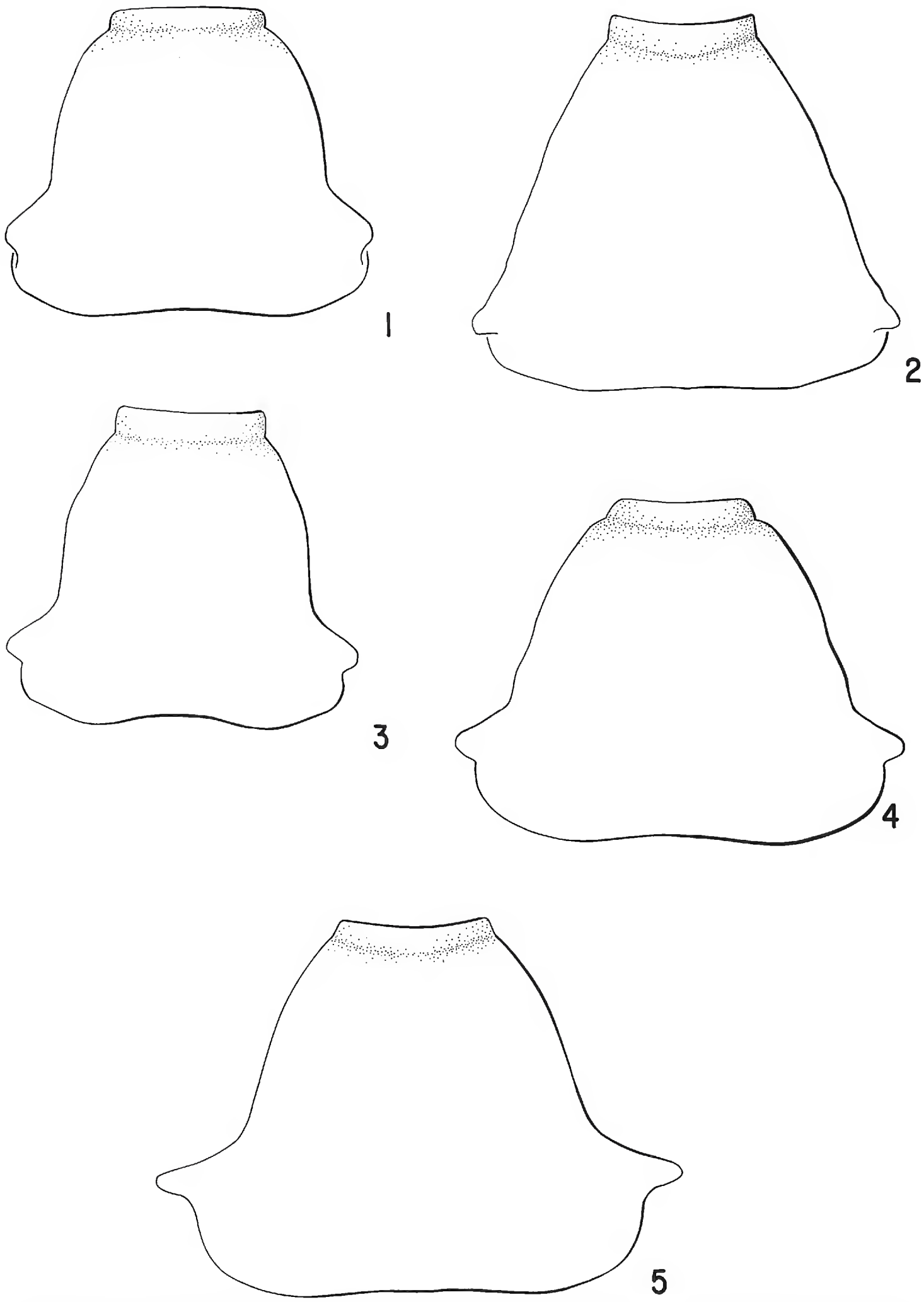
Type Species.—Lybas penicillatus Walker.

Redescription.—Narrow body, moderately elongated, with an average length from 16.48 mm to 20.15 mm. *Head.* Longer than wide, elongate, cylindrical and slightly narrowed basally; tylus unarmed, apically truncate, extending anterior to jugae, and seen laterally extending above them; antenniferous tubercles unarmed with truncate apex; jugae unarmed; antennal segment I robust, cylindrical, slightly curved outwards and longer than head; segment II longest, segment IV shortest and fusiform; segments II and III cylindrical; ocelli not elevated; preocellar pit deep, diagonally excavated; eyes spherical; tubercles postocular protuberant; side of head in front of eyes straight, slightly convergent; bucculae rounded, short, not projecting beyond antenniferous tubercle, with sharp mesial projection and anterior edges thickened; rostrum long, reaching the medial one-third of abdominal sternite V, or almost to apex of VII; rostral segment IV longest, III longer than II and II longer than I, which is shortest. *Thorax. Pronotum.* Wider than long, moderately sloped; anterior collar wide; anterolateral edges ranging from oblique and gently rounded to almost straight; humeral angles projected into conical tooth, directed upwards and slightly backwards, with variable length (Figs. 1–5); posterior edge straight. Anterior lobe of metathoracic scent gland globose and reniform, posterior lobe sharp, small. *Legs.* Femora with two rows of granules and small spines along ventral surface, less abundant on metafemur; tibiae with shallow sulcus, sometimes difficult to see; metatibiae longer than metafemur. *Scutellum.* Triangular, longer than wide, with sharp apex. *Hemelytra.* Macropterous, reaching median one-third of abdominal segment VII of male or median one-third of VIII, or anterior one-third of IX in female, or coleopteroid and extending to anterior third of abdominal segment V in both sexes (see Slater 1975); claval suture evident or barely so (coleopteroid individuals); claval commissure shorter than total length of scutellum; apical border obliquely straight, with short apical angle not reaching middle one-third of hemelytral membrane; hemelytral membrane with few bifurcate veins. *Abdomen.* Connexival segments higher than body, forming a case where hemelytra rest; posterior angle of connexival complete, or extended into a very short, wide projection; abdominal sternites with medial sternal furrow projecting to posterior border of sternites V or VI. *Integument.* Body surface rather dull. Head, pronotum, scutellum, clavus, corium, thorax, abdominal sterna and exposed parts of genital segments of both sexes strongly punctate. Antennae and legs minutely granulate. Head, pronotum, scutellum, clavus, corium, thorax and abdominal sterna with long, decumbent to suberect conspicuous golden or silvery bristle-like hairs. Pronotum, thorax and abdominal sterna with circular gray-white farinose punctures.

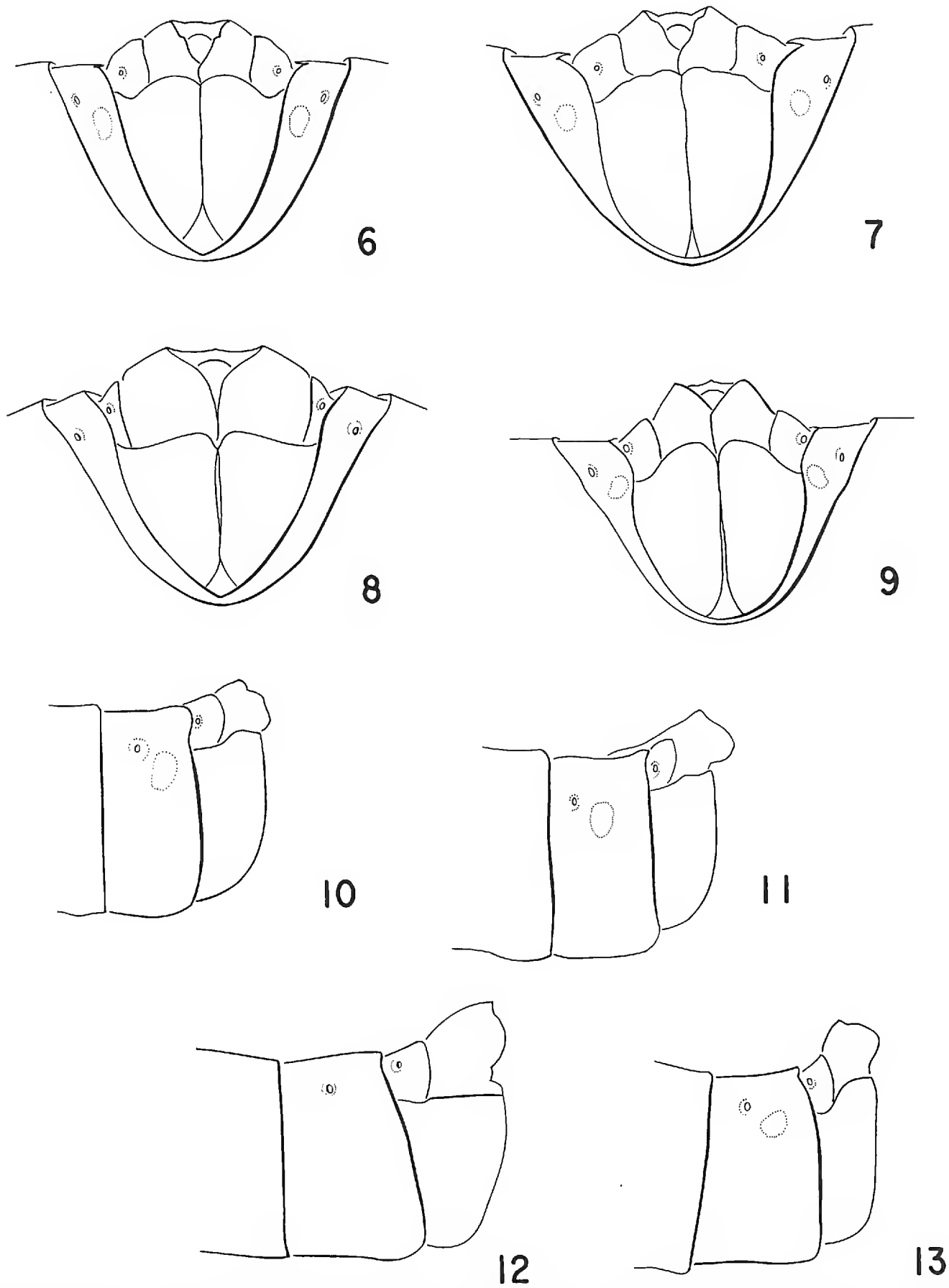
Male Genitalia.—Genital Capsule. Posteroventral edge bidentate (Figs. 14–16). *Parameres.* Simple and straight body; apical projection widened, with the anterior lobe convex or continuous with body and the posterior lobe ending in a sharp and short projection (Figs. 20–24).

Female Genitalia.—Abdominal sternite VII with plica and fissure evident; plica narrow or elevated and transversely evolved; gonocoxae I nearly square, large; paratergite VIII short, square, with spiracle visible; paratergite IX nearly square, larger than former paratergite VIII (Figs. 6–13). *Spermatheca.* Bulb long and dilated, duct coiled, with short membranous duct (Fig. 25).

Diagnosis.—Tachycolpura is the only genus within the Colpurini that has the humeral angles of the pronotum projected into a sharp and robust conical projection, of variable length and trajectory. Other typical characters are an unarmed tylus, jugae and antenniferous tubercles, an armed femora of all three pairs of



Figures 1–5. Pronotum view of *Tachycolpura* spp. Figures 1, 2. *T. penicillata* (Walker). Figure 1. Male. Figure 2. Female. Figure 3. *T. elongata* (Blöte) NEW COMBINATION. Figure 4. *T. luteola,* NEW SPECIES. Figure 5. *T. sumatrana* NEW SPECIES.



Figures 6–9. Frontal view of the female genital plates of *Tachycolpura* spp. Figure 6. *T. penicillata* (Walker). Figure 7. *T. elongata* (Blöte) NEW COMBINATION. Figure 8. *T. luteola* NEW SPECIES. Figure 9. *T. sumatrana* NEW SPECIES. Figures 10–13. Lateral view of female genital plates of *Tachycolpura* spp. Figure 10. *T. penicillata* (Walker). Figure 11. *T. elongata* Blöte NEW COMBINATION. Figure 12. *T. luteola* NEW SPECIES. Figure 13. *T. sumatrana* NEW SPECIES.

legs, and a notoriously elongated head. The presence of a fissure and a plica in the female, together with the spiny projection of the buccula, confirm the generic diagnosis of the genus.

Discussion.—Wing development in the Colpurini is notoriously variable, in-

cluding apterous, coleopteroid, micropterous, submacropterous and macropterous species, even within a genus (*Sciophyrus*) and a species (*Brachylybas* spp.). Therefore, wing character is not a reliable tool for a generic definition.

Blöte (1936) in describing and illustrating *Xenocolpura,* noted that its characteristic features are especially a brachypterous condition, the presence of a subconical tooth in the humeral angles of the pronotum and a thorny projection in the bucula. In examining the type material of *X. elongata* Blöte and *Tachycolpura penicillata* (Walker), both monotypic genera, we could not find any definitive characters to be used. Both species have the same degree of development of the humeral angles, the bucula and of the genital plates of the female. Therefore, we synonymized *Xenocolpura* within *Tachycolpura,* and included *X. elongata* as the second known species of *Tachycolpura.*

Distribution.—Four species are known from Malaya, Sumatra, Singapore and Borneo.

Biology.—Apparently a very scarce genus restricted to forested areas.

Key to *Tachycolpura* Species

1. Coleopteroid individuals, with the hemelytral membrane not extending beyond abdominal segment V; claval suture not evident; gonocoxae I long, with a maximum length of 3.00 mm (Figs. 7, 11); posterior border of genital capsule with two short projections, with robust and truncated apices (Figs. 16, 19) (Sumatra) ..... *T. elongata* (Blöte) NEW COMBINATION

1′. Macropterous individuals, with the hemelytral membrane reaching abdominal segment VII of male, or IX in female; claval suture evident; gonocoxae I shorter than 2.90 mm 2

2(1′). Apical angle and apical margin of corium yellow; genital capsule elongate, with posterior margin oblique and convergent, with two short projections with rounded apices (Figs. 15, 18) (Borneo) ..... *T. luteola* NEW SPECIES

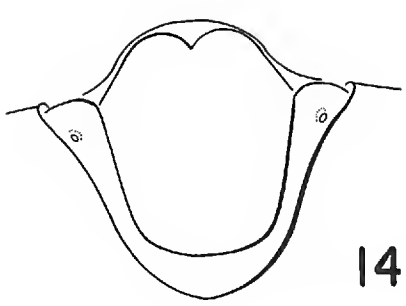
2′. Apical angle and apical border of corium black or brown-red; genital capsule globose, with the posterior edge widened, with two short rounded lobes (Figs. 14, 17) 3

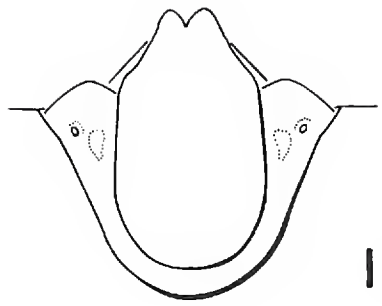
3(2′). Humeral angle of pronotum with long, thin, slender conical projections (Fig. 5); clavus and corium pallid red-orange; tibiae dark orange, with two yellow rings, one subbasal and the other almost apical (Sumatra) ..... *T. sumatrana* NEW SPECIES

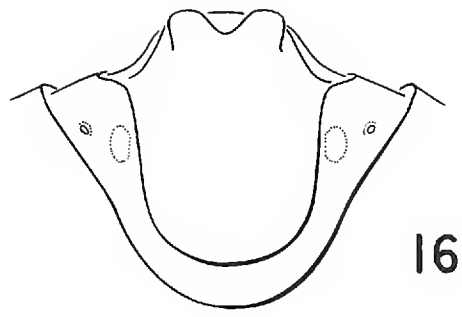
3′. Humeral angles of pronotum with short and robust projections (Figs. 1–2); clavus and corium black; tibiae dark red-brown, without yellow rings (Singapore, Borneo) ..... *T. penicillata* (Walker)

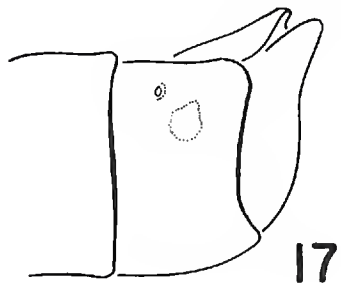
Tachycolpura penicillata (Dallas)
(Figs. 1, 2, 6, 10, 14, 17, 20, 21, 26)

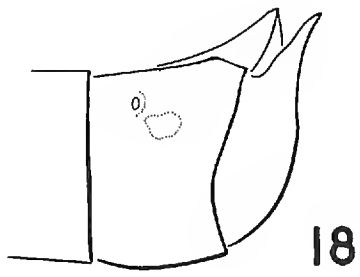
Lybas penicillatus Walker, 1871. Cat. Hem. IV: 150–151.
Lybas penicillatus: Lethierry & Severin, 1894. Cat. Gen. 2: 42.
Tachycolpura penicillata: Breddin, 1900. Rev. d'Entomol. 19: 216.
Colpura penicillatus: Distant, 1901. Ann. Mag. Nat. Hist. Ser. 7(7): 20.
Tachycolpura penicillata: Bergroth, 1913. Mem. Soc. Entomol. Belg. 22: 142.

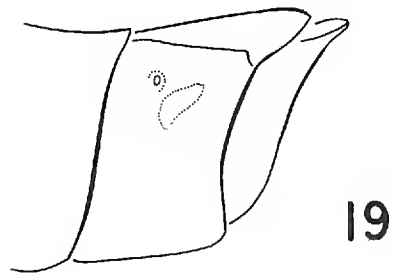


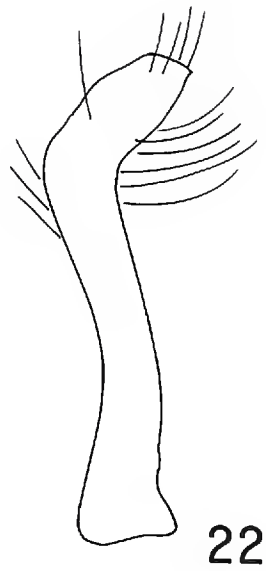


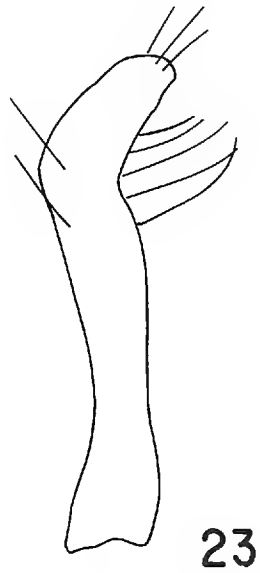


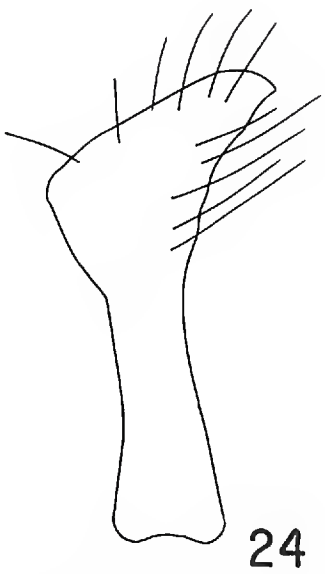












Figures 14–16. Frontal view of the male genital capsule of *Tachycolpura* spp. Figure 14. *T. penicillata* (Walker). Figure 15. *T. luteola* NEW SPECIES. Figure 16. *T. elongata* (Blöte) NEW COMBINATION. Figures 17–19. Lateral view of the male genital capsule of *Tachycolpura* spp. Figure 17. *T. penicillata* (Walker). Figure 18. *T. luteola* NEW SPECIES. Figure 19. *T. elongata* (Blöte) NEW COMBINATION. Figures 20–24. Parameres of *Tachycolpura* spp. Figures 20, 21. *T. penicillata* (Walker) Figures 22, 23. *T. luteola* NEW SPECIES. Figure 24. *T. elongata* (Blöte) NEW COMBINATION. Figure 25. Spermatheca of *Tachycolpura luteola* NEW SPECIES.

Types.—*Lybas penicillatus* Walker. We designate a female, collected in Singapore and deposited in the Natural History Museum, London, as a Lectotype.

Redescription.—*Female. Color.* Black with the following areas pale ochre or pale orange: upper side of the postocular tubercles, apex of scutellum, a very small discoidal dot on middle one-third of apical margin of corium, posterior one-third of connexivum, anterior and posterior lobes of metathoracic scent gland, and posterior angle or pleural margin of abdominal sternites III to VII; antennal segments II and III, rostral segments I to IV and tibiae and tarsi dark red-brown; antennal segment I black, and IV dark ochre, with basal one-third red; hemelytral membrane dirty yellow with veins red-brown, basal angle and anterior margin pale yellow. *Structures.* Rostrum reaching posterior border of sternal segment V; humeral angles of pronotum projecting into a conical, short, robust tooth, pointed backward (Fig. 2); hemelytra macropterous, with claval suture evident and membrane reaching middle one-third of abdominal segment VIII; posterior angle of connexival segments V and VI not projecting out from surface; gonocoxae I conspicuously long, with the maximum width large; paratergite IX nearly square, short and barely reaching beyond the external border of gonocoxae I (Figs. 6, 10). *Measurements:* Head length: 2.85 mm; interocellar space: 0.64 mm; interocular space: 1.44 mm; width across eyes: 2.15 mm; preocular distance: 1.85 mm; length antennal segments: I, 4.00 mm; II, 5.20 mm; III, 3.70 mm; IV, 2.25 mm. Pronotal length: 3.70 mm; width across frontal angles: 1.70 mm; width across humeral angles: 4.90 mm. Scutellar length: 2.35 mm; width: 2.00 mm. Maximum length of gonocoxae I seen frontally: 2.85 mm; maximum length of gonocoxae I seen laterally: 1.35 mm. Total body length: 17.65 mm.

Male.—*Color.* Similar to female, but hemelytral membrane dirty yellow with veins and anterior margin brown and only basal angle yellow. *Structures.* Humeral angles produced into a short conical tooth, barely projecting beyond posterolateral edge of pronotum (Fig. 1). Macropterous hemelytra and membrane reaching middle one-third of abdominal segment VII. Genital capsule globose with posterior margin widened and with two short rounded mounds (Figs. 14, 17). *Parameres.* Figs. 20–21. *Measurements:* Head length: 2.84 mm; interocellar space: 0.64 mm; interocular space: 1.25 mm; width across eyes: 2.13 mm; preocular distance: 1.68 mm; length antennal segments: I, 4.00 mm; II, 5.16 mm; III, 3.70 mm; IV, 2.23 mm. Pronotal length: 3.30 mm; width across frontal angles: 1.70 mm; width across humeral angles: 3.92 mm. Scutellar length: 2.20 mm; width: 1.65 mm. Total body length: 16.48 mm.

Diagnosis.—Macropterous species, characterized by having the humeral angles of the pronotum projected into a short, conical robust tooth (Fig. 1), or very small (Fig. 2), and in each condition pointed backward, with the middle one-third of the apical margin of corium with a discoidal small yellow patch. The male genital capsule is globose, with the posterior margin widened and apices produced into two rounded mounds (Figs. 14, 17). Paratergite IX of female square, short, and barely surpasses the external border of gonocoxae I (Figs. 6, 10). The basal angle of the hemelytral membrane yellow.

Distribution.—Originally described from Singapore and northern Borneo (Sarawak).

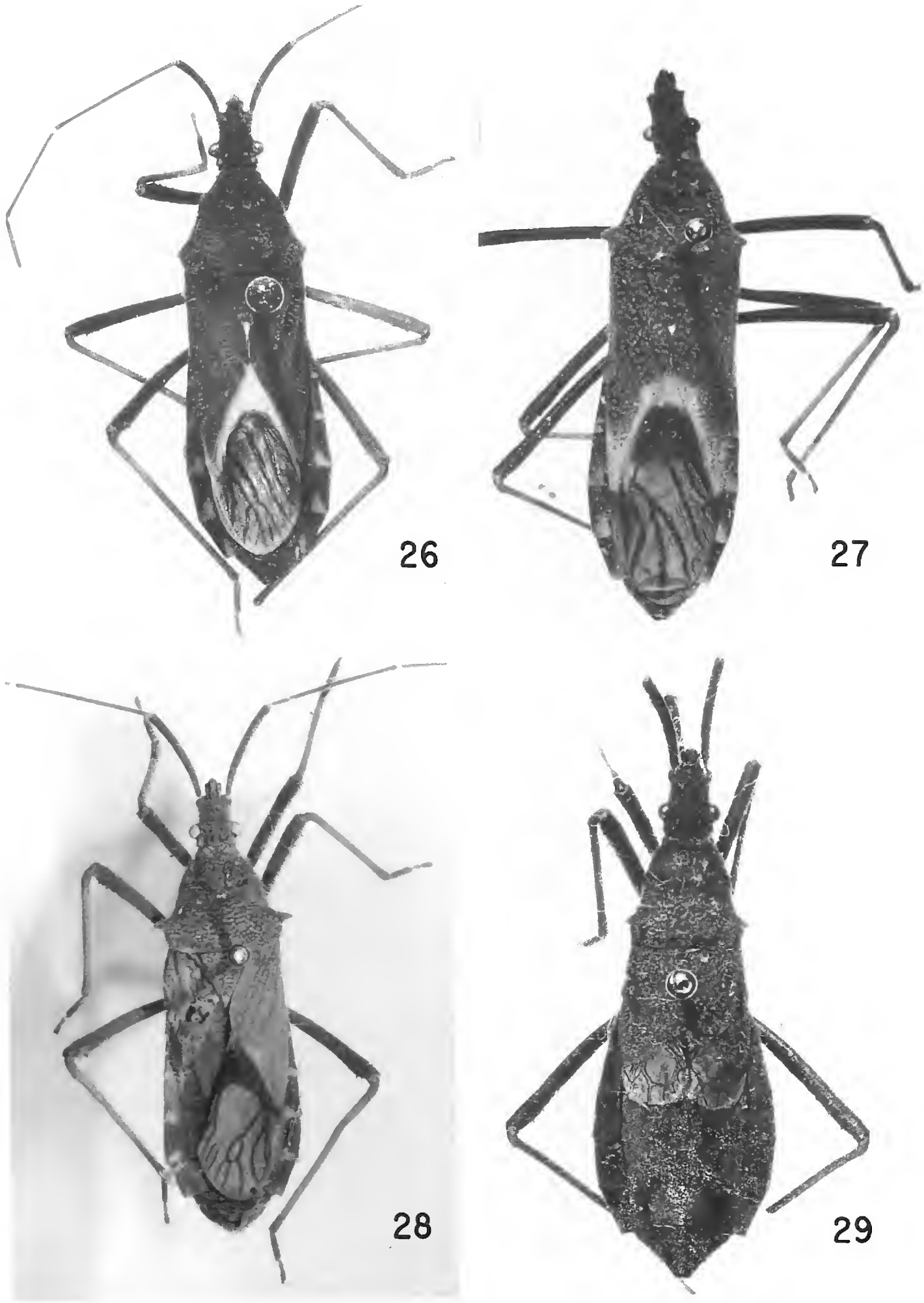
Material Examined.—One male and three females, among them the female lectotype. *Data:* MALAYA. Ulu Gombok. INDONESIA. *BORNEO:* Without localities.

Tachycolpura elongata (Blöte) NEW COMBINATION
(Figs. 3, 7, 11, 16, 19, 24, 29)

Xenocolpura elongata Blöte, 1936. Zool. Meded. 19: 44–45.

Types.—Female holotype deposited in the Rijksmuseum van Naturlijke Histoire, Leiden, Netherlands.

Redescription.—*Female. Color.* Black, with following areas orange ochre: dorsum of postocular tubercles, apex of scutellum, posterior margin of connexivum, and anterior and posterior lobes of



Figures 26–29. Dorsal view *Tachycolpura* spp. Figure 26. *T. penicillata* (Walker). Figure 27. *T. luteola* NEW SPECIES. Figure 28. *T. sumatrana* NEW SPECIES. Figure 29. *T. elongata* (Blöte) NEW COMBINATION.

metathoracic scent glands; rostral segments I to IV, trochanters, most of tibiae and tarsi red-brown; hemelytral membrane dirty yellow, with veins and basal angle red-brown. *Structures.* Rostrum reaching posterior border of sternal segment V; humeral angles of pronotum produced into a robust, short, conical tooth, projected backward (Fig. 3); hemelytra coleopteroid, with claval suture not evident, and membrane reaching anterior one-third of abdominal segment V; posterior angle of connexival segments V–VI well marked against surface; gonocoxae I conspicuously elongated, with well developed maximum width; paratergite IX square, conspicuously surpassing external border of gonocoxae I (Figs. 7, 11). *Measurements:* Head length: 3.06 mm; interocellar space: 0.76 mm; interocular space: 1.40 mm; width across eyes: 2.35 mm; preocular distance: 2.12 mm; length antennal segments: I, 3.90 mm; II to IV absent. Pronotal length: 3.48 mm; width across frontal angles: 1.74 mm; width across humeral angles: 4.55 mm. Scutellar length: 1.95 mm; width: 1.85 mm. Maximum length of gonocoxae I seen frontally: 3.00 mm; maximum length of gonocoxae I seen laterally: 1.80 mm. Total body length: 18.25 mm.

Male.—Color. Similar to female. *Structures.* Rostrum reaching anterior margin of sternal segment VII; coleopteroid, with hemelytral membrane reaching anterior one-third of abdominal segment V. Genital capsule globose, posterior margin widened, with two short robust lateral projections with truncate apices (Figs. 16, 19). *Parameres.* Fig. 24. *Measurements:* Head length: 3.00 mm; interocellar space: 0.67 mm; interocular space: 1.38 mm; width across eyes: 2.30 mm; preocular distance: 2.00 mm; length antennal segments: I, 3.83 mm; II to IV absent. Pronotal length: 3.09 mm; width across frontal angles: 1.69 mm; width across humeral angles: 3.90 mm. Scutellar length: 1.80 mm; width: 1.55 mm. Total body length: 17.18 mm.

Diagnosis.—This is the only species in the genus with coleopteroid hemelytra; the claval suture is not evident and the membrane is very short, not extending beyond the anterior one-third of abdominal segment V. The aspect of the humeral angles of the pronotum, as well as the length of the gonocoxae I, place it near *T. penicilliata* (Walker), but in *T. elongata* (Blöte) the gonocoxae I is clearly wider and paratergite IX extends well beyond the external border of gonocoxae I (Figs. 6, 7, 10, 11).

The genital capsule of *T. elongata* is wide and posseses two robust projections with truncated apices (Figs. 16, 19), whereas the other species have two very short mounds with rounded apices (Figs. 14, 17).

Distribution.—Restricted to Sumatra, from Lubu Raja and Tapanuli.

Material Examined.—One male and three females, among which was the holotype. INDONESIA. (*WEST*) *SUMATRA:* PADANG: Pandjang.

Tachycolpura luteola Brailovsky, Barrera & Lopez-Forment NEW SPECIES (Figs. 4, 8, 12, 15, 18, 22, 23, 25, 27)

Types.—Holotype: male; data: INDONESIA. (*CENTRAL*) *BORNEO:* Sg. Pajau, 1925, Mjoberg. Deposited in the Zoologisches Museum, Universiteit Van Amsterdam, Netherlands. Paratypes: 3 males, 5 females; same data as holotype. (2 males and 4 females deposited in the Zoologisches Museum, Universiteit Van Amsterdam, Netherlands and 1 male and 1 female in the "Colección Entomológica del Instituto de Biología, UNAM, México"); INDONESIA. (*NORTHWEST*) *BORNEO:* Kuching, Jan 1900, Dyak, 4 females (3 deposited in the Rijksmuseum van Naturlijke Histoire, Leiden, Netherlands and 1 in the "Colección Entomológica del Instituto de Biología, UNAM, México").

Description.—Male (*holotype*). *Color.* Black, with the following areas ochre or yellow ochre, sometimes with orange reflections: apex of scutellum, apical angle and apical margin of corium, posterior margin of connexivum, internal side of trochanters, anterior and posterior lobes of metathoracic scent glands, and angle or posterior margin of pleural margin of abdominal sternites IV to VII; antennal

segments II, III and tibiae dark red-brown; rostral segments I to IV and tarsi lighter red-brown; antennal segment I black, IV yellow with basal one-third brown; external side of trochanters shiny red-brown; hemelytral membrane dirty yellow with veins and subbasal large brown blotch and pallid yellow basal angle. *Structures.* Rostrum reaching anterior border of sternal segment VI; pronotal humeral angles projecting into a short, robust, conical tooth pointed outwards and slightly downwards (Fig. 4); macropterous hemelytra, claval suture evident, membrane reaching middle one-third of abdominal segment VII; posterior angle of connexival segments V and VI not marked on surface. Genital capsule long, posterior margin becoming narrower with conspicuous oblique border, and two short lateral projections with rounded apices (Figs. 15, 18). *Parameres.* Figs. 22, 23. *Measurements:* Head length: 3.00 mm; interocellar space: 0.72 mm; interocular space: 1.26 mm; width across eyes: 2.15 mm; preocular distance: 1.95 mm; length antennal segments: I, 4.75 mm; II, 6.70 mm; III, 4.65 mm; IV, 2.70 mm. Pronotal length: 3.45 mm; width across frontal angles: 1.62 mm; width across humeral angles: 4.10 mm. Scutellar length: 2.25 mm; width: 1.90 mm. Total body length: 17.80 mm.

Female.—Color. Similar to male. *Structures.* Macropterous, with hemelytral membrane reaching posterior margin of abdominal segment IX. Gonocoxae I short lengthwise with well developed width; paratergite IX square, reaching beyond external margin of gonocoxae I (Figs. 8, 12). *Spermatheca.* Fig. 25. *Measurements:* Head length: 2.85 mm; interocellar space: 0.70 mm; interocular space: 1.17 mm; width across eyes: 2.10 mm; preocular distance: 1.90 mm; length antennal segments: I, 4.15 mm; II, 5.70 mm; III, 4.05 mm; IV, 2.40 mm. Pronotal length: 3.60 mm; width across frontal angles: 1.65 mm; width across humeral angles: 4.85 mm. Scutellar length: 2.20 mm; width: 1.95 mm. Maximum length of gonocoxae I, seen frontally: 2.25 mm; maximum length of gonocoxae I, seen laterally: 1.55 mm. Total body length: 17.90 mm.

Diagnosis.—This distinctive species is recognized by the light yellow color of the apical angle and apical margin of the corium. In *T. penicillata* and *T. elongata,* the corium are entirely black. The length of the gonocoxae I is very short (2.25 mm) and the posterior margin of the genital capsule is narrowed apically, with conspicuously oblique margins and two short rounded apical projections (Figs. 15, 18). In the other species, the gonocoxae I is longer (2.80–3.00 mm), and the genital capsule is wider and globose, with both projections truncated apically (Figs. 16, 19), or rounded (Figs. 14, 17).

Etymology.—The taxon name is based on the yellow color of the apical angle and the apical margin of the corium.

Material Examined.—See types.

Tachycolpura sumatrana, Brailovsky, Barrera & Lopez-Forment NEW SPECIES

Type.—Holotype: female; data: INDONESIA. *SUMATRA:* Deli (Bed Pict), without date. Deposited in the Museum d'Histoire Naturelle, Geneva, Switzerland. The left wing of the holotype is destroyed.

Description.—Female (holotype). Color. Head, pronotum, scutellum, thorax and abdominal sternites black with pale red reflections at apex of tylus, scutellar disc, acetabula of three pairs of legs, abdominal sternites, genital plates and pleural margin of abdominal sternites III to VII; ochre yellow on: upper side of postocular tubercles, apex of scutellum, semi-discoidal spot on middle one-third of apical margin of corium, posterior margin of connexival, anterior and posterior lobes of metathoracic scent gland, and posterior margin of pleural margin of abdominal sternites III to VII; antennal segment I dark red-brown, segments II and III pale red-orange, IV yellow with basal one-third pale orange; clavus, corium, connexivum and dorsal segments of abdomen red-orange; hemelytral membrane dirty yellow with veins and large subbasal brown spot and basal angle dark ochre; coxae and femora red-brown; trochanters bicolored, with external side red-brown, and internal side yellow; tibiae dark orange with two yellow rings, one subbasal, other almost apical; orange tarsi with ochre reflections; rostral segments I to IV brown ochre. *Structures.* Rostrum reaching posterior border of sternal segment V; humeral angles of pronotum produced into long, thin, slightly backwards inflected conical prominence

(Fig. 5); macropterous hemelytra with claval suture evident and membrane reaching middle one-third of abdominal segment IX; posterior angle of connexival segments V and VI slightly remarked on surface; gonocoxae I well developed longitudinally and transversely widened; paratergite IX square, length exceeding posterior margin of gonocoxae I (Figs. 9, 13). *Measurements:* Head length: 3.05 mm; interocellar space: 0.65 mm; interocular space: 1.30 mm; width across eyes: 2.30 mm; preocular distance: 1.90 mm; length antennal segments: I, 4.10 mm; II, 5.65 mm; III, 3.80 mm; IV, 2.25 mm. Pronotal length: 3.60 mm; width across frontal angles: 1.80 mm; width across humeral angles: 5.85 mm. Scutellar length: 2.45 mm; width: 2.15 mm. Maximum length of gonocoxae I, seen frontally: 3.00 mm; maximum width of gonocoxae I, seen laterally: 1.60 mm. Total body length: 17.30 mm.

Male.—Unknown.

Diagnosis.—The peculiar long and slender (Fig. 5) projections of the humeral angles of the pronotum, the pale red-orange coloration of the clavus, corium, connexivum and the abdominal segments, and the two yellow rings on the tibiae, are diagnostic characters of *T. sumatrana.* All the other species have shorter and more robust conical projections of the humeral angles; their clavus, corium, connexivum and abdominal segments are black, and their tibiae lack two yellow rings.

Etymology.—Named for its occurrence on the Island of Sumatra.

Material Examined.—See types.

Acknowledgment

We are indebted to the following individuals and institutions for the loan of specimens and other assistance: Gordon M. Nishida (Bernice P. Bishop Museum, Honolulu); J. Palmer and Janet Margerison Knight (British Museum [Natural History], London); Jan Van Tol (Rijksmuseum van Naturlijke Histoire, Leiden); W. Hogenes (Zoologisches Museum, Universiteit Van Amsterdam); B. Hauser (Museum d'Histoire Naturelle, Geneva).

Special thanks are extended to the Dirección General de Asuntos del Personal Académico of the Universidad Nacional Autónoma de México (DGAPA) and to the Consejo Nacional de Ciencia y Tecnología (CONACyT) for financial assistance to the senior author.

We thank the reviewers for reading and comments.

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Received 1 July 1991; accepted 18 October 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 133–139, (1992)

DESCRIPTIONS OF IMMATURES OF *EOEURYSA FLAVOCAPITATA* MUIR FROM TAIWAN (HOMOPTERA: DELPHACIDAE)

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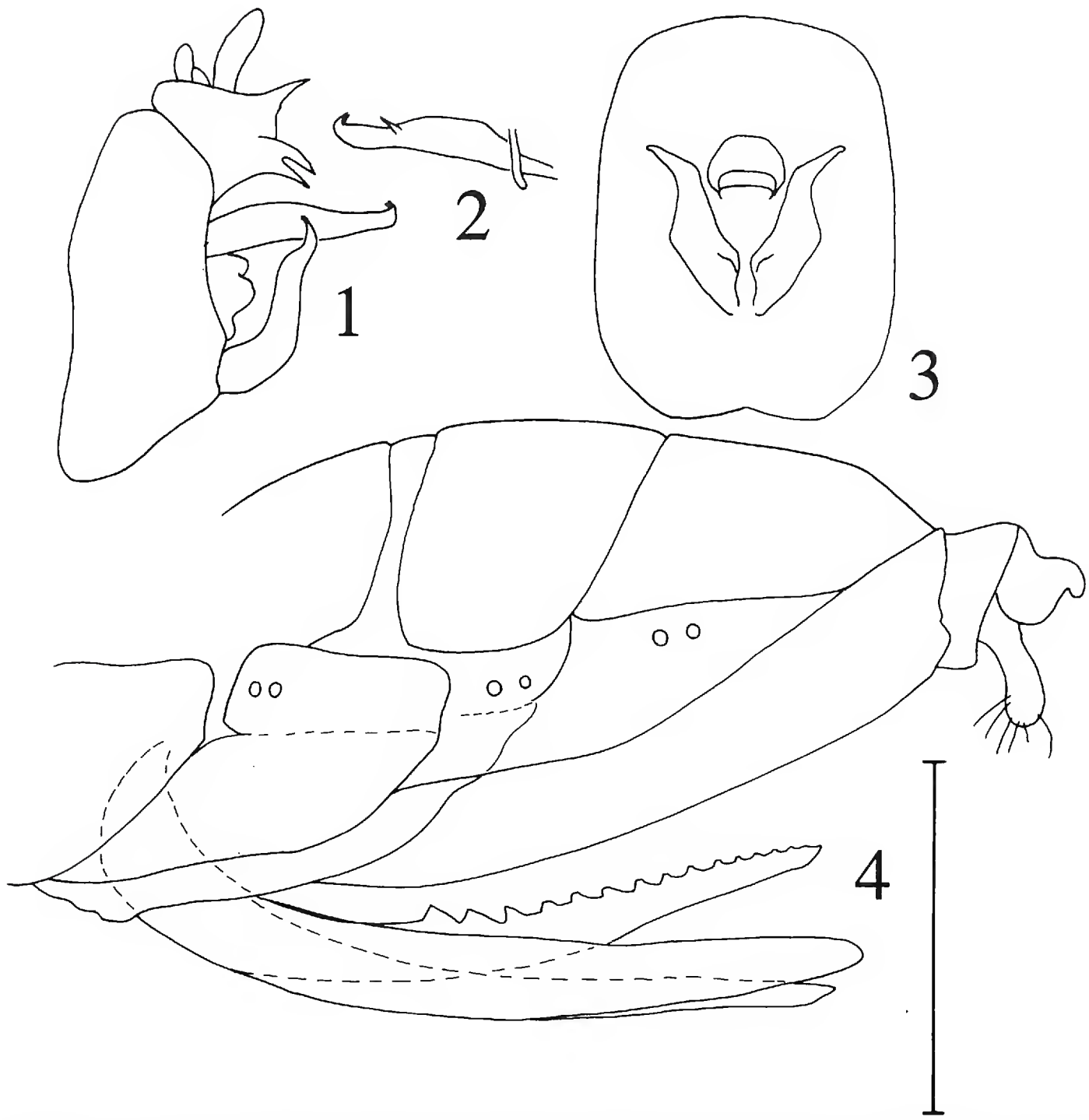
Abstract.—Adult male and female genitalia, the egg, and first through fifth instar nymphs of the delphacid planthopper *Eoeurysa flavocapitata* Muir, collected from sugarcane (*Saccharum officinarum* L.) from Taiwan are described and illustrated and a key to instars is provided. Features useful in separating nymphal instars include differences in body size and proportions; spination of metatibiae, metatibial spurs, and metatarsomeres; and number of metatarsomeres.

Key Words.—Insecta, Homoptera, Delphacidae, *Eoeurysa flavocapitata,* immature stages, Taiwan, sugarcane

The delphacid planthopper *Eoeurysa flavocapitata* Muir has been recorded from northeastern India, Bangladesh, Malaysia, China, Indonesia, and Taiwan (Chatterjee 1971, Chatterjee & Choudhuri 1979, Chu & Chiang 1975, Metcalf 1943, Mirza & Qadri 1964, Qadri 1963). Adult females insert eggs in, and adults and nymphs feed on, leaves of sugarcane (*Saccharum officinarum* L.). Feeding causes leaf desiccation, development of red streaks on damaged tissue, and growth of sooty mold on the honeydew produced by the planthopper (Chatterjee & Choudhuri 1979, Fennah 1969). Sugarcane is the only recorded host, and *E. flavocapitata* may be monophagous on this grass as are over 20 species of sugarcane delphacids in the genus *Perkinsiella* (Wilson 1988). However, the Neotropical sugarcane pest *Saccharosydne saccharivora* (Westwood) was found to have two species of *Andropogon* as its natural hosts (Metcalfe 1969) and apparently included the related grass sugarcane (all in the tribe Andropogoneae [Clayton and Renvoize 1986]) in its range of food plants after introduction of sugarcane to the New World. The only other *Eoeurysa, E. arundina* Kuoh and Ding, has been found only on *Arundo donax* L. (Yang 1989), another economically important grass, which is not closely related to sugarcane (Clayton & Renvoize 1986).

The biology of *E. flavocapitata* on sugarcane was studied by Chatterjee & Choudhuri (1979) and Jiang (1976) who provided information on oviposition, feeding sites, and duration of stadia. Adults were described and illustrated by Chu & Chiang (1975), Jiang (1976) and Yang (1989). Brief descriptions of immatures were provided by Chatterjee & Choudhuri (1979), who also included somewhat diagrammatic illustrations, and Jiang (1976 [in Chinese]); the fifth instar was described, and partial illustrations provided, by Wu & Yang (1985). The present paper includes detailed descriptions and illustrations of adult male and female genitalia, and the immature stages; it also gives a key for the separation of nymphal instars.



Figures 1–4. *Eoeurysa flavocapitata* adult genitalia. Figure 1. Male, left lateral view of complete genitalia. Figure 2. Male, right lateral view of aedeagus. Figure 3. Male, caudal view of pygofer and styles. Figure 4. Female, lateral view of complete genitalia. Scale bar = 0.5 mm.

Methods

Terminology used in the description of the female genitalia follows Asche (1985) and Heady & Wilson (1990). The fifth instar is described in detail but only major differences are described for fourth through first instars. Arrangement and number of pits is provided for the fifth and fourth instars; this information is not given for earlier instars because the pits are extremely difficult to discern (those that could be observed relatively easily are illustrated). Measurements are given as mean ± SD. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the body, and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum. Eggs were obtained by excising them with a fine needle from sections of field collected sugarcane leaves.

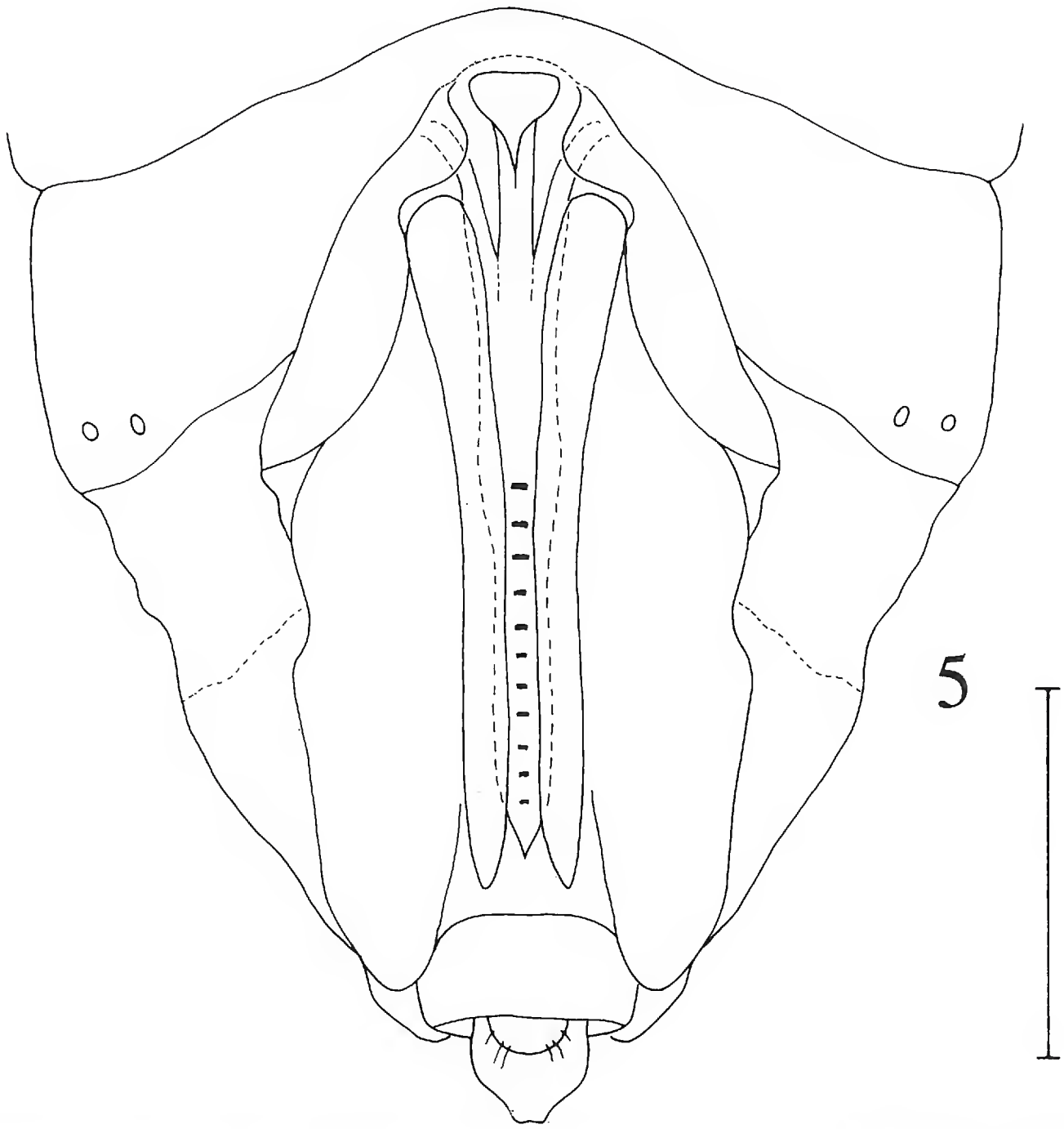


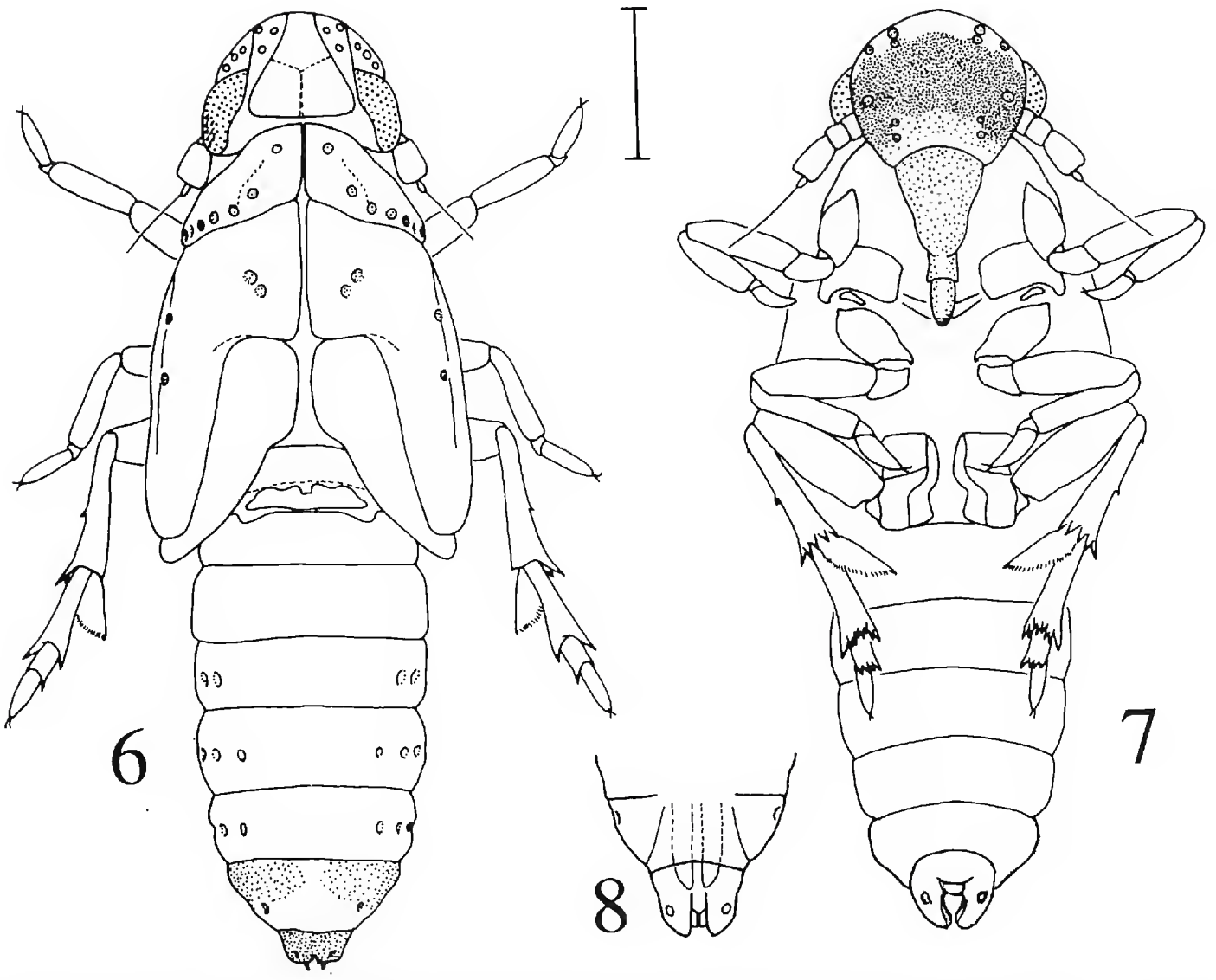
Figure 5. *Eoeurysa flavocapitata* female, ventral view of complete genitalia. Scale bar = 0.5 mm.

Eoeurysa flavocapitata Muir

Descriptions.—Adults (Figs. 1–5). Adult *E. flavocapitata* were briefly described by Muir (1913); detailed descriptions and illustrations provided by Jiang (1976) and Yang (1989) should be referred to for non-genitalic adult morphology.

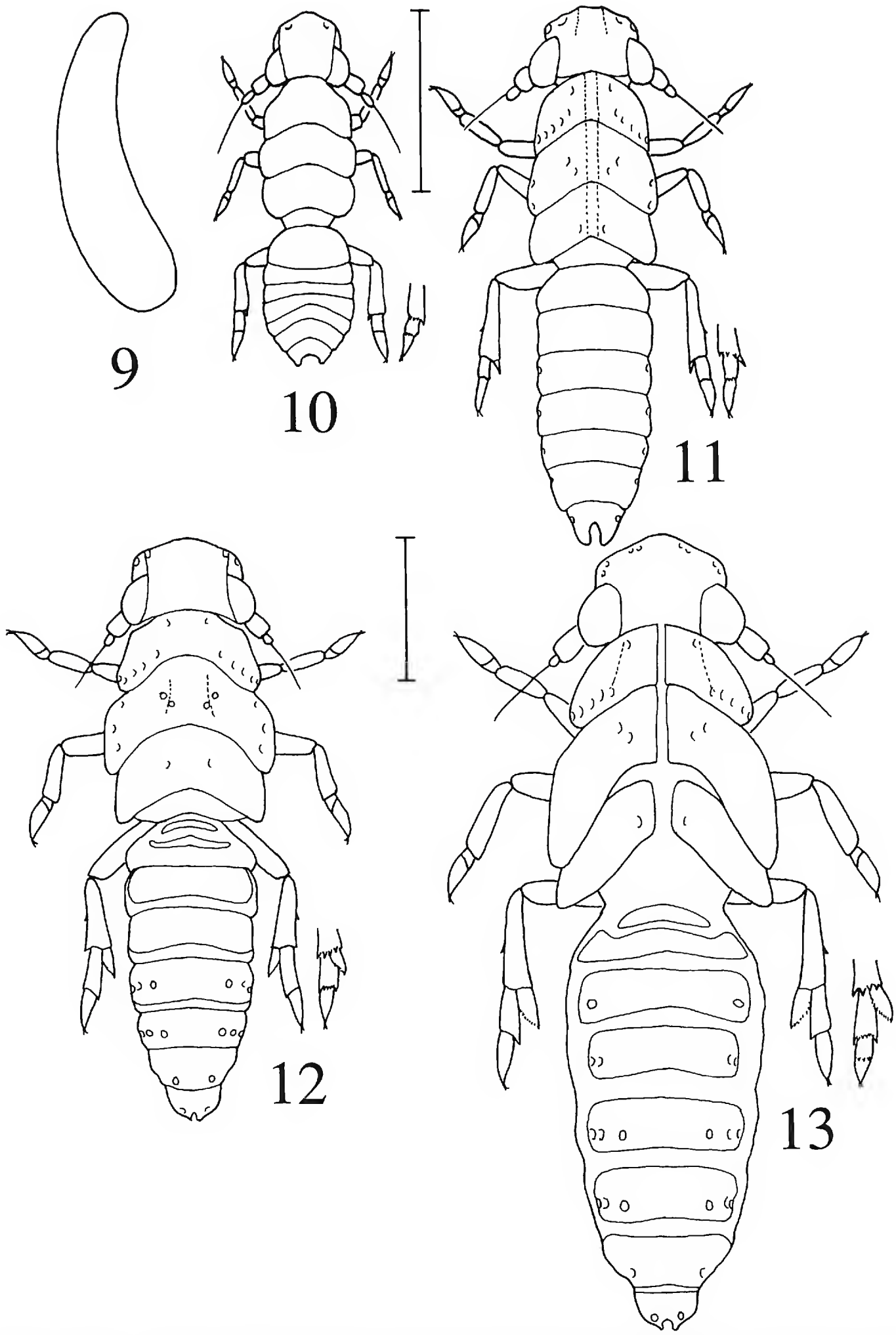
Male genitalia (Figs. 1–3).—Pygofer, in lateral view, subquadrate, with broadly produced diaphragm armature. Anal tube, in lateral view, with a single spinose process originating at the dorsocaudal aspect of the tube, and a pair of bifid spinose processes each originating at the ventrocaudal aspect of the tube. Styles, in caudal view, broadest across basal one-third, narrowing and strongly divergent in apical one-third. Aedeagus subcylindrical, with a dorsally directed terminal bifid tooth and a dorsocaudally directed process in apical one-third on right side.

Female genitalia (Figs. 4, 5).—Tergite nine oriented anteroventrally (see Asche 1985), elongate, longitudinally concave in ventral midline. Anal tube subcylindrical, style somewhat bulbous. Genital scale (or atrium plate) subtriangular. Valvifers of segment eight each covering approximately one-third of tergite nine anterolaterally; medial margin deeply notched in anterior one-third. Lateral gonapophyses of segment nine elongate, broadly rounded posteriorly. In lateral view, median gonapophyses of segment nine saber-shaped, with approximately 15 strong teeth on dorsal margin in distal one-half (not all teeth apparent in ventral view). Gonapophyses of segment eight slender, subacute apically.



Figures 6–8. *Eoeurysa flavocapitata* fifth instar. Figure 6. Habitus, dorsal view. Figure 7. Ventral view of male. Figure 8. Apical part of venter of female abdomen. Scale bar = 0.5 mm.

Fifth instar nymph (Figs. 6–8).—Length 3.6 ± 0.17 mm; thoracic length 1.1 ± 0.06 mm; width 1.2 ± 0.08 mm (n = 10). Body white with gray to fuscous markings on frons, clypeus, and apex of abdomen. Form elongate, subcylindrical, flattened dorsoventrally, widest across mesothoracic wingpads. Vertex subtriangular; posterior margin nearly straight, narrowing anteriorly. Frons border with clypeus concave; lateral margins strongly convex and carinate (outer carinae) and paralleled by second pair of very weak carinae (inner carinae) continuous with lateral margins of vertex; area between inner and outer carinae with nine pits on each side (six visible in ventral aspect, three in dorsal aspect); three pits between each outer carina and eye. Clypeus subconical, narrowing distally. Beak three-segmented, cylindrical, segment one hidden by anteclypeus, segment two subequal in length to segment three, segment three with black apex. Antennae three-segmented; scape short, cylindrical; pedicel subcylindrical, 2.0× length of scape; flagellum bulbous basally, with elongate bristle-like extension distally, bulbous base approximately 0.3× length of pedicel. Thoracic nota divided by middorsal line into three pairs of plates. Pronotal plates subtriangular (in dorsal view); anterior margin convex; posterior border sinuate; each plate with a weak posterolaterally directed carina and seven pits extending anteriorly from near middorsal line posterolaterally to lateral margin (lateralmost pits often not visible in dorsal view). Mesonotum with median length 2.0× that of pronotum; elongate lobate wingpads almost extending to tips of metanotal wingpads; each plate with very weak posterolaterally directed carina (not illustrated); two pits near middle of non-lobate portion of plate and two pits near lateral margin. Metanotum with median length approximately 0.7× that of mesonotum; lobate wingpads extending to fourth tergite; each plate with one very weak pit near middle of plate (not illustrated). Pro- and mesocoxae elongated and directed posteromedially; metacoxae fused to sternum. Metatrochanter short and subcylindrical. Metatibia with two spines on lateral aspect of shaft, an apical transverse row of five black-tipped spines on plantar surface and a subtriangular flattened movable spur with one apical tooth and 13–15 other teeth on posterior margin. Pro- and mesotarsi with two



Figures 9–13. *Eoeurysa flavocapitata* immature stages. Figure 9. Egg. Figure 10. First instar. Figure 11. Second instar. Figure 12. Third instar. Figure 13. Fourth instar. Scale bars = 0.5 mm (top = 9–11, bottom = 12, 13).

tarsomeres, tarsomere one wedge-shaped; tarsomere two subconical, with pair of apical claws and median membranous pulvillus. Metatarsi with three tarsomeres; tarsomere one with apical transverse row of eight black-tipped spines; tarsomere two cylindrical, approximately 3.5× length of tarsomere one, with apical transverse row of four black-tipped spines on plantar surface; tarsomere three subconical, slightly longer than tarsomere two, with pair of apical claws and median pulvillus. Abdomen nine segmented; flattened dorsoventrally; widest across fourth abdominal segment. Tergite one small, subtriangular, hidden by juncture of thorax and abdomen (not visible in illustration); two subrectangular, not extending to lateral aspect of segment; tergites five to eight each with three pits on each side (lateralmost pits not always visible in dorsal view). Segment nine surrounding anus, with three pits on each side; female with one pair of acute processes extending from juncture of sternites eight and nine; males lacking processes.

Fourth instar nymph (Fig. 13).—Length 2.8 ± 0.18 mm; thoracic length 0.8 ± 0.04 mm; width 0.08 ± 0.04 mm (n = 10). Antennal flagellum with basal portion approximately 0.5× length of pedicel. Mesonotal wingpads shorter, each covering approximately two-thirds of metanotal wingpad laterally. Metanotal median length 1.5× that of mesonotum; wingpad extending to tergite two. Metatibial spur slightly smaller, with one apical tooth and eight teeth on margin. Metatarsi with two tarsomeres; tarsomere one with apical transverse row of seven black-tipped spines; tarsomere two subconical with three black-tipped spines in middle of tarsomere on plantar surface. Abdominal segments four to eight each with the following number of pits on either side of midline: tergite four with one pit, five with two, six to eight each with three, segment nine with three.

Third instar nymph (Fig. 12).—Length 2.0 ± 0.12 mm; thoracic length 0.6 ± 0.02 mm; width 0.6 ± 0.03 mm (n = 10). Mesonotal wingpads shorter, each covering one-third of metanotal wingpad laterally. Metanotal wingpad extending to tergite one. Metatibial spur smaller; with one apical and one or two marginal teeth. Metatarsomere one with apical transverse row of six black-tipped spines on plantar surface.

Second instar nymph (Fig. 11).—Length 1.5 ± 0.06 mm; thoracic length 0.5 ± 0.01 mm; width 0.4 ± 0.02 mm (n = 10). Mesonotal median length subequal to that of pronotum; wingpads undeveloped. Metanotal median length subequal to that of mesonotum; wingpads undeveloped. Metatibia with apical row of three black-tipped spines; spur small with no marginal teeth, approximately 3.0× length of longest metatibial spine; metatarsomere one with four apical black-tipped spines.

First instar nymph (Fig. 10).—Length 1.0 ± 0.06 mm; thoracic length 0.4 ± 0.02 mm; width 0.3 ± 0.02 mm (n = 10). Bulbous base of antennal flagellum subequal in length to that of pedicel. Metatibia lacking spines on shaft; metatibial spur smaller, approximately 1.5× length of longest metatibial spine.

Egg (Fig. 9).—Length 0.8 ± 0.05 mm; width 0.2 ± 0.02 mm (n = 5). Eggs laid singly; white, cylindrical, narrower at apical end; chorion translucent, smooth.

Material Examined.—Specimens used for description have the following data: REPUBLIC OF CHINA. *TAIWAN:* Taichung, 5 Dec 1989, ex sugarcane, (10 males, 12 females, 5 eggs, 19 first instars, 14 second instars, 15 third instars, 25 fourth instars, 19 fifth instars).

Key to *E. flavocapitata* Nymphal Instars

1. Metatibial spur with more than five marginal teeth (Figs. 7, 13); mesonotal wingpads overlapping more than one-half length of metanotal wingpads (Figs. 6, 13) 2
– Metatibial spur with fewer than five marginal teeth; mesonotal wingpads overlap less than one-half length of metanotal wingpads (Figs. 10–12) 3
2(1). Metatarsi with three tarsomeres; metatibial spur with more than 10 marginal teeth; mesonotal wingpads extending to or almost to apex of metanotal wingpads (Figs. 6, 7) ..... fifth instar
– Metatarsi with two tarsomeres; metatibial spur with eight marginal teeth; mesonotal wingpads not extending to apex of metanotal wingpads (Fig. 13) ..... fourth instar
3(2). Metatibia with transverse row of four apical spines, spur with one or two marginal teeth (Fig. 12) ..... third instar

– Metatibia with transverse row of three apical spines, spur lacking marginal teeth (Figs. 10, 11) 4

4(3). Metatibia with lateral spine near middle on outer surface; spur approximately 3.0× length of longest metatibial apical spine (Fig. 11) . . . . . second instar

– Metatibia without lateral spines; spur approximately 2.0× or less length of longest metatibial apical spine (Fig. 10) . . . . . first instar

Acknowledgment

Florida Agricultural Experiment Station Journal Series R-01742.

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Received 24 July 1991; accepted 23 October 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 140–143, (1992)

A REDESCRIPTION OF *ORDOBREVIA NUBIFERA* (FALL) (COLEOPTERA: ELMIDAE)

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Abstract.—Newly found variation in the size, sculpturing and color of *Ordobrevia nubifera* (Fall) is described. This variation may be linked to varying larval developmental rates.

Key Words.—Insecta, Coleoptera, Elmidae, *Ordobrevia,* variation, development

The genus *Ordobrevia* was erected in 1953 by Sanderson, with *Stenelmis nubifera* Fall, 1901 as its type species. At that time, *S. nubifera* was the sole member of the "*nubifera* group" of *Stenelmis* (Sanderson 1938). Twelve more species of *Ordobrevia* have been described since 1953. Four are from the Palaearctic region (Japan) and eight are from the Oriental region (Brown 1981). It thus appears that *Ordobrevia nubifera* represents an intrusion of the Palaearctic/Oriental fauna into the Nearctic fauna. *Zaitzevia* (Elmidae) and *Eubrianax* (Psephenidae) show similar intrusions (Brown 1981).

Ordobrevia nubifera occurs only in North America, and its known range extends from California to Washington (Brown 1972). More is known about California populations than those in other areas. Within California, *O. nubifera* occurs widely throughout all the various mountain ranges. It inhabits streams of all sizes from first order to much larger. It seems to prefer microhabitats with faster flows and coarser substrates.

Several years ago I found what seemed to be a new species of *Ordobrevia.* It was larger and more robust, and it had more coarse granulation and a distinctly different color pattern. I came embarassingly close to describing it as a new species. Subsequent collections have shown it to be the end of a previously unknown range of variation within *O. nubifera.* Recent studies of the elmid fauna of Taiwan by M. L. Jang and P. S. Yang, and an ongoing revision of *Stenelmis* by Kurt Schmude have called into question the status and identity of *Ordobrevia.* Because of these two recent studies and discovery of additional intraspecific variation in *O. nubifera,* I decided to review what was known about *Ordobrevia nubifera.*

Existing work that illustrates *O. nubifera* includes the following: for larvae, ninth abdominal tergum (Sanderson 1953: fig. 24), mesothorax (Leech & Chandler 1956: fig. 13:51h), habitus (Brown 1972: figs. 163 and 164), head (White et al. 1984: fig. 19.246); and for adults, aedeagus (Sanderson 1938: fig. 1), antenna (Sanderson 1938: fig. 7), elytral pattern (Sanderson 1938: fig. 19), elytron (Leech & Chandler 1956: fig. 13:52g), and habitus (Brown 1972: fig. 25, White et al. 1984: fig. 19.272).

ORDOBREVIA NUBIFERA (FALL) 1901

Redescription.—(both sexes, except as indicated).—BODY: Body elongate, slender (Fig. 1) to robust (Fig. 2), parallel sided; sculpturing and granulation slight to very coarse. Pronotum narrower than

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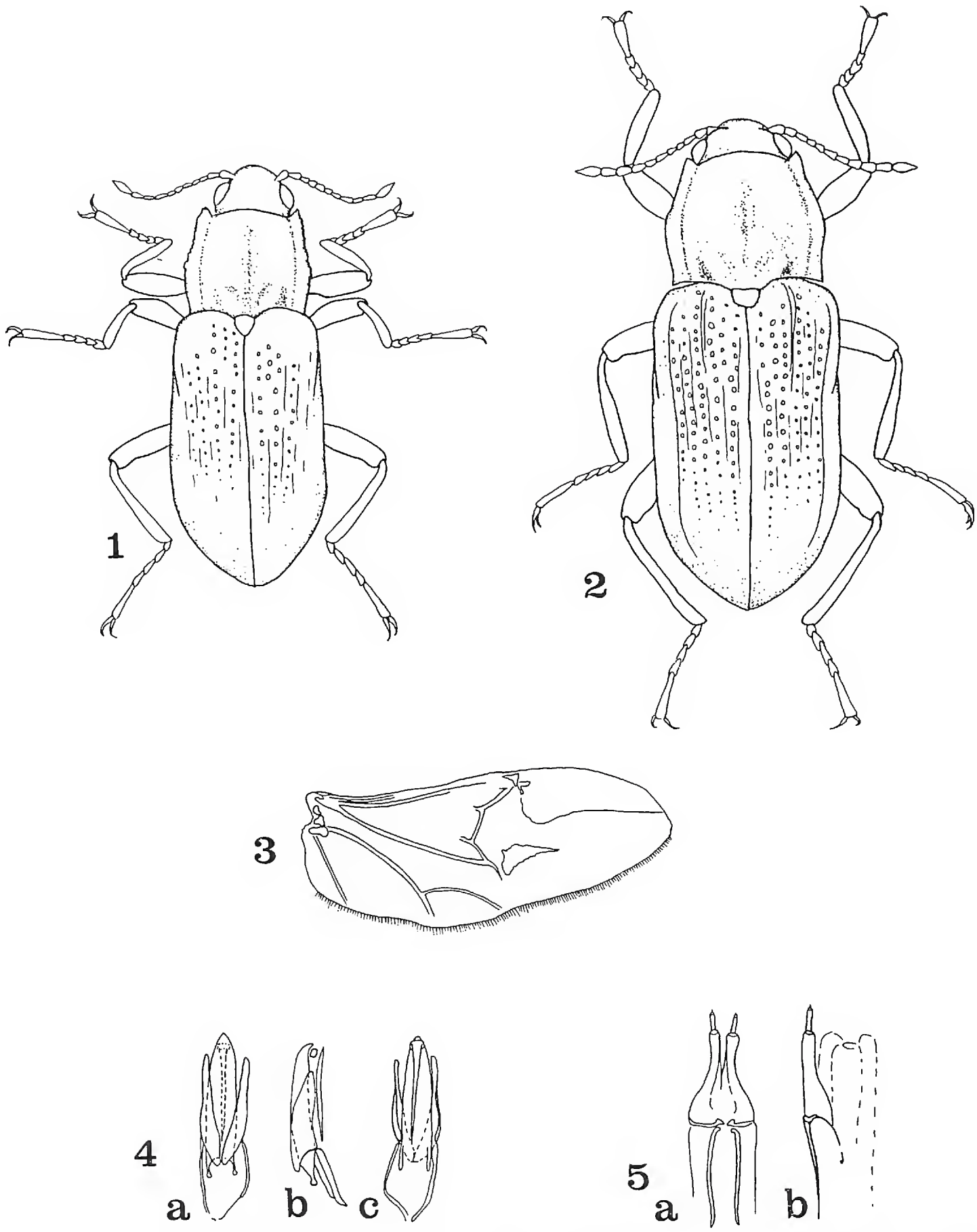

Figures 1–5. *Ordobrevia nubifera.* Figure 1. Typical morph. Figure 2. Large morph. Figure 3. Right wing. Figure 4. Aedeagus (a—dorsal view, b—lateral view, c—ventral view). Figure 5. Ovipositor (a—dorsal view, b—lateral view).

elytra. Body uniformly brown to testaceous, with a transverse yellow band across the middle of the elytra. Length 2.0–2.6 mm; width 0.8–1.2 mm. HEAD: Head covered with granules. Granules longitudinally elongate on the epicranial surface, less elongate elsewhere. Antennal ridges prominent dorsally. Fronto-clypeal suture absent. Clypeus with coarse setae on apical margin. Labrum dark brown, shiny, coriaceous; apical margin with thick medially curved setae. Mandibles prominent; tips trifid. Palpi three-segmented, last segment broad and apically truncate; labial palpi lighter than maxillary palpi. Antennae eleven-segmented; segments one to six narrow; segments seven to eleven apically

widened forming a weakly defined club, possessing lateral tufts of whitish setae. PRONOTUM: Pronotum usually wider than long, width greatest just behind middle. Base of pronotum wider than apex, lateral margins sinuate and weakly serrate. Entire surface covered with close-set granules and punctures. Median longitudinal sulcus in basal three-fourths of pronotum; sulcus deeper anteriorly. Base of median sulcus with two depressions on each side. ELYTRA: Elytra with punctae arranged in striae. Punctures smaller and less distinct in apical one-third, obsolete at tip. Surface between punctures smooth and shiny to coarsely granulate. First and accessory striae join in basal one-fourth. Intervals raised; third intervals carinate in basal third; sixth intervals forming sublateral carinae that reach almost to apex. Humeri distinct and produced beyond basal pronotal margins. Epipleura extend almost to tip of elytra. WINGS: Wings entire (Fig. 3); posterior edge with fringe of fine setae. Venation reduced. VENTER: Hypomera, pro-, meso-, and metasternum covered with granules separated by less than their own width. Prosternal margin projecting anteriorly under head and labium. Prosternal process parallel-sided, projecting beyond coxae, with apex apically rounded. Mesosternum very short, broadly truncate apically, reaching only to middle of mesocoxae; median longitudinal sulcus present. Metasternum similar to mesosternum but longer, with apex broadly emarginate. Abdomen with five visible segments; males with segment V with lateral margins produced into short wide spines and narrowly emarginate apically; females with lateral margins only weakly spiniform and apex broadly emarginate. Granules on segment I rounded, separated by own width, those on segments II–V elongate, more widely separated. All segments with lateral flanges closely fitting into the epipleura. LEGS: Pro- and mesocoxae rounded, metacoxae transverse. Metathoracic legs slightly longer than others. Granules on coxae rounded, close-set. Granules on trochanters 2.0× as long as wide. Granules on femora and tibiae very elongate, arranged parallel to the axes of the legs. GENITALIA: Male genitalia (Fig. 4) with parameres shorter than median piece; accessory sclerites include a longitudinally elongate ventral sclerite and a short transverse rectangular sclerite located between the tips of the median piece and the ventral piece; basal piece weakly sclerotized, varying from a flattened U-shape to a complete ring. Female genitalia (Fig. 5) typical for elmids.

Discussion

This species shows considerably more size variation than previously stated. However, I think that size ranges given in the literature are often the result of repetition of earlier measurements that may have been based on relatively few specimens. The morph that I earlier almost mistook for a new species is now considered to be the upper range of size for *O. nubifera.* It is longer and much wider than "typical" specimens. A more strongly developed granulation, punctation and sculpturing, and a trend toward uniformly dark brown color is correlated with increasing size. Other morphologic characters remain unchanged, albeit somewhat larger in proportions.

There seem to be higher percentages of larger individuals of *Ordobrevia nubifera* in populations in the northern Coastal Mountains and the Warner Mountains than in other parts of California (unpublished data). These larger individuals of *O. nubifera* often occur with "typical" specimens. However, the larger morph is a larger percentage of the population in rather cold streams, or in areas that experience rather cold winter weather. I now think that they represent larvae in which the normal developmental rate was retarded allowing the normal growth rate to produce a larger-than-normal individual. Larger larvae, of course, mean larger adults. Differential manipulation of developmental rates has been shown to cause different sized morphs in the worker caste of ants (Oster & Wilson 1978). I have found similar, larger-than-normal individuals in several other elmid genera. Retardation of developmental rates could be a result of intrinsic factors (e.g., genetic recombinations, random mutations) or extrinsic factors (e.g., cold temperatures, limited supplies of specific nutrients). My experiences lead me to favor the cold temperatures as the major influencing factor. Some described variations

in *Microcylloepus,* another elmid, appear to be temperature correlated (Shepard 1990). However, in this case, smaller-than-normal individuals (and species) occur in warmer habitats. There, I believe, the developmental rate is accelerated while the growth rate remains unaffected. Thus the individuals mature at a smaller body size. More study is warranted concerning the influences of varying temperatures upon life cycle events in natural populations.

My near description of a new species of *Ordobrevia* should alert other taxonomists to sample extensively and pay more attention to intraspecific variation. Even though I had previously collected and identified hundreds of the "typical" *O. nubifera,* I did not have an accurate idea of the total intraspecific variation until I collected in streams that were perennially cold, or were very cold during large parts of the year. I am also reminded of the necessity of obtaining population samples large enough to contain the rarer morphs within a population. This is especially a problem when sampling aquatic insects in such an ecologically diverse area as California. Larger population samples have led me to question the validity of several California elmid species.

Acknowledgment

Harley P. Brown kindly loaned specimens from his collection for this study, and generously offered his comments on the manuscript. Part of this study was supported by a summer research position at the University of Oklahoma Biological Station.

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Received 25 June 1991; accepted 1 November 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 144–152, (1992)

A REVIEW OF THE SWEETPOTATO WHITEFLY IN SOUTHERN CALIFORNIA

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Abstract.—The sweetpotato whitefly, *Bemisia tabaci* Gennadius, of Palaearctic origin was originally introduced into California in the late 1920s. Since that time it has been restricted to the state's southern desert valleys and has, at times, been a significant agricultural problem. In the mid-1980s, however, a new "strain" of *B. tabaci* was introduced to southern California and has wreaked great havoc in the area. This strain, from poinsettia plants, has become known as the B strain, poinsettia strain or poinsettia whitefly. This paper documents the new introduction, notes the poinsettia strain's differences from other *B. tabaci,* and assesses the possibilities for its control.

Key Words.—Insecta, Aleyrodidae, *Bemisia tabaci,* sweetpotato whitefly, California

California has been experiencing serious problems with whiteflies during the last several years. Of the approximately 1160 described species of whiteflies in the world, 54 occur in the state along with approximately a dozen undescribed native species. Of California's described species, at least 11 were introduced by man's activities, and five have been introduced in the last 15 years. Several of the introduced species have become serious pests and two are currently quite problematic: the ash whitefly, *Siphoninus phillyreae* (Haliday), and the sweetpotato whitefly, *Bemisia tabaci* (Gennadius). These species currently have extremely large populations in areas of California.

The ash whitefly, an easily recognized species, was introduced into the state in the late 1980s, and although it spread rapidly with tremendous population explosions (Sorensen et al. 1991), a successful parasite was found (Bellows et al. 1991) and effective biological control has progressed rapidly. The sweetpotato whitefly (SPW), however, has been in California since the 1920s (Russell 1975), but only in the last two decades, particularly the early 1980s, has it been a serious agricultural problem (Natwick & Zalom 1984) and a taxonomic and ecological curiosity. Currently, it is in a disastrous expansion phase in southern California, which involves the acquisition of many new hosts. This paper documents the ecological history and potential taxonomic problems with SPW in southern California.

BACKGROUND

The *Bemisia tabaci* was originally described as an *Aleyrodes* from tobacco in Greece in 1889 (Gennadius 1889). Since then, the species has been redescribed in synonymy many times (Table 1). The insect has spread to most tropical and subtropical areas of the globe, occasionally causing serious damage upon colonization. It was first recorded from India in 1905 (Misra & Lambda 1929, Reddy & Rao 1989, Immaraju 1989), and by 1919 had become a serious pest of cotton in the Punjab (now Pakistan) (Immaraju 1989). It has been reported as a serious

Table 1. Taxonomic synonyms of sweetpotato whitefly.[a]

Genus	Species	Author	Date	Type locality
Aleyrodes	*tabaci*	Gennadius	1889	Greece
Aleyrodes	*inconspicua*	Quaintance	1900	Florida
Bemisia	*emiliae*	Corbett	1926	Sri Lanka
Bemisia	*costa-limai*	Bondar	1928	Brazil
Bemisia	*signata*	Bondar	1928	Brazil
Bemisia	*bahiana*	Bondar	1928	Brazil
Bemisia	*gossypiperda*	Misra & Lambda	1929	Pakistan
Bemisia	*acyranthes*	Singh	1931	Pakistan
Bemisia	*hibisci*	Takahashi	1933	Taiwan
Bemisia	*longispina*	Priesner & Hosny	1934	Egypt
Bemisia	*gossypiperda* var. *mosaicaivectura*	Ghesquiere	1934	Zaire
Bemisia	*goldingi*	Corbett	1935	Nigeria
Bemisia	*nigeriensis*	Corbett	1935	Nigeria
Bemisia	*rhodesiaensis*	Corbett	1936	Rhodesia
Bemisia	*manihotis*	Frappa	1938	Madagascar
Bemisia	*vassyierei*	Frappa	1939	Madagascar
Bemisia	*lonicerae*	Takahashi	1957	Japan
Bemisia	*minima*	Danzig	1964	U.S.S.R.
Bemisia	*miniscula*	Danzig	1964	U.S.S.R.

[a] See Taxonomic Assessment and Biological Control section for comments on *B. poinsettiae* Hempel, 1923.

pest of various crops in: the West Indies, Nicaragua, Venezuela, Brazil, Turkey, Israel, Egypt, Sudan, Iran, Thailand, and the Philippines. In addition, it is known from southern Europe, the Middle East, much of Africa, Madagascar, Sri Lanka, China, Malaya, Australia, New Guinea, Fiji, and Hawaii, among other locations. By 1978, SPW was known from at least 420 plant species in 18 families (Mound & Halsey 1978, Greathead 1986), but new hosts are being continually added as the current infestation in California and Arizona grows. Currently, SPW is a major economic pest of cotton, tobacco, cassava, sweetpotato and soy bean in many areas of the world.

After its introduction to the U.S., SPW was redescribed as *Bemisia inconspicua* by A. L. Quaintance (1900) from material collected on okra and sweetpotato in Florida between 1897 and 1898. Later, museum specimens were found to have been collected in Pomona, Putnam County, Florida in 1894 (Russell 1975). It has since spread across the southern part of the U.S. Prior to 1985, it was found in outdoor environments in Florida, Georgia, Texas, Arizona and California. Recently, it has been found in extremely high populations in the agricultural areas of Arizona, California, Texas and northwestern Mexico.

History in California

Specimen records at the U.S. National Museum of Natural History indicate it had been introduced into California by at least 1928 (Russell 1975), when it was collected on cotton at Calipatria, Imperial County. Subsequent records of early spread in California are shown in Table 2. Although SPW was in California in the late 1920s, it was found outdoors only in the desert valleys of Imperial,

Table 2. The earliest records of the spread of *Bemisia tabaci* within California, after its 1928 introduction (Calipatria, Imperial Co.) on cotton.

Year	County	Location	Host
1947	Riverside Co.	Coachella	sweetpotato
1950–1954	Riverside Co.	Indio	cotton
1951	Imperial Co.	Calexico	cotton
1952	Riverside Co.	Coachella	cotton
1953	Riverside Co.	Thermal	sweetpotato
1953	Riverside Co.	Mecca	sweetpotato
1954	Imperial Co.	Imperial	cotton
1954	Riverside Co.	Riverside	cotton[a]
1955	Riverside Co.	Riverside	euphorbia[a]
1961	San Bernardino Co.	Yucca Valley	*Hibiscus* sp.

[a] In greenhouse.

Riverside, San Bernardino and San Diego Counties. It was seldom, if ever, found in greenhouses in California, and then usually on plants imported recently from other states.

In the Imperial Valley of California, a curious and disastrous phenomenon occurred with SPW in the summer and fall of 1981; its populations exploded on numerous crops, including cotton, melons and lettuce. D-Vac® monitoring by University of California Agricultural Extension personnel collected over 60,000 whiteflies per 100 sweeps of the devices (Natwick & Leigh 1984). The large numbers of whiteflies were severely debilitating the infested crops, and also transmitting serious viral diseases to the crops. High incidences of squash yellow leaf curl and lettuce infectious yellows resulted in premature plow-down and total crop loss in many lettuce and melon fields in fall 1981 (Duffus & Flock 1982, Natwick & Zalom 1984).

Although 1981 was a disastrous year for the growers in the Imperial, Bard and Palo Verde Valleys of California, SPW had actually been building up populations over the preceding several years. University of California extension personnel had been making routine whitefly counts for many years (Natwick & Leigh 1984) because SPW and another species, banded-winged whitefly [*Trialeurodes abutiloneus* (Haldeman)] were found on cotton infested with cotton leaf crumple, a viral disease. Prior to 1975, D-Vac® catches for SPW were running consistently lower than 300–400 per 100 sweeps. However, in 1975 the number jumped to nearly 4300 whiteflies per 100 sweeps. Numbers dropped the next year, only to leap to an incredible 35,000 whiteflies per 100 sweeps in 1977. The populations dropped again to near zero in 1978, only to be followed by the disastrous rebound seen in 1981.

There are several possible causes for these population explosions, which probably result from several interrelated concurrent events. Starting in 1975, the southern California desert areas experienced unusually warm winter temperatures, with a virtual absence of days below freezing (only two years out of nine had recorded temperatures below 0° C) (Flock & Christopherson 1985). Because SPW is apparently of tropical origin, cool or cold temperatures appear to prevent normal development, while high summer temperatures and humidity probably enhance development. Comparing the warm winter temperature ranges in the Imperial

Valley with the sudden upsurges observed in SPW populations shows an intriguing, yet not exactly corresponding, correlation.

A second event in the Imperial Valley area in 1975 involved the first use there of synthetic pyrethroid insecticides for general pest control (E. T. Natwick, personal communication). Such pyrethroids have a devastating effect on the natural enemies (primarily parasitoids) of SPW. Essentially the lack of cold winter temperatures allowed SPW to maintain larger than normal populations through the winter, and a reduced natural enemy population allowed SPW an unencumbered pathway to the devastating populations that were encountered between 1975 and 1990. By 1986, researchers and growers were discovering ways to deal with the SPW problem. They observed that the SPW population was building up on cotton to such large levels that by the time the cotton was ready for the normal fall defoliation and harvest, it would be heavily covered with honeydew and sooty mold. When the cotton was defoliated, the whiteflies would move in large numbers into other crops including squash, melons, lettuce, sugar beets, tomatoes and other specialty crops, transmitting viral diseases presumably picked up from weeds and other virus infected hosts. By defoliating cotton early, it was found that SPW did not have time to develop large populations that could move onto other crops, and the cotton would be fairly free of honeydew and sooty mold (Meyerdirk et al. 1986).

By 1990, just when the SPW problem seemed to be under control in the desert southwest, a second disastrous phenomenon occurred, this time as a result of events in Florida four years earlier. SPW had maintained a foothold in Florida for many years, seldom being more than a scientific curiosity. Inexplicably in 1986, growers of greenhouse poinsettias had a devastating outbreak of SPW that appeared overly resistant to chemical control (Hamon & Salguero 1987). As the summer of 1986 wore on, these SPW jumped to numerous other greenhouse bedding plants and nursery stock; they also began infesting outdoor vegetable crops and gardens with disastrous results. By 1987, the large poinsettia nurseries of San Diego County were found to be infested, and over the next year or two SPW was found on poinsettias in many greenhouses throughout California. Shortly thereafter, in late 1990, SPW moderately infested commercial citrus groves near Phoenix, Arizona; it had never been found on this crop in economically damaging populations before (D. N. Byrne, personal communication). SPW was observed to spend the winter in fairly large numbers on this plant.

Prior to the find of SPW on citrus, researchers in Florida and Arizona were beginning to evaluate some of the characteristics and effects of the SPW "strain" (hereafter referred to as poinsettia SPW) that began attacking greenhouse poinsettias and other crops in Florida in 1986. Poinsettia SPW was found to cause virus-like symptoms in cucurbits (Yokomi et al. 1990; Costa & Brown 1990, 1991a, b) that were quickly called "squash silver leaf." These symptoms probably are related to a phytotoxin injected into the plant by poinsettia SPW, because the plants recovered from the effects when the whiteflies were removed.

In contrast, it was found that the original "strain" of SPW (hereafter referred to as cotton SPW) reared from cotton, squash and other crops in Arizona (Costa & Brown 1990, 1991) and California (Perring et al. 1991) did not produce these same symptoms in squash plants. Shortly thereafter, researchers in Arizona (Costa & Brown 1990, 1991) and California (Perring et al. 1991) investigated the isozymic

variation in poinsettia versus cotton SPW "strains" using several different electrophoretic techniques. Populations of poinsettia SPW from poinsettias were found to show slight, but consistently different, esterase banding patterns from those cotton SPW populations that had existed in the southwest prior to 1986. Taxonomists, however, have not been able yet to show a morphological difference between these populations, and they are both currently considered to be *B. tabaci.*

After SPW was discovered on citrus in Arizona, it was assayed using electrophoretic techniques and found to be poinsettia SPW (D. N. Byrne, personal communication). By early spring 1991, it became evident that SPW was occurring in large numbers over the winter on cole crops, particularly broccoli, in the Yuma and Imperial Valleys; the presence of SPW on cole crops in winter had never been experienced in these areas before. These whiteflies also were determined to be poinsettia SPW (T. M. Perring, personal communication).

By July 1991, it was obvious that a major and catastrophic change had taken place in the SPW situation in the Imperial and Palo Verde Valleys (Weddle & Carson 1991, Perring et al. 1991). Observers in the field made many startling discoveries. Some cotton was covered completely by adult whiteflies before the plants could produce more than three or four leaves. The first leaves of squash plants were being devastated before the plants could send out three or four inches of runners. Many fields were disced under. The cotton that did mature was hopelessly sticky with honeydew before the bolls could open. Fields of alfalfa were so sticky they could not be baled. In late August, table grape vineyards on the north shore of the Salton Sea in Riverside County were found heavily infested and sticky with SPW. The same was found on new growth of grapefruit plantings and on many weed species in the immediate vicinity. Some of this infestation apparently originated from clouds of SPW that have been observed flying across the Salton Sea from breeding grounds in the Imperial Valley. These whiteflies are generally considered to be the poinsettia SPW.

After just one season, cotton SPW is now believed to be practically nonexistent in California (T. M. Perring, personal communication), due either to interbreeding, competition between the two strains, the extreme cold temperatures of December 1990, or possibly all of these reasons. Cross breeding experiments that are now being conducted in Arizona and California may shed light on this phenomenon. However, work that had been done on the two strains prior to this summer has also produced some other interesting differences between the two SPW strains. Poinsettia SPW is more cold tolerant. The time required to complete a generation has been found to be slightly shorter in poinsettia SPW, or identical in the two strains (usually 16–23 days), but poinsettia SPW is considered to be five times as prolific (T. M. Perring, personal communication). Poinsettia SPW has been found to extract five times as much nutrient material from plants and, therefore, produces five times as much honeydew as cotton SPW. Although cotton SPW is thought to be a better virus disease vector, at least with lettuce infectious yellows (J. E. Duffus, personal communication), poinsettia SPW has produced such large populations that plants die before virus symptoms appear (F. Laemmlin, personal communication), so its effectiveness in virus transmission is unknown. Furthermore, poinsettia SPW severely attacks more crops, including some not previously utilized by cotton SPW.

By the first week in October 1991, SPW had been found in moderate numbers in dooryard vegetable gardens in the city of San Bernardino. This is the first

important record for any SPW outdoors in California outside of the desert valleys. One week later, SPW was found on established, outdoor poinsettia bushes in Riverside, Riverside County. The owners of these bushes said that the whiteflies had been a problem since the previous year. By December, SPW had been found in three southern San Joaquin Valley counties in field situations not associated with nurseries.

Taxonomic Assessments and Biological Control

As was done with ash whitefly, the first step that should be taken to find an effective biological control for SPW is to identify the native home of the insect, so that natural enemies can be found. In the case of SPW, however, this creates an immediate dilemma. Up until recently, the native home of SPW was thought to be either the Orient or Africa/the Middle East (Mound 1963, Lopez-Avila 1986, Anonymous 1987). Other *Bemisia* are prevalent in southern Russia and are also known from mainland Asia, southeast Asia along the Pacific rim, Africa, and one species each from South America and the western United States (Mound & Halsey 1978). Certainly, the area to the north and west of Pakistan shows the greatest diversity in parasitoids of *Bemisia* (Mound & Halsey 1978, N. Mills 1992), reputedly an indication of a genus epicenter.

SPW was probably moved around the world at a very early date, but was not described until 1889. Because SPW has probably been reintroduced into many countries numerous times, it becomes extremely difficult to trace the origin of the whitefly. Because poinsettia and cotton SPW cannot presently be separated morphologically, we cannot effectively access pre-1986 museum specimens to ascertain where poinsettia SPW occurred prior to 1986. Lacking adequate surveys using electrophoretic analysis to separate the strains, we so far have very limited knowledge of where poinsettia SPW presently occurs in the world. We know only that it has been transported over most of the U.S. and the Caribbean on poinsettia and other nursery crops (J. K. Brown, personal communication). It has also been transported to Canadian greenhouses (Broadbent et al. 1989), from where it escaped to the field but probably could not survive the Canadian winters.

Recently, however, evidence is emerging that indicates *B. tabaci* may be of New World origin. For example, it seems to do best on hosts that are of New World origin (unpublished data), such as sweetpotato, poinsettia, tomato, common bean, squash, peppers, and tobacco. Further, in Puerto Rico (Bird 1957), a strain of *B. tabaci* was identified that feed solely on *Jatropha gossypifolia* L., a plant of New World origin, despite numerous trials on other hosts; a feeding pattern that seems highly unlikely if *B. tabaci* were of Old World origin. A New World origin hypothesis for *B. tabaci* would have important ramifications for searching for natural enemies, switching the search emphasis to the Neotropics.

New studies of genetic variance may also suggest a New World origin for *B. tabaci.* Wool et al. (1991) examined isozymes of *B. tabaci* populations in Israel and found genetic uniformity, with no geographical races existing there. However, in examining *B. tabaci* from Columbia, they found differing esterase patterns among populations from various Columbian regions. In fact, the esterase pattern found in samples from the Valle, near Cali, were "very similar to the Israeli pattern" (Wool et al. 1991: 228). Similar circumstances exist in other homopterans, suggesting that centers of origin for a species probably have higher genetic

variability than do invaded areas. For example, among now cosmopolitan aphids, such as *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas), electrophoretic surveys of variance in North America indicate that the former, with zero variability in the Nearctic, probably had a limited introduction to that continent, whereas the latter, with a higher heterozygosity level, is probably a Nearctic endemic (May & Holbrook 1978).

This limited "founder effect" variance appears contrary to implied increasing genetic variance in other invasive whiteflies, such as *Siphoninus phillyreae* recently in California, where Sorensen et al. (1991) proposed a mutation-driven expansion of feeding-range, caused by explosive invasive populations in the absence of population controls. (A situation also similar to poinsettia SPW there.) Clearly, electrophoretic surveys of *S. phillyreae* in California should be (or *should have been*) conducted to monitor its heterozygosity during the geographical expansion. If limited genetic variability were maintained for *S. phillyreae* during its California explosion, then theories of expansions in the range of host-feeding during invasions might require modification (J. T. Sorensen, personal communication).

SPW, like several other whiteflies and scale insects, tends to be morphologically variable depending on both its host and on its location on the plant (Mound 1963). In SPW, the last stage nymph ("pupa") usually has a smooth dorsal surface if the host leaf is smooth. Alternatively, if the underside of the host leaf is covered with stiff hairs or spines, the pupa usually possesses very long (usually two to eight) dorsal setae arising on the head, thorax and abdominal areas. The pupa also tends to develop other unique characteristics on given hosts, as has been demonstrated by cross-rearing various populations on different hosts. Before interhost morphological variability was realized, numerous *Bemisia* synonyms were described as distinct species, but are now considered to be *B. tabaci* (Russell 1957) (Table 1).

Partly because of host induced morphological variation, conventional taxonomists have not been able to find characters in any of the life stages of SPW that would indicate that more than one species is present. Current diagnostic methods require either live insects to test for the ability to induce squash silver leaf symptoms, or adults that have been adequately preserved for electrophoretic analysis.

What poinsettia SPW actually represents remains in question. Because no differentiating morphological traits have been found it must currently be considered to be the same species as cotton SPW, *B. tabaci.* Yet its explosive population growth and host acquisitions in the presence of cotton SPW suggest that it probably represents something more than a simple biotype, perhaps a sibling species. (Interestingly, type material of *Bemisia poinsettiae* Hempel, 1923, described from Brazil on *Poinsettia* [obtained by E. Delfosse], shows no conventionally used morphological characters that can be used to separate it from *B. tabaci,* with which it thus may be synonymous.) Although there are a few taxonomic tools that are still available to use (e.g., morphometric multivariate analyses), it may take a while before they can be adequately developed on this problem. However, even if we can satisfactorily determine the relationships between the two SPW "strains," we will still require satisfactory control measures. Cotton SPW caused as much as $100 million in agricultural losses in southeastern California in 1981 (Duffus & Flock 1982). With recent developments, losses in 1991 may go well beyond that mark, because now crops are being attacked that were not infested previously.

Acknowledgment

I thank J. K. Brown, D. N. Byrne, E. Delfosse, J. E. Duffus, F. Laemmlin, N. Mills, E. T. Natwick, and T. M. Perring for providing information used in this review. John T. Sorensen also provided information, and expanded parts of the last section of the article in galley.

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Received 1 November 1991; accepted 26 November 1991.

PAN-PACIFIC ENTOMOLOGIST
68(2): 153–154, (1992)

Scientific Note

A NEW ANT INTRODUCTION FOR NORTH AMERICA: *PHEIDOLE TENERIFFANA* (FOREL) (HYMENOPTERA: FORMICIDAE)

During the spring of 1989, while spraying weeds at Admiral Kidd Park in western Long Beach, California, I discovered several foraging columns of small brown ants. The ants were nesting in the southeastern corner of the park, in sandy soil. I was able to identify the ants to the genus *Pheidole*; later, I sent samples to the Departments of Agriculture in Orange and Los Angeles counties, the California Department of Food & Agriculture, and the Los Angeles County Natural History Museum. Ultimately, the ants were identified to species as *Pheidole teneriffana* (Forel) on 20 Feb 1990 by E. O. Wilson of Harvard University. This species, a native of north Africa and the Canary Islands, has never been recorded from North America, although it had been previously found in Cuba in 1932 (Aguayo, T. 1932. Bull. Brooklyn Entomol. Soc., 22: 219). Between 1989 and 1991, this ant had spread to infest about five acres of the seven acre park site where it was discovered.

The workers of *P. teneriffana* are 2.5 mm long, with a black-brown head and gaster, and a lighter brown thorax. Soldiers of the species have oversized heads with powerful mandibles, and are the same colors as the workers, but larger and 3.75 mm long. The queen is entirely a shining dark brown, and 5.5 to 6.0 mm long, while males are dull light brown to medium brown and 4.0 to 4.5 mm long. The main function of the soldiers is to defend the nest, although both they and the workers will fight with other ants over food or when they are invading new territory.

In Admiral Kidd Park, I have observed on several occasions *P. teneriffana* displacing the Argentine ant, *Iridomyrex humilis* Mayr, another introduced pest species. Between 13 Mar and 5 Jun 1990, and on 9 Sep 1991, *P. teneriffana* advanced into Argentine ant territories, attacking and destroying colonies and taking over their nest sites. Similar interactions have been observed between *Iridomyrex humilis,* and another *Pheidole* sp., *P. megacephala* (Fabr.), in Hawaii and Bermuda (Haskins, C. P. & E. F. Haskins. 1965. Ecology, 46: 736–740; Crowell, K. L. 1968. Ecology, 49: 551–555; Fluker, S. S. & J. W. Beardsley. 1970. Ann. Entomol. Soc. Am., 63: 1290–1296).

In contrast, in the park, a native fire ant, *Solenopsis xyloni* McCook, often raids the nests of *P. teneriffana* and may annihilate whole colonies. Curiously, however, *S. xyloni* is itself displaced, at least partially, by *I. humilis,* so that a repetitious cycle of displacement might occur. It may be possible that *I. humilis* is repelled by a kariomone produced by *P. teneriffana,* but which does not repel *S. xyloni*; whereas, *S. xyloni* might be repelled by a kariomone produced by *I. humilis*?

Pheidole teneriffana seems to have few "conflicts" with less aggressive native ants in the park, but I have observed it attacking workers of the California red harvester ant, *Pogonomyrmex californicus* Buckley. Other ant species present in

the park are: *Conomyrma bicolor* Wheeler, *Conomymra insana* Buckley, *Tapinoma sessile* Say, *Formica pilicornis* Emery, *Monomorium minimum* Buckley and *Cardiocondyla ectopia* Snelling.

Pheidole teneriffana nests have many inseminated queens; 23 were observed in one colony that was changing its nest site. The nests occur as large colonies with low mounds in the soil, along curbs or sidewalks, at the edges of lawns, in cracks in pavement, and at the bases of trees. New colonies are started by budding, with new queens mating in the nest and moving with part of the existing colony to form new nests in adjacent territory. The workers forage night and day, unless it gets too hot (>26° C). However, if the nest is in a shady location, they will remain active on the hottest days. Colony members are predacious on live insects, such as noctuid or beetle larvae. They may also harvest seeds and scavenge dead or dying insects. I have not observed them tending aphids, but they do feed on sweet or greasy materials.

Records.—CALIFORNIA. *LOS ANGELES Co.:* Long Beach, Admiral Kidd Park, 7 Mar 1989, M. J. Martinez.

Acknowledgment.—I thank Edward O. Wilson, Harvard University, for the determination of this ant to species, and Roy Snelling, Los Angeles County Natural History Museum, for his assistance and support in identifying the ants. I also thank Phil Hester and his staff of the Recreation and Marine Department, Park Bureau, Long Beach Parks, for their cooperation, and my wife, Charlean, for her help and patience.

Michael J. Martinez, *Department of Parks and Recreation, City of Long Beach, Long Beach, California 90815.*

Received 30 September 1991; accepted 10 October 1991.

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The PAN-PACIFIC ENTOMOLOGIST

Volume 68 July 1992 Number 3

Published by the PACIFIC COAST ENTOMOLOGICAL SOCIETY
in cooperation with THE CALIFORNIA ACADEMY OF SCIENCES
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This issue mailed 10 November 1992

The Pan-Pacific Entomologist (ISSN 0031-0603)

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044, U.S.A.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PAN-PACIFIC ENTOMOLOGIST
68(3): 157–168, (1992)

THE FIRST ENDEMIC TROGLOBITIC CARABID BEETLES IN HAWAIIAN LAVA TUBES (COLEOPTERA: CARABIDAE)

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Abstract.—The first troglobitic Hawaiian carabid beetles are described from lava tube caves on Haleakalā, Maui Island. The species—*Atelothrus howarthi* Samuelson & Liebherr, NEW SPECIES, and *Atelothrus aaae* Samuelson & Liebherr, NEW SPECIES—are members of the tribe Platynini, subtribe Platyni, a group that has radiated extensively on the islands. Both cave species are members of a complex of *Atelothrus* species found on the windward slopes of Haleakalā, but they do not appear to be sister species, suggesting that they represent two independent colonizations of the lava tube habitat.

Key Words.—Insecta, Coleoptera, Carabidae, Platynini, *Atelothrus,* Hawaii, caves

The Hawaiian Carabidae make up the largest assemblage of beetles endemic to the Hawaiian Islands, and are perhaps the largest predaceous insect group to have radiated in the islands (Zimmerman 1948). Of these, the Platynini (= Anchomenides of Sharp) has speciated extensively, resulting in description of 111 species in 23 genera (Sharp 1903, Perkins 1917, Csiki 1931). In recent years, F. G. Howarth of Bishop Museum has investigated the arthropods of Hawaiian lava tubes. The species described below come from dark zones of lava tubes in the upper reaches of Kipahulu Valley, on the eastern part of East Maui Island.

Sharp (1903) established genera for the Hawaiian platynines based on the configuration of the metathoracic flight-wings and pronotal setation. He was aware that setal presence was highly variable within some species, and that "contemporary members of one generation may possibly belong to two different genera, though having the same specific parentage" (Sharp 1903: 177). Thus it is likely that comprehensive cladistic analysis will result in synonymization of many generic names in this fauna. The two cave species we describe appear related to a complex of five epigean species on East Maui: *Atelothrus erro* (Blackburn), *A. dyscoleus* Sharp, *A. gracilis* Sharp, *A. longicollis* Sharp, and *A. politus* Sharp. The two new species do not appear to be sister taxa, supporting the hypothesis that cave colonization by platynine carabids occurred at least twice on East Maui.

MATERIALS AND METHODS

Specimens were relaxed in warm soapy distilled water before dissection. For males, the intersegmental membranes posterad the apical visible abdominal segment were cut, and the male terminalia extracted. The aedeagus and associated sclerites of abdominal segment IX were placed in cold 10% KOH overnight, acidified with dilute acetic acid, and examined. The aedeagal internal sac was everted while the dissection was in the acetic acid wash. The disassociated ae-

deagus and abdominal sclerites were then placed in glycerin for microscopic examination, thereafter stored in glycerin microvials under the specimens.

For females, the abdomen was removed from water-relaxed specimens and placed overnight in cold 10% KOH. After clearing, the abdominal tergites for segments I–VII were removed along the pleural sutures, and the remaining segments removed from the visible sternites I–VI. The alimentary canal, defensive glands, and reproductive structures were placed in Chlorazol Black® in methyl cellosolve. The defensive glands and associated sclerites of segment VIII were removed, and the reproductive tract and alimentary canal mounted ventral side upward on a temporary glycerin mount. Reproductive structures were examined at × 100 to × 400 using phase-contrast microscopy. All internal cuticular structures were subsequently placed in plastic glycerin vials and stored with the specimens.

Body length is the sum of three dimensions: median length of head from anterior margin of labrum to cervical collar, median length of pronotum, and distance from basal groove of scutellum to apex of left elytron.

Each description is accompanied by a diagnosis sufficient to differentiate the species from all other species assignable to *Atelothrus* sensu Sharp (1903).

Atelothrus howarthi Samuelson & Liebherr, NEW SPECIES

Type Material.—Holotype (male): HAWAIIAN ISLANDS. *(E) MAUI I:* Haleakalā National Park, Kipahulu Valley, West Camp, 1800 m [6100 ft], in dark zone of Luamanuiwi Lava Tube, from top of large talus slope at end of lava tube, 14 Jul 1983, F. G. Howarth. The holotype is deposited in the B. P. Bishop Museum, Honolulu (BPBM type no. 14,799). Allotype (female): same data (except 15 Jul 1983) and deposition as holotype. Paratype (female): same data (except Jul 1983) and deposition as holotype; paratype (male): same data (except 4 Mar 1984) and deposition as holotype.

Description.—Head: form narrow, elongate, eyes flat, facets barely protruding from genal region of head; neck constricted laterally, obsoletely constricted dorsally. Mandibles elongate, apex finely acuminate. Labrum broadly emarginate medially; six setae along anterior margin, the two outer pairs stout, long, and set in foveate articulatory sockets, the inner pair much finer, shorter, and set in fine sockets. Maxillae elongate; laciniae narrow, acuminate; galeae elongate, apical segment bowed mesally; palps glabrous; palpomere IV fusiform, apex with small flat area. Ligula broad apically, bisetose; second palpomere anteriorly bisetose. Basal three antennomeres with very short microsetae on surfaces (× 125); antennomeres IV–XI elongate, antennomere IV with length 4.40× greatest width. Mentum with bifid or broadly emarginate median tooth; depressions of mentum deep, a round fovea evident at deepest part; submentum with inner and outer pairs of lateral setae present. Eyes reduced, maximal diameter from lower anterior to dorsal posterior margins crossing 12 facets (Fig. 3). Clypeus transverse, width 2.50× length; one seta each side about middle of length. Frons with shallow broad frontal grooves; two supraorbital setae each side, anterior setae above median dimension of eye, posterior just anterad constriction of neck. *Prothorax:* pronotum rhadiniform, lateral margin anteriorly convex before broadly concave and raised basolateral margin, basal margin broadly concave meeting nearly right, bluntly rounded hind angles; median base with slight longitudinal wrinkles, basal marginal bead absent; median longitudinal impression fine; anterior transverse depression deep medially, becoming obsolete one-quarter distance to front angles; area anterad anterior transverse depression weakly longitudinally strigose; anterior marginal bead present just inside front angles, absent medially; front angles narrowly rounded and slightly forward-projecting; lateral marginal depressions broad anteriorly, narrowest at lateral setae, and wider toward hind angles; laterobasal depressions deep, broad, with rounded depression mesad hind seta; lateral marginal seta normally single, unilaterally doubled on right side of female paratype. Prosternal projection narrowly rounded at apex, with a broad marginal bead weakly indicated by a slightly depressed area between procoxae. *Elytra:* lateral margins broadly curved from humerus to weakly developed subapical sinuation; disc flattened medially; basal groove

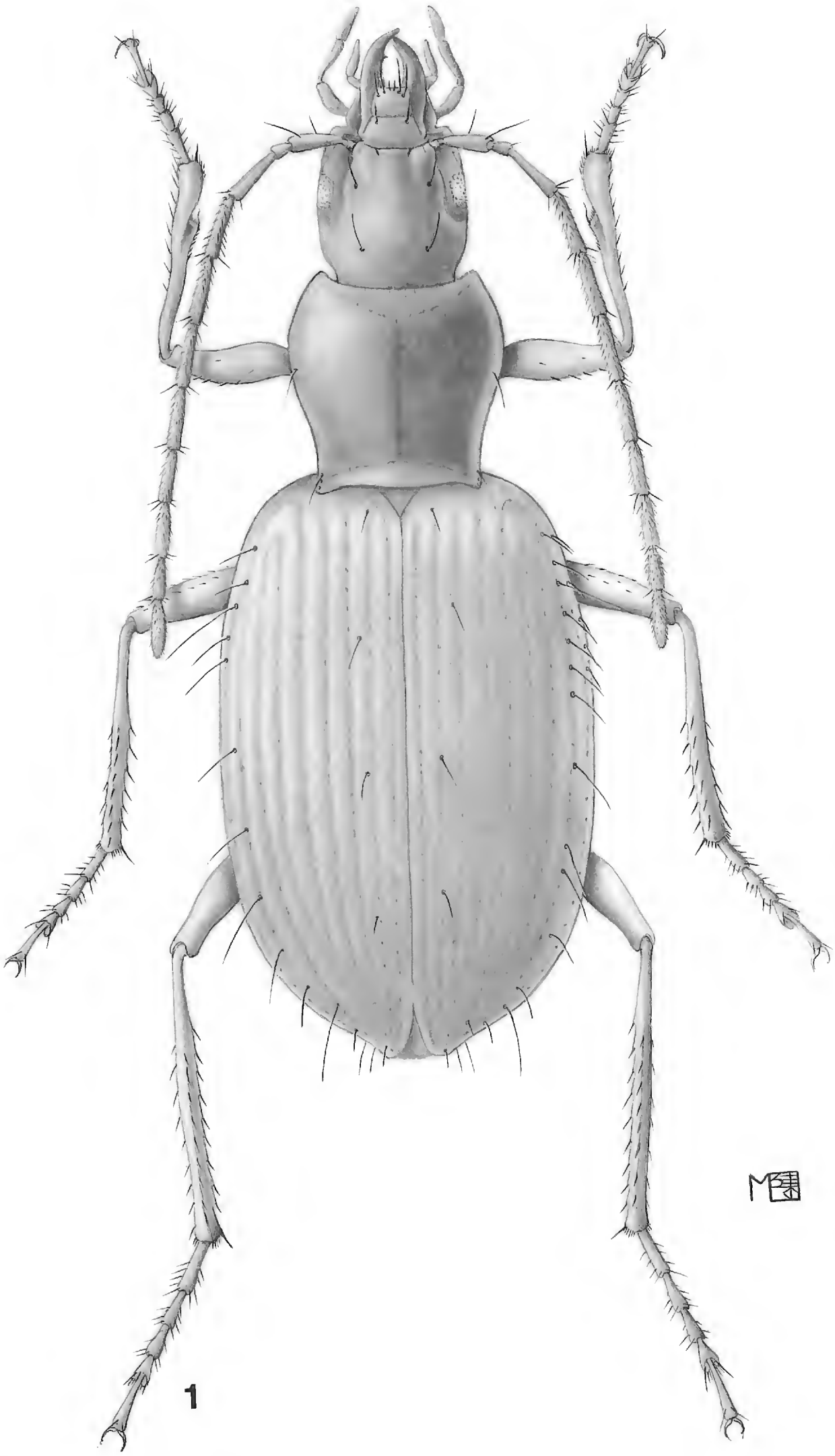
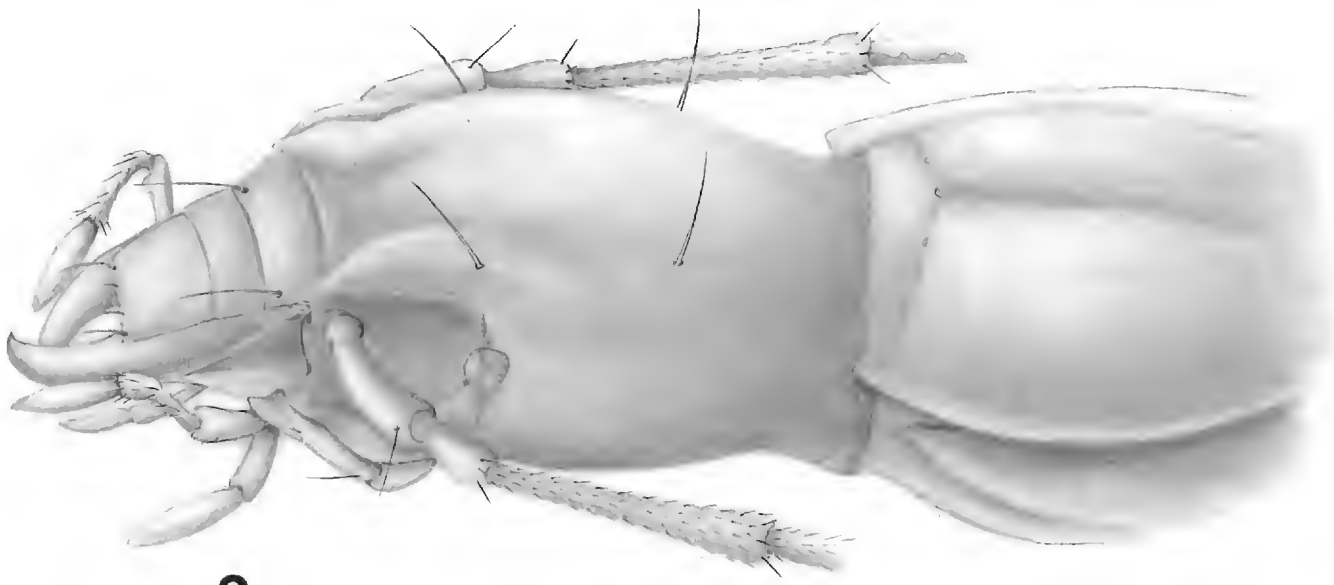
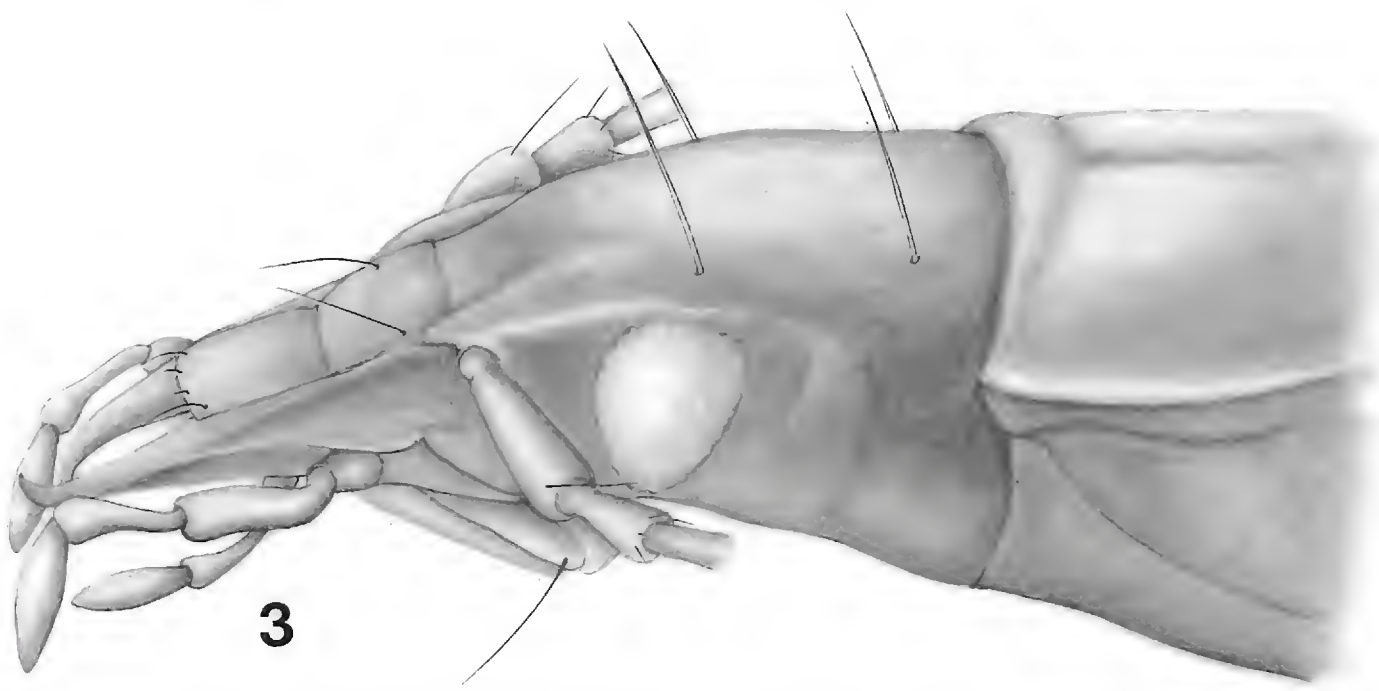


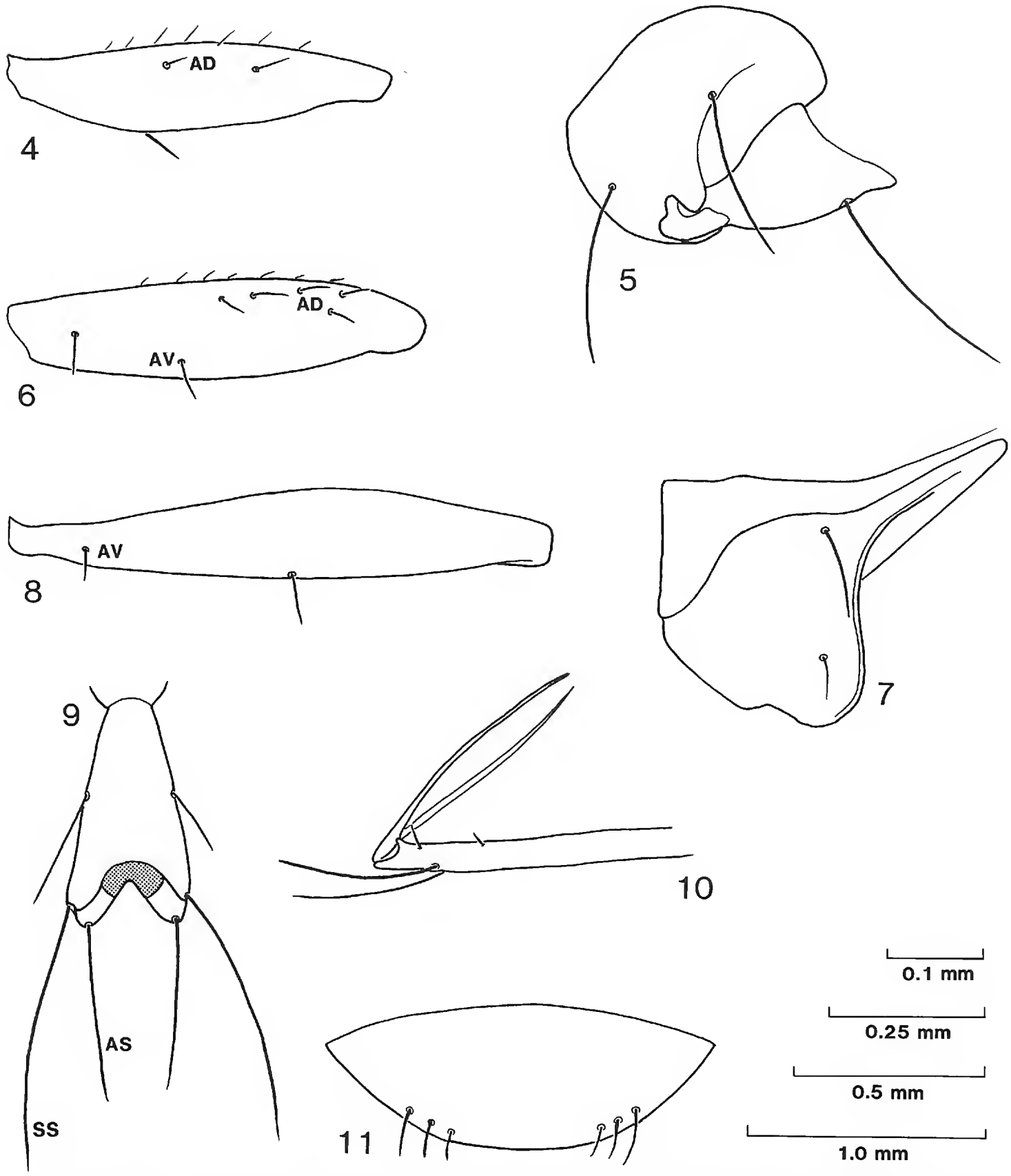
Figure. 1. *Atelothrus howarthi,* female allotype.





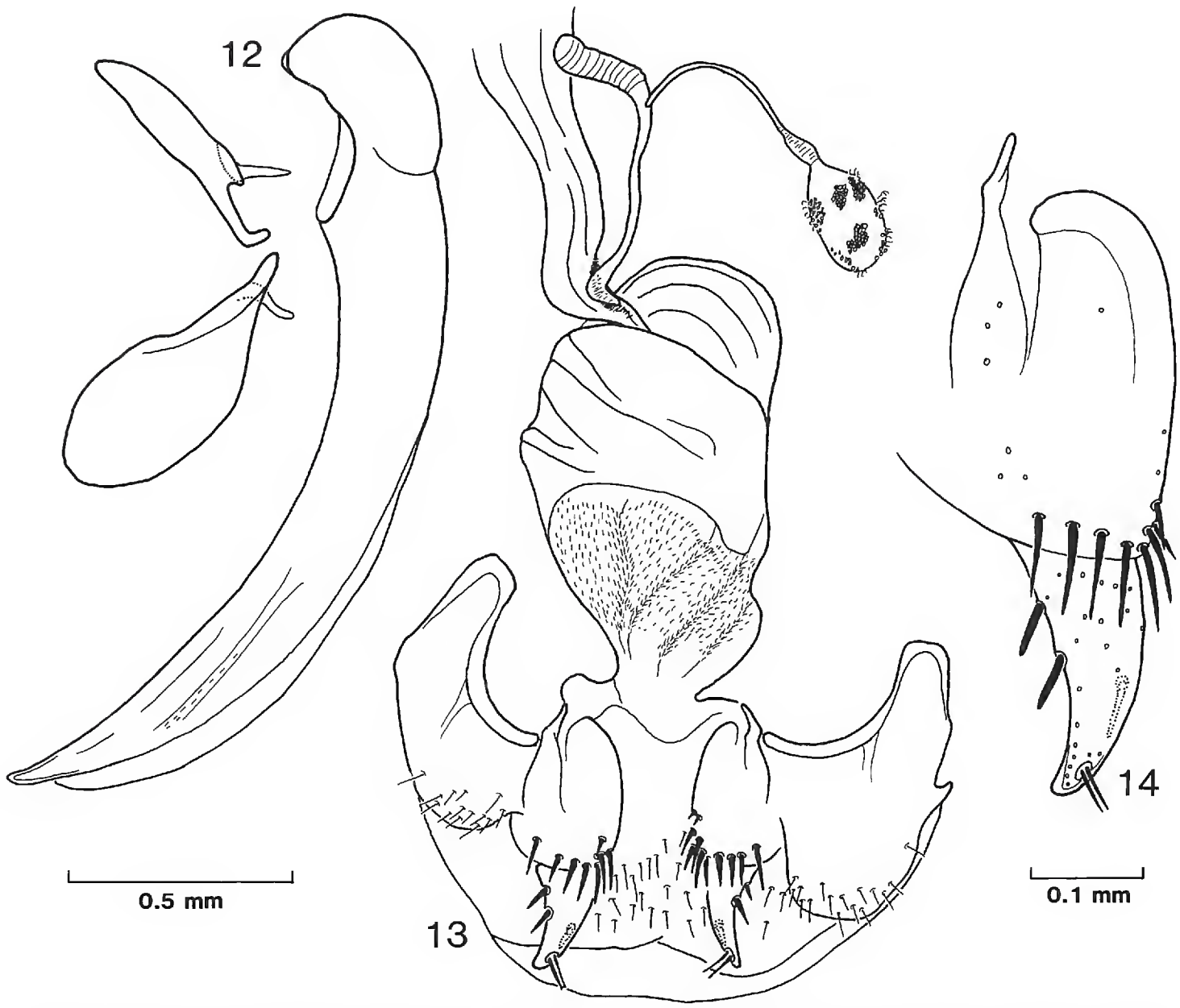
Figures. 2–3. Lateral view of head capsule showing development of compound eye. Figure 2. *Atelothrus aaae.* Figure 3. *Atelothrus howarthi.*

straight from second to fourth stria, recurved anteriorly from fourth stria outward, evenly rounded at humerus; striae continuous, slightly wavering, giving the impression of faint punctulae; intervals moderately and broadly convex; scutellar seta present; three dorsal elytral setae in third interval, the anterior seta in medial half of interval, the posterior two in second stria; 12 to 14 setae along lateral margin from humerus to subapical sinuation; a single seta near apex of seventh stria inside subapical sinuation; a single seta at elytral apex posterad second stria; sutural apex rounded. *Pterothorax:* metepisternum slightly elongate, lateral margin 1.25× length of anterior margin; hind wings vestigial, scalelike flaps about as long as metepisterna. *Legs:* profemur with a single ventral seta and two anterodorsal setae (Fig. 4), approximately seven smaller setae along dorsal surface; posterior surface glabrous. Mesocoxa with one ridge seta and one ventral seta (Fig. 5); mesofemur with two anteroventral setae, four to five anterodorsal setae, and about seven smaller dorsal setae (Fig. 6). Metacoxa bisetose, inner seta absent (Fig. 7); metafemur with two anteroventral setae, apex glabrous (Fig. 8); basal three metatarsomeres with sharp keellike median carina and broad internal and external dorsal sulci; fourth metatarsomere smooth, glabrous dorsally, with inner and outer mediolateral, subapical, and apical setae (Fig. 9); apical margin medially emarginate, inner and outer apical lobes equally elongate; metapretarsus with two pairs of short ventral setae and longer apicolateral setae (Fig. 10). *Abdomen:* apical margin of last visible abdominal sternite with one (holotype) or two (paratype) setae each side in males, three marginal setae each side in females (Fig. 11). *Microsculpture:* vertex with evident isodiametric mesh, stronger along upper margins of eyes. Pronotal disc with lightly impressed transverse mesh connected by weak crosslines, the surface faintly alutaceous; laterobasal depressions and



Figures. 4–11. *Atelothrus howarthi.* Figure 4. Left profemur (anterior view). Figure 5. Left mesocoxa and trochanter (anteroventral view). Figure 6. Left mesofemur (anterior view). Figure 7. Left metacoxa (ventral view). Figure 8. Left metafemur (anterior view). Figure 9. Right fourth metatarsomere (dorsal view, fifth tarsomere articulatory socket stippled). Figure 10. Left metapretarsus and claws (outer lateral view). Figure 11. Apical visible abdominal sternite of female (ventral view). Scale bar for Figs. 4, 6, 8, 11, 1.0 mm; for Fig. 7, 0.5 mm; for Figs. 5 and 10, 0.25 mm; for Fig. 9, 0.1 mm. AD = anterodorsal setae; AS = apical setae; AV = anteroventral setae; SS = subapical setae.

median base with granulate isodiametric mesh. Elytral intervals with faintly developed isodiametric mesh, more well developed in lateral intervals. Abdominal sternites with regular transverse mesh, mesh more isodiametric near lateral margins and laterad metacoxae. *Color:* vertex rufobrunneous to rufopiceous; anterior of frons, clypeus, and labrum rufous with testaceous cast; palps and antennae testaceous. Pronotum rufous to rufobrunneous, distinctly lighter in color than vertex; apical and lateral margins and laterobasal depressions more testaceous. Elytra rufotestaceous, thin, translucent. Pronotal



Figures. 12–14. *Atelothrus howarthi.* Figure 12. Male aedeagal median lobe and disassociated parameres (dorsal view for median lobe; ventral view of ventral (= right) paramere shown above dorsal view of dorsal (= left) paramere). Figure 13. Female external genitalia and reproductive tract (ventral view). Figure 14. Right gonocoxa (ventral view; dorsal ensiform seta on apical gonocoxite shown stippled). Scale bar for Figs. 12 and 13, 0.5 mm; for Fig. 14, 0.1 mm.

and elytral epipleura testaceous, venter of body rufous. Coxae, trochanters, and femora testaceous; tibiae and tarsi brunneous. *Body Size:* male holotype and female allotype 7.5 mm body length; male paratype 7.9 mm length; female paratype 8.0 mm length. *Male Genitalia:* aedeagus lightly melanized, testaceous to brunneous; ventral (= right) paramere narrow with subparallel sides (Fig. 12); dorsal (= left) paramere slightly longer and more rounded apically; median lobe slender, elongate, evenly curved, the apex finely acuminate; sagittal crest of basal bulb extremely small to absent; internal sac with inconspicuous microtrichia. *Female Reproductive Tract:* bursa copulatrix elongate with medial band of simple lumenal microtrichia (Fig. 13). Spermatheca tubular with short duct; spermathecal gland duct short, joining base of spermathecal reservoir. Hemisternite IX with setose lateral margin, 14–16 setae laterad basal gonocoxite. Basal gonocoxite with apical fringe of 8 to 11 setae (Figs. 13 and 14). Apical gonocoxite moderately stout with two lateral and one dorsal ensiform setae, and apical depression bearing two nematiform setae.

Diagnosis.—Pronotum with two lateral setae, one at middle, the other before hind angle (Fig. 1); hind wings vestigial; mandibles elongate, narrow apically; eyes reduced, surface barely protruding from flattened lateral areas of head; basal groove of elytra anteriorly recurved at humerus, humerus rounded; female with three marginal setae each side on apical visible abdominal sternite (Fig. 11).

Etymology.—This species is named to honor Frank Howarth and his many contributions to the knowledge of Hawaiian cave animals.

Related Species.—Sharp (1903) placed only two species in the genus *Platynus,* basing placement in that taxon on possession of dorsally bisulcate tarsomeres and bisetose pronotal lateral margins. These include *P. ambiens* Sharp from Kauai and *P. calathiformis* Sharp from Maui. The former character diagnoses the five genera Sharp proposed as his Division II of the Hawaiian Platynini. We discount the latter character for inclusion of any Hawaiian species in the Holarctic *Platynus,* due to the plasticity of pronotal setal presence and absence throughout the Platynini (e.g., Liebherr 1988). Such a decision follows Perkins' (1920) opinion that the two species placed in *Platynus* by Sharp are not closely related. We hypothesize that *A. howarthi* is most closely related to *A. longicollis,* a species found in Kipahulu Valley from 900 to 1900 m (A. C. Medeiros, Jr., and J. K. Liebherr, unpublished data), and ranging westward on the windward side of Haleakalā to Waikamoi Gulch. *Atelothrus longicollis* and *A. howarthi* share the derived states of: basolateral pronotal margin concave with hind angles projecting posterad; body pale with elytra translucent; metacoxae bisetose, inner seta lacking; apical margin of apical abdominal segment with three setae each side in female. This hypothesis interprets lateral pronotal setal presence in *A. howarthi* as an autapomorphy, and setal absence in related *Atelothrus* as the primitive state. *Atelothrus howarthi* exhibits developmental plasticity at this setal position—the female paratype has two setae on the right side, and a single seta on the left.

Material Examined.—See type material.

Atelothrus aaae Samuelson & Liebherr, NEW SPECIES

Type Material.—Holotype (female): HAWAIIAN ISLANDS. *(E) MAUI I:* Haleakalā National Park, Kipahulu Valley, West Camp, 1830 m [6000 ft], in dark zone of Pukamoa Lava Tube, under stone on mud bank above stream, 29 Apr 1988, F. G. Howarth. The holotype is deposited in the B. P. Bishop Museum, Honolulu (BPBM, type no. 14,800).

Description.—*Head:* vertex convex, domelike; lateral surfaces of head evenly convex from strong neck constriction to eyespot; constriction of neck broad, visible in lateral view. Mandibles moderately elongate, terebral surface broad, apex acuminate. Labrum trapezoidal, anterior margin 0.75× width of posterior margin, six setae along apical margin, the median pair 0.80× length neighboring more lateral setae, the outer pair nearly twice as long as more mesal neighbors. Maxillary palps with longer apical setae on second and third palpomeres, and sparse pelage of short microsetae over surface of palpomeres II–IV; palpomere IV fusiform, finely acuminate apically. Second labial palpomere with two longer anteromedial setae plus sparse pelage of fine microsetae. Mentum with acuminate median tooth; depressions of mentum deep, with pitlike foveae at deepest part; submentum with inner and outer pairs of lateral setae present. Antennae elongate; basal three antennomeres with sparse pelage of fine setae in addition to longer apical setae, the fine setae as long as pelage on antennomeres IV–XI; antennomere III slightly bowed posteriorly. Clypeus transverse, trapezoidal, anterior margin 0.70× length of posterior margin; one seta each side at middle of length. Eyes reduced to an obscurely faceted eyespot composed of four ommatidia, the ommatidial corneae flat, obscuring their margins (Fig. 2). Frons with broad, shallow, irregular frontal grooves, two supraorbital setae each side, anterior setae just above eyespot, posterior somewhat before neck constriction. *Prothorax:* pronotal lateral margins explanate, marginal bead depressed from front angle to mid-length, raised gradually to position of hind seta, gradually depressed posteriorly to hind angle; lateral margins evenly convex anterad hind setae, subparallel basad setae; hind angles right but bluntly rounded; median base with faint longitudinal wrinkles; basal marginal bead obsolete; median longitudinal impression foveate just anterad basal

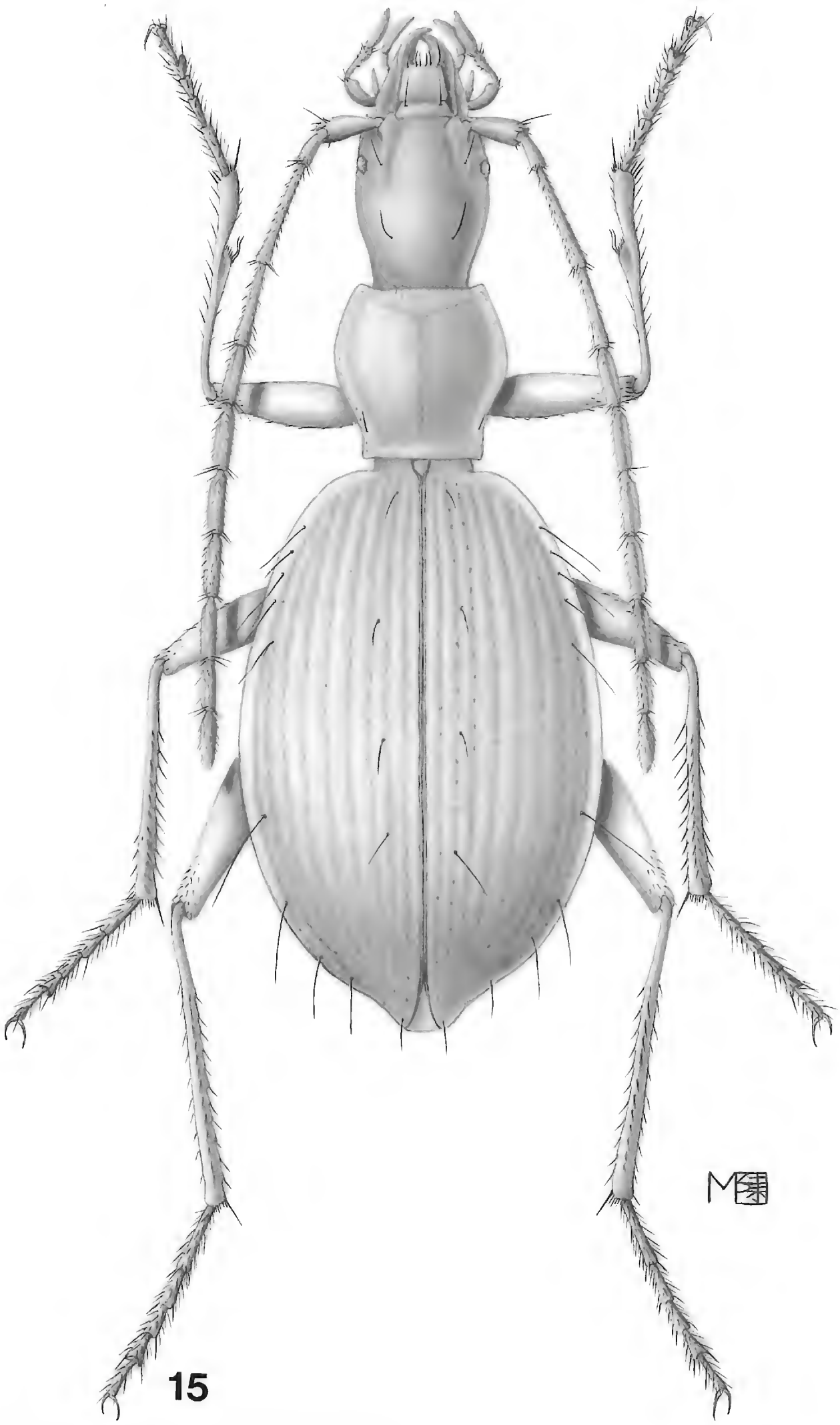
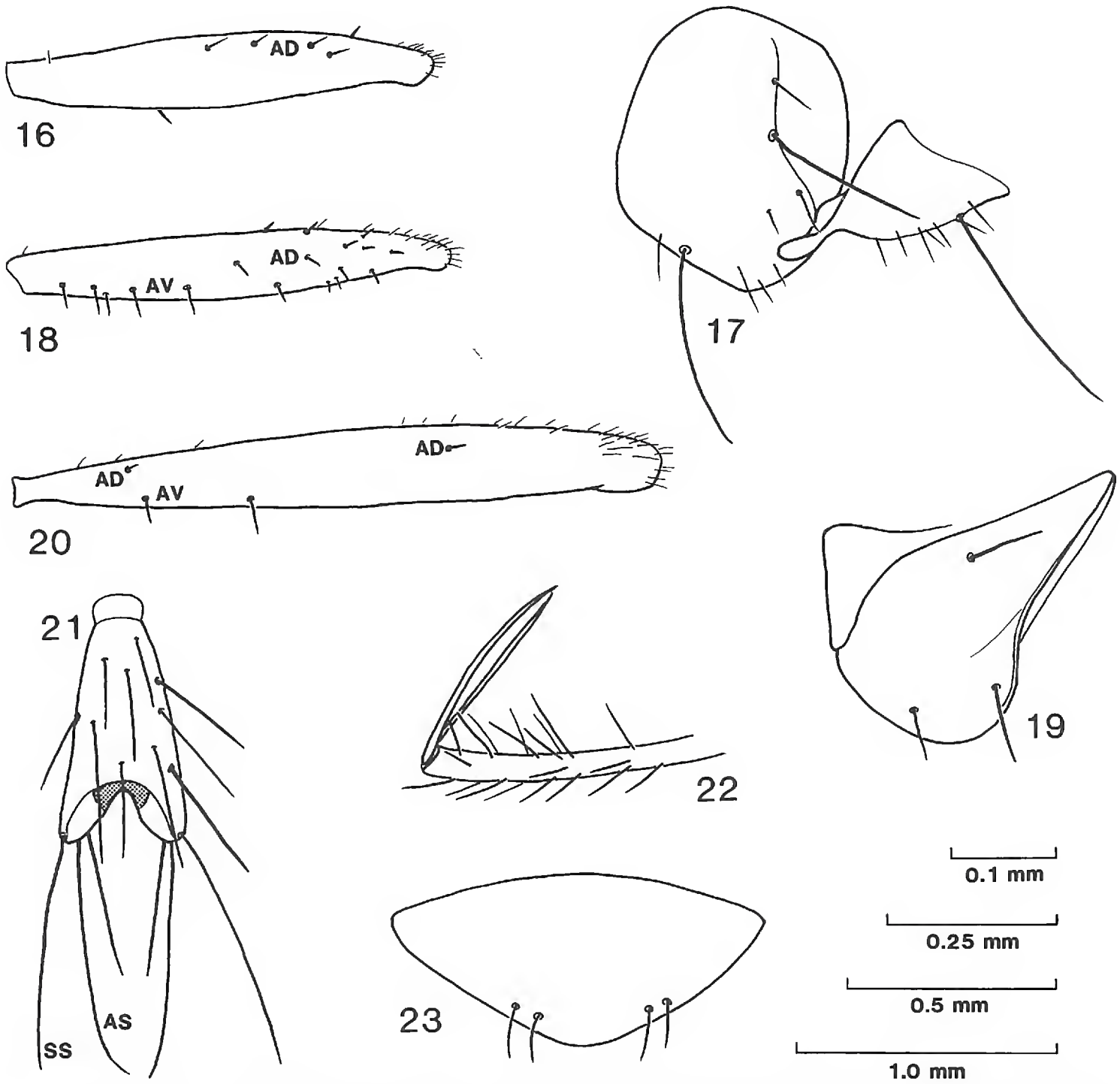
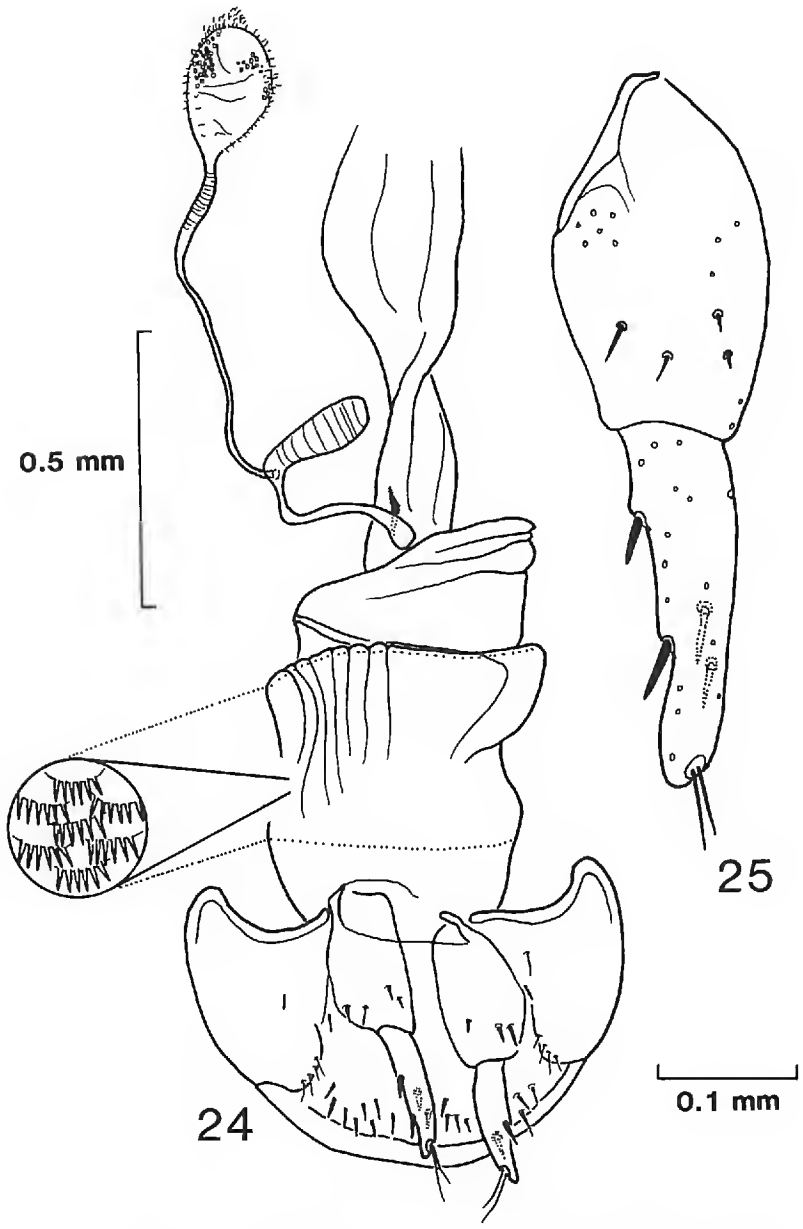


Figure. 15. *Atelothrus aaae,* female holotype.



Figures. 16–23. *Atelothrus aaae.* Figure 16. Left profemur (anterior view). Figure 17. Left mesocoxa and trochanter (anteroventral view). Figure 18. Left mesofemur (anterior view). Figure 19. Left metacoxa (ventral view). Figure 20. Left metafemur (anterior view). Figure 21. Right fourth metatarsomere (dorsal view; fifth tarsomere articulatory socket stippled). Figure 22. Left metapretarsus and claws (outer lateral view). Figure 23. Apical visible abdominal sternite of female (ventral view). Scale bar for Figs. 16, 18, 20, 23, 1.0 mm; for Fig. 19, 0.5 mm; for Figs. 17 and 22, 0.25 mm; for Fig. 21, 0.1 mm. AD = anterodorsal setae; AS = apical setae; AV = anteroventral setae; SS = subapical setae.

collar, fine near mid-length; anterior transverse depression deep, triangular medially, disappearing one-fifth distance to front angles; anterior margin with well-developed longitudinal wrinkles from middle to just inside lateral marginal depressions; anterior marginal bead obsolete; front angles slightly protruding, tightly rounded; lateral marginal depressions wide, of equal width along anterior half of notum, widened posteriorly to meet laterobasal depressions; basal seta positioned at basal 0.19 to 0.25 of length; weak carina extending medially from seta; laterobasal depressions smooth, with circular depression each side posterad basal setae. Prosternum depressed anterad procoxae, narrowly convex medially; prosternal projection with flattened ventral surface, ventral and posterior surfaces meeting at angulate apex; setae sparsely covering ventral surface. *Elytra:* form ovoid, humeri weakly developed, lateral margins nearly straight from rounded humeri to 0.40 of length, evenly convex posteriorly to well-developed subapical sinuation before rounded, protruding apex; basal groove faintly indicated inside fourth stria, evident and rounded on humerus; striae continuous, wavering basally, faintly punctate apically; intervals slightly convex; scutellar seta present; three dorsal elytral setae in third



Figures. 24–25. *Atelothrus aaae.* Figure 24. Female external genitalia and reproductive tract (ventral view; circular detail shows cristate bursal scales that occur between dotted lines, each cristate scale approximately 0.01 mm across). Figure 25. Right gonocoxa (ventral view; dorsal ensiform setae on apical gonocoxite shown stippled). Scale bar for Fig. 24, 0.5 mm; for Fig. 25, 0.1 mm.

interval, the anterior seta in middle of interval narrowed at its position by coming together of striae two and three, the posterior two setae just laterad second stria; nine lateral setae adjacent eighth stria, five in basal half behind humerus, four in apical half before subapical sinuation; a single seta in apex of first elytral interval; lateral reflection wide from humerus to middle of length, narrower posteriorly, absent laterad subapical sinuation. *Pterothorax:* metepisternum slightly elongate, lateral margin 1.33 × length of anterior margin; hind wings vestigial, small scalelike flaps much shorter than metepisterna. *Legs:* profemur elongate, slender, with one ventral seta, four anteroventral setae (Fig. 16), three posteroventral setae, and numerous fine setae apically. Mesocoxa with one larger ridge seta, one larger ventral seta, plus a sparse covering of fine setae, two of which are on mesocoxal ridge (Fig. 17); mesotrochanter with one large ventral seta and numerous short, fine setae over surface; mesofemur with approximately seven larger anteroventral setae, five anterodorsal setae, and numerous smaller setae along dorsal edge and on apical surfaces (Fig. 18). Metacoxa trisetose, inner seta present (Fig. 19); metafemur with two anteroventral setae, two anterodorsal setae, and numerous smaller setae along dorsal edge and apical surfaces (Fig. 20); basal three metatarsomeres with very shallow inner and outer dorsal sulci and a fine median carina, the dorsal surfaces of tarsi with a sparse pelage of microsetae; fourth metatarsomere convex dorsally, dorsal surface with sparse microsetae, subapical and apical setae present, apical margin medially emarginate with inner and outer lobes equally developed (Fig. 21); metapretarsus covered with sparse pelage of setae (Fig. 22). *Abdomen:* apical visible abdominal sternite of female with two setae on each side of apical margin (Fig. 23). *Microsculpture:* vertex with slightly transversely stretched isodiametric mesh, more transverse on constriction of neck. Pronotal disc with well-developed transverse mesh, more isodiametric mesh anterad anterior trans-

verse depression and on basal collar; laterobasal depressions with transverse mesh in deepest portions, mesh stretched parallel to lateral margin before hind setae. Elytral intervals with well-developed transverse mesh. Abdominal sternites with regular transverse mesh. *Color:* vertex yellow-brown, palps and antennal scape yellower, antennomeres II to XI brunneous. Pronotal disc slightly darker than vertex, anterior and lateral pronotal margins darker, brunneous. Elytra brunneous near scutellum, lighter, more flavous apically, translucent. Pronotal and elytral epipleura flavous; venter of body slightly darker, rufotestaceous. Coxae, trochanters, and femora flavous, concolorous with epipleura; tibiae and tarsi darker, concolorous with venter of body. *Body Size:* female holotype body length 7.05 mm. *Female Reproductive Tract:* bursa copulatrix elongate, with cristate scales lining the medial portion of the lumenal wall (Fig. 24). Spermatheca tubular with short duct; spermathecal gland duct 2.0× length of spermathecal reservoir, entering at base of reservoir. Hemisternite IX with four setae along apical margin. Basal gonocoxite glabrous apically (Figs. 24 and 25), with several short setae on ventral surface. Apical gonocoxite narrow and elongate with rounded apex; two widely separated lateral ensiform setae (right side of holotype) or one lateral ensiform seta (left side), and two (right side) or one (left side) dorsal ensiform setae; apical depression bearing two nematiform setae.

Diagnosis.—Pronotum with single seta before base of lateral margin (Fig. 15); hind wings vestigial; eyes very small, obscurely faceted (Fig. 3); basal antennomeres, palps, and tarsi covered with sparse pelage of microsetae; humeri weakly developed; legs and antennae elongate, legs slender, antennae 5.0 mm long; body length 7.05 mm.

Etymology.—The species epithet signifies that this species has been found in lava tubes; ʻ aʻ aʻ ā being the Hawaiian word for lava tube.

Related Species.—The presence of a single pronotal lateral seta just before the hind angle, the dorsally bisulcate tarsomeres, and vestigial flight wings are sufficient to diagnose this species as an *Atelothrus*. *Atelothrus aaae* has diverged extensively in morphology relative to geographically proximate epigean species. Its specializations typical of cave adapted taxa include elongation of legs and antennae, reduction of eyes, narrowing of the body, reduced melanization, and increased setosity (Casale 1988). We suggest that it is a member of the East Maui *Atelothrus* complex, but defer specifying a sister group pending comprehensive cladistic analysis. Based on its possession of symplesiomorphous character states of trisetose metacoxae and laterally bisetose female apical abdominal segment, *A. aaae* would not appear to be the sister taxon of *A. howarthi,* supporting two independent colonizations by *Atelothrus* species of the Kipahulu Valley caves.

Material Examined.—See type material.

Acknowledgment

We thank Arthur C. Medeiros, Jr., Haleakalā National Park, for support and assistance in the study of the Hawaiian biota. Michelle Chun, Honolulu, prepared the habitus drawings. Field work was supported, in part, by the National Science Foundation under grant BSR-85-15183 to the Bishop Museum.

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Received 29 August 1991; accepted 14 January 1992.

PAN-PACIFIC ENTOMOLOGIST
68(3): 169–173, (1992)

ENDEMIC PHYTOPHAGOUS INSECTS ASSOCIATED WITH YELLOW STARTHISTLE IN NORTHERN IDAHO

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Abstract.—A survey of endemic phytophagous insects associated with yellow starthistle in northern Idaho was conducted during 1981 and 1982, prior to the introduction of biological control agents. These data were supplemented with later observations. Eight species of insects were confirmed feeding on parts of the weed, other than pollen and nectar. None of these significantly impacted yellow starthistle populations. This is contrasted with the situation in Europe where numerous species exploit the weed. The significance of these data to biological control efforts is discussed.

Key Words.—Insecta, *Centaurea solstitialis,* yellow starthistle, phytophagous insect fauna, survey

Yellow starthistle, *Centaurea solstitialis* L. (Asteraceae), is a Eurasian annual or biennial that now occupies over 3 million hectares in the western U.S. (Maddox et al. 1985, Maddox & Mayfield 1985). In northern Idaho, the weed infests approximately 100,000 ha, primarily in five counties along the Snake and Clearwater Rivers (Callihan et al. 1989). *Centaurea solstitialis* is capable of forming solid stands that eliminate grazing capacity on rangelands in this area.

In northern Idaho, *C. solstitialis* typically germinates in the fall. Rosettes with seven or eight leaves form in the spring. The plants bolt during May and June, with flowering occurring from mid-June through early August. Thus, it blooms and senesces later in the season than most plants in the area.

A survey to assess the impact of endemic insects on *C. solstitialis* was conducted prior to the release of biological control agents. The data also allow comparison with the European insect fauna of *C. solstitialis.* These comparisons may identify open niches that could be exploited by introduced biocontrol agents.

Materials and Methods

Site Descriptions.—Three sites in the primary *C. solstitialis* infestation (100,000 ha) area of Nez Perce County in northern Idaho were selected for study. Site 1 was a 1 ha plot on a SE facing 30° slope, located 5.1 km ENE of Culdesac. This site had a loam soil and was relatively little disturbed, retaining some native vegetation. The mean elevation was 965 m. *Centaurea solstitialis* density was 187.6 plants/m^2, forming 14.5% of the ground cover. Other common species were *Poa secunda* Presl, *Ventenata dubia* (Leers) Cosson & Durieu, *Agropyron spicatum* (Pursch) Scribner & Smith (Poaceae), *Symphoricarpus albus* (L.) Blake (Caprifoliaceae), *Allium douglasii* Hooker (Liliaceae), *Balsamorhiza sagittata* (Purschall) Nuttall (Asteraceae) and *Lomatium dissectium* (Nuttall) Mathias & Constance (Apiaceae).

Site 2 was a 1 ha plot on a SE facing 40° slope, 8 km NW of Culdesac. The soil was a silt loam loess. The mean elevation was 645 m. *Centaurea solstitialis* density averaged 632.7/m^2 and formed 24.5% of the vegetative cover. The second most

abundant plant species was *Dipsacus sylvestris* Hudson (Dipsacaceae) with 140.3 plants/m^2 forming 21.4% of the ground cover. Other common species were *Hypericum perforatum* L. (Clusiaceae) and *Poa pratensis* L.

Site 3 was a 4 ha plot located 8 km S of Lapwai on a 5–20° SW facing slope. The soil was a skeletal loam. The mean elevation was 650 m. *Centaurea solstitialis* density averaged 177.2/m^2 and formed 15.3% of the ground cover. Other common species included four grasses, *Poa bulbosa* L., *Festuca myuros* L., *Bromus tectorum* L. and *B. secalinus* L. (Poaceae), and two forbs *Erodium cicutarium* (L.) L'Heritier (Geraniaceae) and *Balsamorhiza sagittata.*

Sampling Methods.—Arthropods were sampled weekly from the rosette stage to senescence, May through October, 1981 and 1982, using pitfall traps, sweepnets and hand-picking. Ten pitfall traps were set at 10 m intervals along a transect that ran up the slope at each site. The traps consisted of removable 8 oz plastic cups (7.2 cm diameter) filled to a depth of 2–3 cm with ethylene glycol. These were set in permanently positioned 10 oz cups of the same diameter to minimize soil disturbance. Samples were collected by pouring the ethylene glycol through a fine-mesh (4 threads/mm) aquarium net. Items caught in the net were transferred to 70% ethyl alcohol for storage and transport to the laboratory. Fifty sweepnet samples were collected by taking 180° sweeps along a transect 10 m from, and parallel to, the line of pitfall traps. Net contents were put into a cyanide jar to kill the insects collected, then transferred to a plastic bag for transport to the laboratory. These two collecting methods yielded qualitative assessments of the abundance of arthropods in the yellow starthistle-dominated habitats. A 20–30 min period of observation and hand-picking of insects feeding on *C. solstitialis* was conducted on each sample date throughout the study and later as opportunities arose. Specimens were identified as far as taxonomically possible.

Results and Discussion

The sampling yielded over 11,000 collections that included 488 recognizable arthropod taxa. Of these, 453 were insects, representing 17 orders and 131 families. Only 50 species in nine orders and 25 families were directly associated with *C. solstitialis.* Eight endemic species were observed to feed on *C. solstitialis,* other than as a source of pollen and nectar. Only two species appeared to regularly exploit *C. solstitialis.* Unless otherwise noted, the species discussed below occurred at all sites.

The species observed feeding on *C. solstitialis* included the western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), meadow spittlebug, *Philaenus spuramrius* (L.) (Homoptera: Cercopidae), plum leaf curl aphid, *Brachycaudus helichrysi* (Kaltenbach) (Homoptera: Aphididae), larvae of the moth *Sparganothus tunicana* (Walshingham) (Lepidoptera: Tortricidae), an ant, *Formica* sp. (Hymenoptera: Formicidae), the migratory grasshopper, *Melanoplus sanguinipes* (Fabr.) (Orthoptera: Acrididae), a cutworm larva (Lepidoptera: Noctuidae) and the European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae).

Western flower thrips were regularly found in *C. solstitialis* flowers during visual inspections. They were also abundant in sweepnet samples taken while flowers were present. The thrips did not appear to damage *D. solstitialis.*

Meadow spittlebugs were often found on lower foliage of *C. solstitialis* through-

out the spring and summer. Spittlebug densities as high as 14 per plant were observed. There was no obvious damage to *C. solstitialis* in the field attributable to spittlebug feeding.

Plum leaf curl aphids were occasionally found on the apex of elongating *C. solstitialis* stems during June. They caused the stem to curl, but were too scarce to contribute to controlling the weed. This aphid host alternates between plum trees and a wide variety of composites, including spotted knapweed, *Centaurea maculosa* Lambert (J. P. McCaffrey, unpublished data).

A population of the moth, *S. tunicana* was found feeding and developing on *C. solstitialis* at Site 1. It was first found on plants during 1985. Beginning in May of 1986, the site was visited weekly to check for the occurrence of *S. tunicana.* Larvae were not found until 30 May, at which time mid-instar larvae were found. This suggests that larvae overwinter. A related species *S. sencionana* (Walsingham) also overwinters as larvae that move to low-growing herbs (J. A. Powell, personal communication). Damage by *S. tunicana* frequently resulted in partial to complete lodging of the stem and in several instances caused the terminal portions of the plant to die back. The larvae were less common in 1987, and many were parasitized by an external parasitoid.

A single colony of *Formica* sp. at Site 2 chewed into maturing *C. solstitialis* seedheads and consumed the seeds. The impact of the ants was limited to a radius of approximately 10 m from their colony. Other colonies of apparently conspecific ants occurred at Site 2, but no other evidence of this behavior was observed.

Three other insect taxa were seen feeding on *C. solstitialis.* Late in the summer grasshoppers occasionally consumed *C. solstitialis* foliage when other vegetation in the area had senesced. A single cutworm larva was observed consuming *C. solstitialis* foliage. Rearing was attempted, but three days later it died, though it is not clear that this was due to being restricted to a diet of *C. solstitialis.* Lastly, earwigs were occasionally observed feeding in *C. solstitialis* blossoms, consuming pollen and doing minor damage to the flowers.

Pollen and nectar feeders were numerous, representing eight orders, 41 families and approximately 80 species. Most of these were Hymenoptera, especially bees (*Apis mellifera* L., *Bombus* spp. (Apidae); *Melissodes bimaculata* (Lepeletier) (Anthophoridae); and *Dialictus* spp. (Halictidae)), or Diptera (most commonly Syrphidae, e.g., *Eumerus strigatus* (Fallen) and *Sphaerophoria mehthastri* (L.)). Included in this group were a few agricultural pests (e.g., the pea leaf weevil, *Sitona lineatus* (L.) (Coleoptera: Curculionidae)). However, numerous beneficial insects also utilized this resource, including Hymenoptera such as *Dacnusa* sp. (Braconidae), *Banchus* sp. (Ichneumonidae), and numerous Chalcidoidea. *Hyalomyodes* sp. and *Eugymnogaster* sp. (Diptera: Tachinidae) were also commonly observed feeding within the flowers.

In addition to these taxa, many adult phytophagous insects were found on *C. solstitialis,* but were not observed feeding. The dominant groups in this category were Hemiptera, especially *Lygus* spp. (Miridae), *Coenus delius* (Say) and *Neotiglossus tumidifrons* Downes (Pentatomidae), and Homoptera, primarily *Dikraneura* spp. and *Deltocephalus* spp. (Cicadellidae). Despite the lack of direct observation, it is likely that some of these polyphagous species fed on *C. solstitialis* to a limited extent.

Thus, it appears that *C. solstitialis* in northern Idaho is exploited only by a few

generalist ectophages and flower visitors. These insects appear to have no significant impact on *C. solstitialis* populations. This situation contrasts with reports from Europe.

The entomofauna of *C. solstitialis* in its home range has been studied by entomologists since the late 1950s (Zwölfer 1965). These studies have characterized European populations of *C. solstitialis* as primarily occurring in pastures, open fields, and ruderal situations (Sobhian & Zwölfer 1985, Clement 1990), as they do in the U.S. However, the populations of *C. solstitialis* typically encountered in southern Europe occupied <3.5 ha (Clement 1990) and were far less dense than commonly found in the U.S. (S. Clement, personal communication). Despite the reduced abundance of *C. solstitialis,* numerous insect taxa have been found associated with the weed in Europe. Clement (1990) reported 42 species of herbivores associated with *C. solstitialis* in southern Europe. Homoptera, Coleoptera, Lepidoptera, Diptera and Hymenoptera dominated in all three surveys. Many of the insect species associated with *C. solstitialis* are capitulum-feeders, but all parts of the plant are exploited (Clement 1990). Many of the species are stenophagous endophages and some appeared to be monophagous, particularly among the capitulum-feeders (Maddox & Sobhian 1987, Clement 1990, Groppe et al. 1990, Maddox et al. 1990, Clement & Sobhian 1991, Fornasari et al. in press).

Thus, it seems likely that native phytophagous insects will not interfere with introductions of biological control agents on *C. solstitialis* in northern Idaho. The resident fauna is sparse and comprised of generalists. The European fauna includes at least 18 monophagous to oligophagous taxa that might be suitable for introduction, although five capitulum-feeding species appear to have the greatest potential for use in biological control (Clement 1990). Four of these have already been released in the U.S.: *Bangasternus orientalis* (Capiomont), *Eustenopus villosus* (Boheman) (Coleoptera: Curculionidae), *Chaetorellia australis* Hering and *Urophora sirunaseva* (Hering) (Diptera: Tephritidae). As of yet, only *B. orientalis* has become widespread and well established (Turner et al. in press), so it is too early to assess their impact on *C. solstitialis* in the U.S.

Acknowledgment

We thank Robert Gillespie, Jude Sirota, John Jenkins, Russell Clausen, Terry Miller, Bradley Harmon and Gregory Wheeler for their assistance with field and laboratory work. We are very grateful to Jerry A. Powell for identifying *S. tunicana* and providing biological information on related species. Stephen Clement and Charles Turner reviewed earlier drafts of this manuscript. This work was supported by USDA-ARS Coop. Agr. 58-91H2-9-251 and Idaho Agricultural Experiment Station Project, 061-R838, a contributing project to Western Regional Project, W-84. Journal article number 91744 of the Agricultural Experiment Station, University of Idaho, Moscow, Idaho.

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Received 28 June 1991; accepted 10 February 1992.

PAN-PACIFIC ENTOMOLOGIST
68(3): 174–191, (1992)

NEW AMERICAN MEINERTELLIDAE (ARCHAEOGNATHA, MACHILOIDEA)

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Abstract.—*Praemachilellus* NEW GENUS and its type-species *P. rentzii* NEW SPECIES from Mexico are described. The genus *Machilinus* Silvestri, 1905 is redescribed and subdivided into the three subgenera *Machilinus* s. str., *Neotropolinus* NEW SUBGENUS and *Nearctolinus* NEW SUBGENUS. *Machilinus* (*Neotropolinus*) *chilensis* NEW SPECIES and *Machilinus (N.) abulbiferus* NEW SPECIES are described; *M. (N.) chilensis* is the first species of *Machilinus* for Chile. *Machilinus* (*Nearctolinus*) *aurantiacus* (Schött), 1896 from western United States is redescribed and *M.* (*N.*) *a. setosus* NEW SUBSPECIES is described. The phylogenetical relations of the taxa are briefly discussed.

Key Words.—Insecta, Arachaeognatha, Microcoryphia, Meinertellidae, *Machilinus, Praemachilellus*

With approximately 450 described species the Archaeognatha (= Microcoryphia) constitute a relatively small order of the primary apterous insects. The recent representatives are subdivided into two families: the more primitive Machilidae, which are centered mainly in the northern hemisphere, and the more derived Meinertellidae, which are predominantly distributed over the southern hemisphere. In North America and Mexico, both families occur.

In attempting to clarify the phylogenetic relations within the genera of recent Archaeognatha, it became apparent that the widely distributed genus *Machilinus* had not been adequately described. With the inclusion of the South American and North American *Machilinus,* it was necessary to redescribe the genus and to subdivide it into three subgenera. In material received from Mexico, specimens of a new genus were found, the females of which have ovipositors with setae that were strongly thickened in part, a characteristic that up to now has been restricted to the genus *Kuschelochilis* within the Meinertellidae. The results presented here indicate that our knowledge of the American fauna (sensu New World) of Meinertellidae is still insufficient, in spite of the excellent studies of Wygodzinsky (1950, 1951, 1952, 1967, 1974) and Wygodzinsky & Schmidt (1980).

MACHILINUS SILVESTRI, 1905: 2

Type Species.—*Machilis rupestris* Lucas, 1846: 253.

Redescription.—Small (body length 6–9 mm, rarely 10 mm); hypodermal pigment brown, often unclearly defined; scales absent on head, head appendages, legs and stylets. Head: frons not protruded; eyes very large (ratio width of eyes : width of head, 0.8–0.9), about as long as wide; lateral ocelli sublateral to eyes, in alcohol hyaline, elliptical, ovoid or round; setae on clypeus small to medium sized; frons of males often with strong spine-like setae. Antennae: shorter than the body, generally exceeding one-half body length; flagellum uniformly brown, distal chains generally with eight to nine subarticles. Mandibles: distal end distinctly four-toothed, apex of teeth generally black. Maxillae: apex of terminal teeth of lacinia generally black; longitudinal process near dorsal base of maxillary palp

absent; triangular process on article one of palp well developed, quite digitate; article seven very short; article two of male palp on the distal dorsal border with a hooked process typical in Meinertellidae; inner face of article two or two + three of males with specialized setae (sometimes also the shape of these articles sexually dimorphic). Labium: submentum near base of palps slightly protruded laterad; labial palp article two on dorsal side with almost transversely oriented setae; distal portion of article three only slightly widened, in male often of special form, with field of short setae. Legs: coxal stylets absent; femur I distinctly wider than II and III; ventral margin of all legs from femur distadly with brown or black spine-like setae. Urosternites: sternites I–VII very small (usual in Meinertellidae); spine-like setae on coxites absent; stylets on II–IX present, apex with a tuft of dark setae, terminal spines well developed, partially reduced or completely reduced depending on subgenus; one + one coxal vesicles on II–VII or only on II–V depending on subgenus. Penis: shorter than one-half the length of coxites IX, aperture ventral, triangular; inner margin of aperture with slightly specialized small setae that present a grooved basal part; parameres absent. Ovipositor: long and slender, of primary type, surpassing tips of stylets IX, with more than 55 articles; terminal spines longer than the two to three distal articles; distal articles one to three of each gonapophysis with two to nine sensory rods or small setae; more proximal articles with highly reduced characteristic chaetotaxy, maximum of three setae per article; lateral macrochaetae present on each second or third article of distal one-third to one-half of each gonapophysis present. Caudal appendages: typical hair-like scales absent; cerci with single terminal spine.

Discussion.—*Machilinus* is distributed worldwide: southern Europe to southern European Russia, North Africa, Cape Verde Islands, South Africa, western North America, Argentina and Chile. The genus represents a monophyletic group. This is indicated by the combination of the following characteristics common to this group (apomorphies marked by [A]): eyes very large; lateral ocelli sublateral, round to elliptical and hyaline to light red [A]; apex of teeth on mandible and lacinia generally black [A]; horizontal process on the base of maxillary palp absent [A]; article two of labial palp on dorsal side with distinctly transversely oriented setae [A]; coxal stylets absent from all legs; penis with slightly specialized inner setae; highly reduced chaetotaxy with lateral macrochaetae distributed at odd intervals on gonapophyses VIII and IX [A]. These characteristics indicate not only the natural relationship of the group but also its special position within the Meinertellidae. Its relationship with other genera of the family is not clear. In spite of the many derived characteristics, the worldwide distribution indicates that the genus existed for quite a long time. Those groups that are geographically very far apart have obviously evolved separately and should be subgenera.

Subgenus *Machilinus* s. str.

Type Species.—*Machilis rupestris* Lucas, 1846: 253.

Description.—Terminal spines of abdominal stylets II–IX well developed, distinctly longer than surrounding pigmented setae; distance between inner basal margins of abdominal stylets II and IV not very different, ratio distance IV:II, <1.4; one + one coxal vesicles on abdominal coxites II–VII present.

Discussion.—The normally developed terminal spines on abdominal stylets represent plesiomorphic characteristics within the Meinertellidae (see Sturm 1984). Silvestri (1905) indicates the type-species of *Machilinus rupestris* has coxal vesicles on the abdominal coxites I–VII. The examination of more than ten European and North African species proved that they lack coxal vesicles on abdominal segment I. This, and the reduction of coxal vesicles only on abdominal segment I, indicate that this subgenus is the most primitive of the three subgenera. It includes not only the European and North African species (16) but also the species from Yemen

(1), South Africa (1) and the Cape Verde Islands (1) (Wygodzinsky 1967, Mendes 1981).

Material Examined.—*Machilinus* (*M.*) *rupestris gallicus* Bitsch, 1967: FRANCE. *CORSICA:* Porticcio, 5–15 Aug 1982, M. Bless, 2 males, 2 females.

M. (*M.*) *kleinenbergi* (Giardina), 1900: ROMANIA. nr Histria, 12 Sep 1969, H. Sturm, 2 females.

Neotropolinus Sturm & Bach, NEW SUBGENUS

Type Species.—*Machilinus chilensis* NEW SPECIES.

Description.—As subgenus *Machilinus,* except: terminal spines on all abdominal stylets almost completely reduced, replaced by a tuft of pigmented setae; one + one coxal vesicles on abdominal coxites II–VII present.

Diagnosis.—*Neotropolinus* can be distinguished by its reduced terminal spines of all abdominal stylets (a tiny hyaline remainder—compare Figs. 23, 24—discernible) which have been replaced by a tuft of pigmented setae. It also differs from the subgenus *Nearctolinus* in the coxal vesicles on abdominal coxites II–VII.

Etymology.—The subgenus is named after the biogeographical region, the Neotropics, where the group is found.

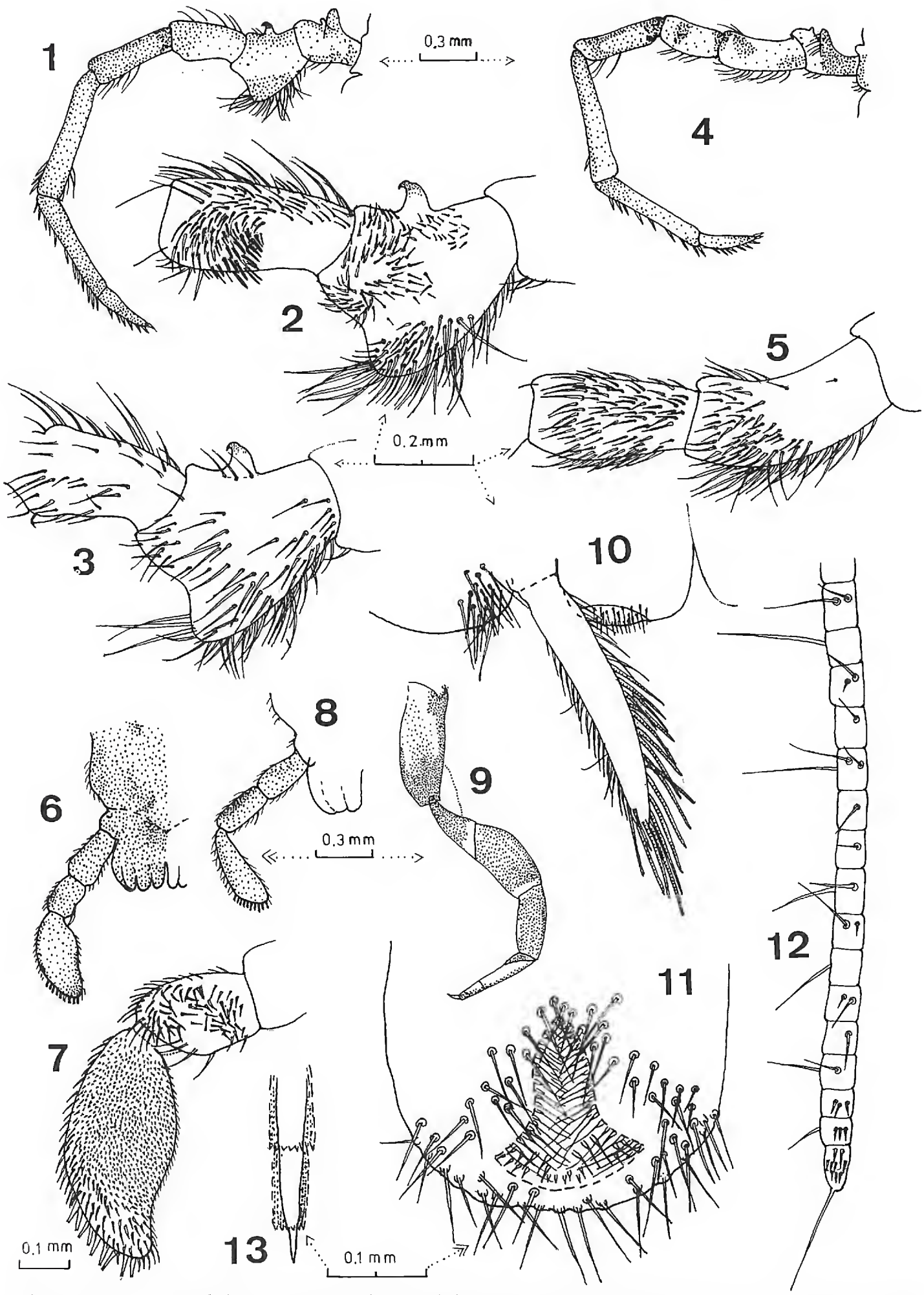
Discussion.—The almost complete reduction of the terminal spines on all abdominal stylets in all South American species of the genus is a unique characteristic within the recent Archaeognatha. It indicates that *Neotropolinus* is more derived than the subgenus *Machilinus. Neotropolinus* comprises six known species from Argentina and Chile (see discussion under *M.* (*N.*) *chilensis* Sturm & Bach NEW SPECIES).

Material Examined.—See *Machilinus* (*N.*) *chilensis* NEW SPECIES and *M.* (*N.*) *abulbiferus* NEW SPECIES.

Machilinus (*Neotropolinus*) *chilensis* Sturm & Bach, NEW SPECIES

Types.—Holotype: male; data: CHILE, nr Valdivia, fundo Zimmermann, base of *Nothofagus dombeyi* trunk, 9 Apr 1989, W. Probst. Allotype: female; same data as type. Holotype and allotype deposited in Zoological Museum of the University, Hamburg. Paratypes: 2 males, same data as type; 3 females above Valdivia, rancho Dr. Martin, forest, on bark of fallen trunk, 13 Apr 1989, W. Probst; deposited in Sturm collection, Hildesheim.

Description.—Body length 6–8 mm; hypodermal pigment yellow to dark brown, very extended on head, mandibles, labium, scapus, pedicellus, legs and some coxites, patches often not clearly defined; black chitinous pigment on apex of mandible on flagellum of antenna and on all spine-like setae. Head: nearly all frontal area more or less densely pigmented; frons and clypeus with medium to small sized setae; eyes in frontal view somewhat longer than wide (ratio width of eyes : width of head approximately 0.9; ratio length of eyes : width, 1.2; ratio line of contact : length of eye, 0.7–0.8); lateral ocelli in alcohol white, sublateral to eyes, ovoid to subrectangular, distance of inner borders 0.5–0.6 × width of both eyes. Antennae: shorter than body (up to 6 mm long); chains of flagellum with up to nine subarticles; scapus about 2 × as long as wide; pedicellus somewhat shorter than wide. Maxillary palps (Figs. 1–5): ratio length of articles seven to four, 0.45–0.5:1.0:1.05–1.15:0.75–0.8 respectively; number of dark-tipped spines on articles seven to five, up to 12, 21, 2, respectively; distribution of hypodermal pigment as in Figs. 1 and 4; highly sexually dimorphic: article two (male) ventrally strongly protruded, with long straight setae, inner side with ring of medium-sized setae oriented differently; article three (male) inner side with characteristic field of setae, partially black and thick. Labium (Figs.



Figures 1–13. *Machilinus* (*Neotropolinus*) *chilensis* NEW SPECIES. Figures 1–3. Maxillary palp (male), lateral view. Figure 1. Survey. Figure 2. Articles 2 + 3, inner side. Figure 3. Outer side. Figures 4, 5. Maxillary palp (female), lateral view. Figure 4. Survey. Figure 5. Articles 2 + 3, inner side. Figures 6–8. Labium in part, dorsal view. Figure 6. Male. Figure 7. Articles 2 + 3 of male palp with transversal setae on article 2 and field of short setae on article 3. Figure 8. Female. Figure 9. Leg I (female). Figure 10. Urosternite II (male), partly. Figure 11. Apex of penis, ventral view. Figure 12. Gonapophysis VIII (female), distal part. Figure 13. Apex of cercus (female) with terminal spine.

6–8): palps sexually dimorphic; article two (male) much shorter (ratio length of article two : one, 0.8 (males), 1.0–1.1 (females)), with group of characteristically oriented setae dorsally; article three (male) flattened, of special form, upper side with proximal field of setulae covering more than two-thirds of area. Legs (Fig. 9): nearly all surface pigmented, pigment concentrations on coxae and trochanters; maximal number of spine-like setae on femur, tibia, tarsomeres is 21, 35, 16, 24, 10 respectively; trochanters with few spine-like setae or with transitional setae. Urosternites (Fig. 10): with diffuse yellow-brown pigment on most of surface; coxites II–VII each with one + one coxal vesicles; coxites II–VIII lateradly of stylet base with well limited group of straight setae, more setae on anterior segments; stylets with characteristic black spine-like setae on median margin, their length increasing apically, forming tuft near tip, terminal spine not discernible; median margin of stylets II characteristically curved; ratio length of coxites : length of stylets for II and VIII, 1.2–1.5:1.0; for V, 1.7:1.0 (male); for IX, 1.3–1.5:1.0 (male); 1.6–1.8:1.0 (female); ratio length of terminal tuft : length of stylet, 0.2–0.4. Penis (Fig. 11): aperture rounded by ring of long straight setae; lateral inner border with row of setae that are slightly grooved on base, and ends of which cross; apical border with one or two rows of shorter grooved (?) setae. Ovipositor (Fig. 12): very long (up to 3.6 mm), slender; with >60 articles (see also description of genus). Caudal appendages (Fig. 13): with black spine-like setae; hair-like scales absent; one long terminal spine on cerci present.

Diagnosis.—*Machilinus chilensis* can be distinguished from the other species of the subgenus by the combination of the following characteristics: the extremely protruded ventral margin of article two of the male maxillary palp, the characteristic chaetotaxy of its articles two and three; the very short article two of the male labial palp and the specific pigment pattern on maxillary and labial palps as well as on leg I.

Discussion.—The new species is the first one of the genus that is clearly identified as coming from Chile. Wygodzinsky (1967: 508, 510) indicates the presence of the genus in Chile, but this information is not supported either by species names or by localities. The ventrad projection on article two of the male maxillary palp and the specialized setae on this article indicate that *M.* (*N.*) *chilensis* is closely related to four other South American species: *M.* (*N.*) *birabeni* Wygodzinsky, 1944, *M.* (*N.*) *inopinatus* Wygodzinsky, 1952, *M.* (*N.*) *muntanolae* Wygodzinsky, 1950 and *M.* (*N.*) *neotropicalis* Wygodzinsky, 1944, all collected in Argentina. Similar sexually dimorphic characters are also present in some European species (cf. *M.* (*M.*) *cisatlanticus* Janetschek, 1953, *M.* (*M.*) *rocai* Bach, 1975, *M.* (*M.*) *valencianus* Mendes & Bach, 1981). In the European species the ventral projection on article two is distinctly less pronounced. In *M. abulbiferus* NEW SPECIES from Argentina, the ventral projection on article two of the male maxillary palps is absent. The description of *M. pampeana* (Silvestri 1902) is insufficient and, therefore, must be regarded as a nomen nudum. Wygodzinsky (1950: 597) mentions in the case of *M. birabeni* two terminal spines on cercus, a trait that is generally considered to be characteristic of the genus. However, in all American specimens of *Machilinus* with well preserved cerci only a single terminal spine was present. Sometimes a tiny and indistinct projection on the base of the larger one could be suggested. The peculiar form of article three of the male labial palp, and the setulae on this article, are described by Wygodzinsky (1944: 90, 91) for *M. neotropicalis*. He illustrated a similar form of article three for males of *M. muntanolae* and *M. inopinatus* (Wygodzinsky 1950: 599, 1952: 438). The presence of grooved setae around the aperture of the penis is mentioned in this paper for the first time, but these could also be encountered in North American and European species and they are probably characteristic of the genus.

Material Examined.—See types.

Machilinus (*Neotropolinus*) *abulbiferus* Sturm & Bach, NEW SPECIES

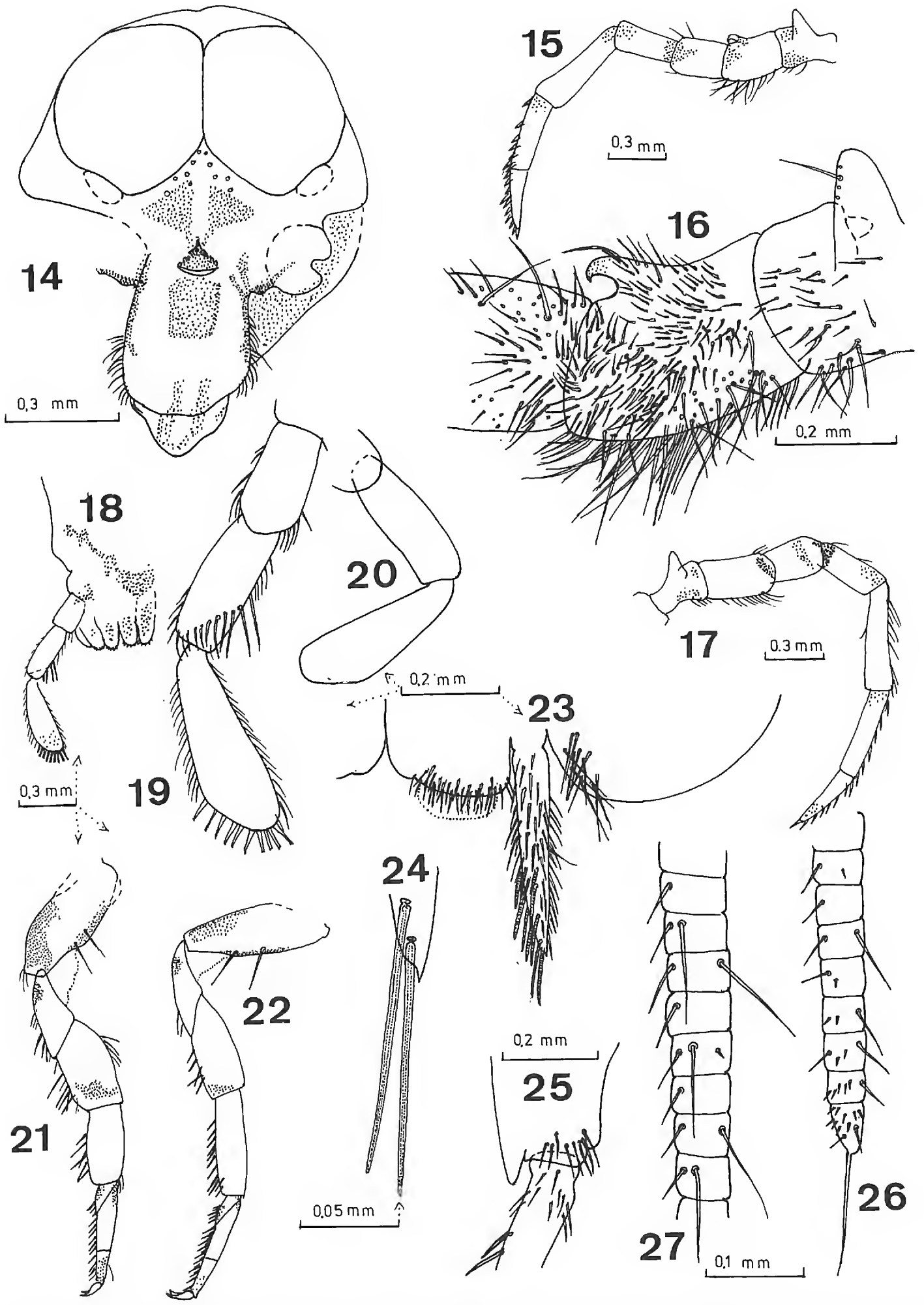
Types.—Holotype: male; ARGENTINA. *CATAMARCA:* El Manchado, 4000 m, Jan 1958, Goldbach. Allotype: female; same data as holotype. Holotype and allotype deposited in the American Museum of Natural History, New York.

Description (for characters not mentioned see *M. chilensis* or the genus description).—Body length approximately 6.5–8.0 mm, brown hypodermal pigment scarcely developed. Head (Fig. 14): two conspicuous triangular patches of pigment on frons; setae on clypeus small to medium sized; ratio width of eyes : width of head, approximately 0.83; length of eyes : width, 1.1–1.2; line of contact : length of eye, 0.5–0.6; lateral ocelli ovoid, not clearly defined. Antennae: up to 5 mm; terminal chains with eight subarticles; scapus and pedicellus conspicuously stout (ratio length : width of scapus, 1.4–1.5, of pedicellus = 0.60–0.75); scapus with distinct, longitudinal stripe of hypodermal pigment. Maxillary palps (Figs. 15–17): ratio length of articles seven : six : five : four = 0.72:1.0:1.2:0.86 (male); 0.62:1.0:1.1:0.73 (female); number of spines with brown colored tips on articles seven/six/five is 9–11/12–13/–; for distribution of hypodermal pigment see Figs. 15 and 17; distinctly sexually dimorphic; article two of male with the usual hook-shaped process near dorsal distal end, on ventral border with many long strong setae, median side with field of medium-sized slightly curved setae forming a whirl on distal part; ventral border not distinctly protruded, comparable field on article two of female absent. Labium (Figs. 18–20): article two of palp in male not distinctly shorter than in female, article three distally only slightly widened, not obviously sexually dimorphic, setulae absent. Legs (Figs. 21, 22): coxae with big patches of hypodermal pigment, trochanters and femora with smaller ones; more distal articles indistinctly pigmented; typical medium-sized spine-like setae on all tarsomeres present, tibiae and femora with longer ones and with transitional setae; all types of spine-like setae light brown; maximum number of spine-like setae (without transitional forms) on trochanter, femur, tibia and the three tarsomeres, 3/11/22/10/14/8 respectively. Urosternites (Figs. 23–25): coxites II–VII with well defined fields of straight setae near base of all coxal vesicles and lateradly from stylet base; coxites IX with group of setae proximadly from stylet base; spine-like setae on coxites absent; long scattered setae especially on coxites I–III; spine-like setae on stylets brown to black; ratio length of coxite : length of stylet for II, 1.35–1.5, for V, 2.4–2.5, for VIII, 1.4–1.5, for IX 1.65–1.75. Penis: no striking differences when compared to that of *M. chilensis*. Ovipositor (Figs. 26, 27): general chaetotaxy quite similar to *M. chilensis*: up to three longer setae per article, interrupted taxy of lateral macrochaetae; slight differences in number and position of sensory rods. Caudal appendages: length of terminal filament of male 6 mm, cerci 3 mm; cerci with long terminal spine in the base of which perhaps a very short one.

Diagnosis.—*M. abulbiferus* is distinguished from all other five species of the subgenus *Neotropochilis* by the absence of a distinct projection on the ventral margin of article two on the male axillary palp and by the different distribution and the lower intensity of hypodermal pigment, especially on head maxillary palps and legs. It is also distinguished apparently by the very stout form of scapus and pedicellus; the form of article three of the male labial palp does not differ from that of the female and lacks setulae.

Etymology.—The species name refers to the absence of a projection on the ventral margin of article two of the male maxillary palp. a (greek), alpha privativum; bulbus (latin), bulb, rounded projection; fere (latin), bear.

Discussion.—A distinctly sexually dimorphic form and chaetotaxy were described for four of the other South American species of the genus. In the fifth species (*M. birabeni*) this characteristic needs to be examined. The absence of distinctly specialized setae on article three of the male maxillary palp of *M. abulbiferus* is in common with *M. chilensis*. *M. abulbiferus* was found at the highest altitude registered for Meinertellidae. In the tropical region of South America species of *Neomachilellus* and *Meinertellus* (Meinertellidae) are found at heights



Figures 14–27. *Machilinus* (*Neotropolinus*) *abulbiferus* NEW SPECIES. Figure 14. Head (female), frontal view. Figures 15–17. Maxillary palp, lateral view. Figure 15. Survey (male). Figure 16. Article 2 (male), median side with hook. Figure 17. Survey (female). Figures 18–20. Labium and labial palp, ventral view. Figures 18, 19. Female. Figure 20. Male. Figure 21. Leg I (female). Figure 22. Leg III (female). Figure 23. Detail of coxites II with stylet (female), ventral view. Figure 24. Tip of stylet II (female). Figure 25. Distal end of stylet IX with base of stylet (female), ventral view. Figure 26. Apex of gonapophysis VIII (female), ventral view. Figure 27. Gonapophysis VIII (female), articles adjacent to Figure 26.

of up to 3500 m (Sturm 1984: 37). In contrast, *Machilanus swani* Wygodzinsky, 1974 was found at heights above 5700 m in the Himalayas.

Material Examined.—See types.

Nearctolinus Sturm & Bach, NEW SUBGENUS

Type Species.—*Machilis aurantiacus* (Schoett), 1897.

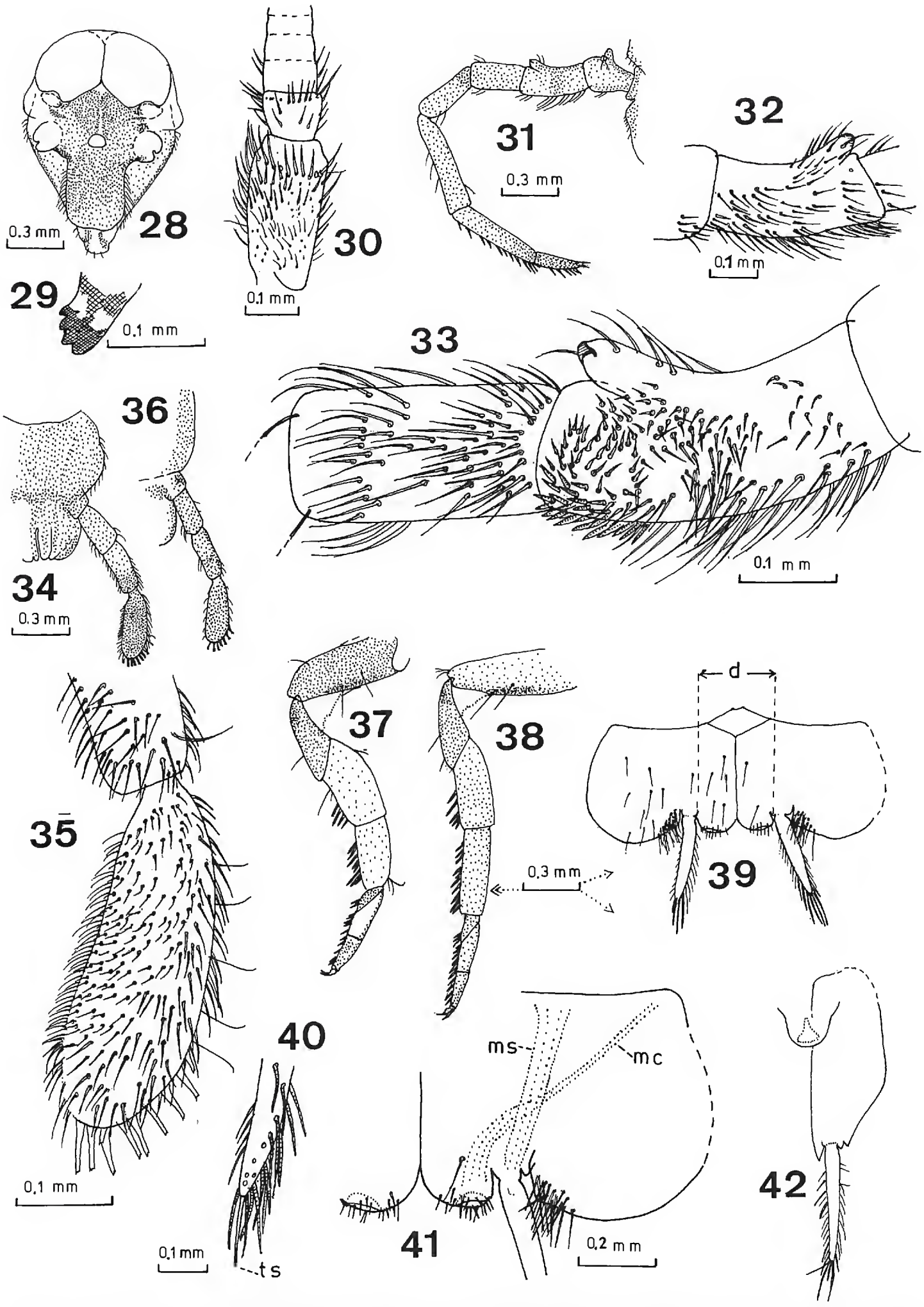
Description.—As subgenus *Machilinus,* except: a reduced form of one + one coxal vesicles on abdominal coxites II–V present; slightly pigmented terminal spines on abdominal stylets II and III well developed, a little longer than surrounding heavily pigmented setae, terminal spines on stylets IV–IX greatly reduced (Fig. 44); difference in distance between median margins of abdominal stylet bases II and IV very great; ratio distance on IV : distance on II, >1.8.

Diagnosis.—*Nearctolinus* can be distinguished from the other subgenera by its: complete reduction of coxal vesicles on abdominal segments I, VI and VII, and reduction of vesicles on II–V; the reduction of terminal spines on abdominal stylets IV–IX and reduction of the inner distance between abdominal stylets II + III are also unique.

Etymology.—The subgenus is named after the biogeographical region, the Nearctic, where the group is found.

Discussion.—The apparently complete reduction of coxal vesicles on abdominal segments I, VI and VII, the reduction of size of vesicles on II–V, the reduction of terminal spines on abdominal stylets IV–IX, as well as the obvious reduction of the inner distance between abdominal stylets II + III, prove that the subgenus *Nearctolinus* is the most derived of the three subgenera. None of the many alcohol-fixed specimens examined had swelled a coxal vesicle, a common case in other genera. Therefore, it is doubtful if the vesicles are still exsertile. The main criterion for the existence of vesicles on segments II–V is morphological: the presence of the retractor muscle (Figs. 41, 43), and of a double lined outer border. By the same criterion, *Kuschelochilis ochagaviae* Wygodzinsky, 1951, a species that according to Wygodzinsky has lost all its coxal vesicles, bears reduced vesicles with distinct retractor muscles on abdominal coxites II–IV (cf. Fig. 83).

The subgenus comprises actually a single well defined species, *M.* (*M.*) *aurantiacus* distributed in the western part of the USA. For the other described species of the subgenus, see the discussion under *M. aurantiacus.* The existence of other species of the subgenus seems possible. Wygodzinsky (1967: 509) has already stated that the different degrees of reduction make it impossible "to derive the recent South American species from the recent North American ones, but the reverse cannot be excluded." This conclusion is based on the supposition that the extreme reduction of parts or organs usually cannot be reversed on the same parts. But this would also mean that the descendence of North American species from the recent South American species group would be extremely improbable as it would require the reduction of the terminal spines on the abdominal stylets II and III to be reversed. There are two other possibilities besides this one. The ancestors of the two subgenera could have evolved separately from the primitive subgenus *Machilinus* or together from an extinct form, the reductions of which were not allowed to exceed the reductions of one of the derived subgenera (*Neotropolinus* and *Nearctolinus*). A decision in favor of one of these hypotheses could perhaps be made on the basis of additional collections and studies.



Figures 28–42. *Machilinus* (*Nearctolinus*) *a. aurantiacus* (Schoett). Figure 28. Head (male), frontal view. Figure 29. Apex of mandible (male) frontal view. Figure 30. Base of antenna (male). Figure 31. Maxillary palp (male), lateral view. Figure 32. Article 2, outer side. Figure 33. Articles 2 + 3, inner side. Figures 34–36. Labium partly, dorsal view. Figure 34. Male. Figure 35. Article 3 (male) with field of short setae. Figure 36. Female. Figure 37. Leg I (male). Figure 38. Leg III (male). Figures 39–41. Sternocoxite II (male), ventral view. Figure 39. Survey, d = inner distance of stylet bases. Figure

Material Examined.—See under *Machilinus aurantiacus.*

Machilinus (*Nearctolinus*) *aurantiacus* (Schoett), 1897

Machilis aurantiacus Schoett, 1897.

Types.—Neoholotype: male (see discussion); CALIFORNIA. *NAPA Cor.:* 3 km NE of Angwin, 396 m, 12 Jun 1980, H. B. Leech. Neoallotype: female; same data as neoholotype. Paratypes: 1 male, 1 female; same data as neoholotype; 1 female, same data as neoholotype except 20 Jun 1979 on garden soil; all types deposited in the California Academy of Sciences, San Francisco.

Redescription.—Small species (adults 6–8 mm); basic color of body and appendages yellow; brown hypodermal pigment widely distributed especially on head and its appendages but not clearly defined; black pigment present on chitinous cover of flagellum, tips of mandibulae and spine-like setae. Head (Figs. 28, 46): eyes very large (ratio width of head : width of eyes, 0.8–0.85), about as long as wide (ratio length of eye : width, 0.9–1.1); line of contact, 0.5–0.6 × length of eyes; lateral ocelli white to transparent, sublateral to eyes, elliptical to suboval; distance of inner margins 0.5–0.6 × width of both eyes; frons not protruding; pigment on frons and clypeus present but not clearly defined; hairs on clypeus of medium size; frons of male with short spine-like setae. Antennae (Fig. 30): shorter than body (up to 5 mm); ratio length of scapus : width, 1.6–1.9; distal chains of flagellum with up to eight subarticles, flagellum uniformly brown, scattered subcircular flat sense organs present (see Wygodzinsky 1950: 595–599). Mandibles (Fig. 29): distal end black with four distinct teeth. Maxillary palps (Figs. 31–33): distal spines of lacinia black; ratio length of articles seven : six : five, 0.45–0.55:1.0:1.0–1.1: 0.7–0.75 respectively; maximal number of spines on articles seven/six/five: 13/4/1; inner side of article two (male) with well developed hook and characteristic field of setae oriented differently, distal ventral margin with relatively short and strong darkly pigmented setae. Labal palps (Figs. 34–36): distal end of article three only slightly widened; sensory cones long and slender; male with field of short setae on median edge of dorsomedian side of article three; hairs on dorsal side of article two inclined up to 90° to longitudinal axis of article. Legs (Figs. 37, 38): coxal stylets absent; femora I distinctly wider than II and III; median (ventral) side of femur, tibia, tarsomeres with characteristic black spine-like setae, maximal numbers registered: 14/21/10/17/10 respectively; in legs III coxa also with up to four spine-like setae. Urosternites (Figs. 39–45): coxal vesicles I absent, on II–V one pair of reduced vesicles with adhering muscles present (reduction progressing distadly), on VI and VII vesicles or adhering muscles not discernible; sternites small (ratio length of sternites I–VII : length of coxites, 0.15–0.25; width of sternites I–VII : width of coxites, 0.2–0.3), median angle obtuse; well limited fields of setae on coxites laterad-distadly from base of stylets, number and length of setae decreasing from II to VIII; scattered long setae on all coxites, spine-like setae absent; terminal spines of stylets II and III well developed, slightly longer (II) or slightly shorter (III) than surrounding setae; stylets IV–IX with greatly reduced terminal spines (Figs. 43, 44); all stylets with many dark colored spine-like setae increasing distadly in number and length; lateral distance of inner stylet bases in II and III very small, approximately one-fourth of width of both coxites; ratio of distance between inner margins of stylet base II: III:IV, 1.0:1.0–1.1:1.9–2.1, on V–VIII distance continually decreasing. Ovipositor (Figs. 47–50): with 60 or more articles; terminal spines well developed, longer than the three terminal articles; distal articles with hyaline sensory rods or short setae, on gonapophyses VIII approximately seven/four/three/two (from distal), on IX approximately seven/three/one; number of setae on more proximal articles greatly reduced, on VIII one to three setae per article, on IX zero to one; setae on proximal one-half of gonapophyses very short or absent. Caudal appendages: filum terminale little longer than body; cerci longer than one-third body length; one terminal spine on cerci present; typical hair-like scales absent; longer scales in male and female present.

Diagnosis.—The species can be determined by the characteristics of the subgenus.

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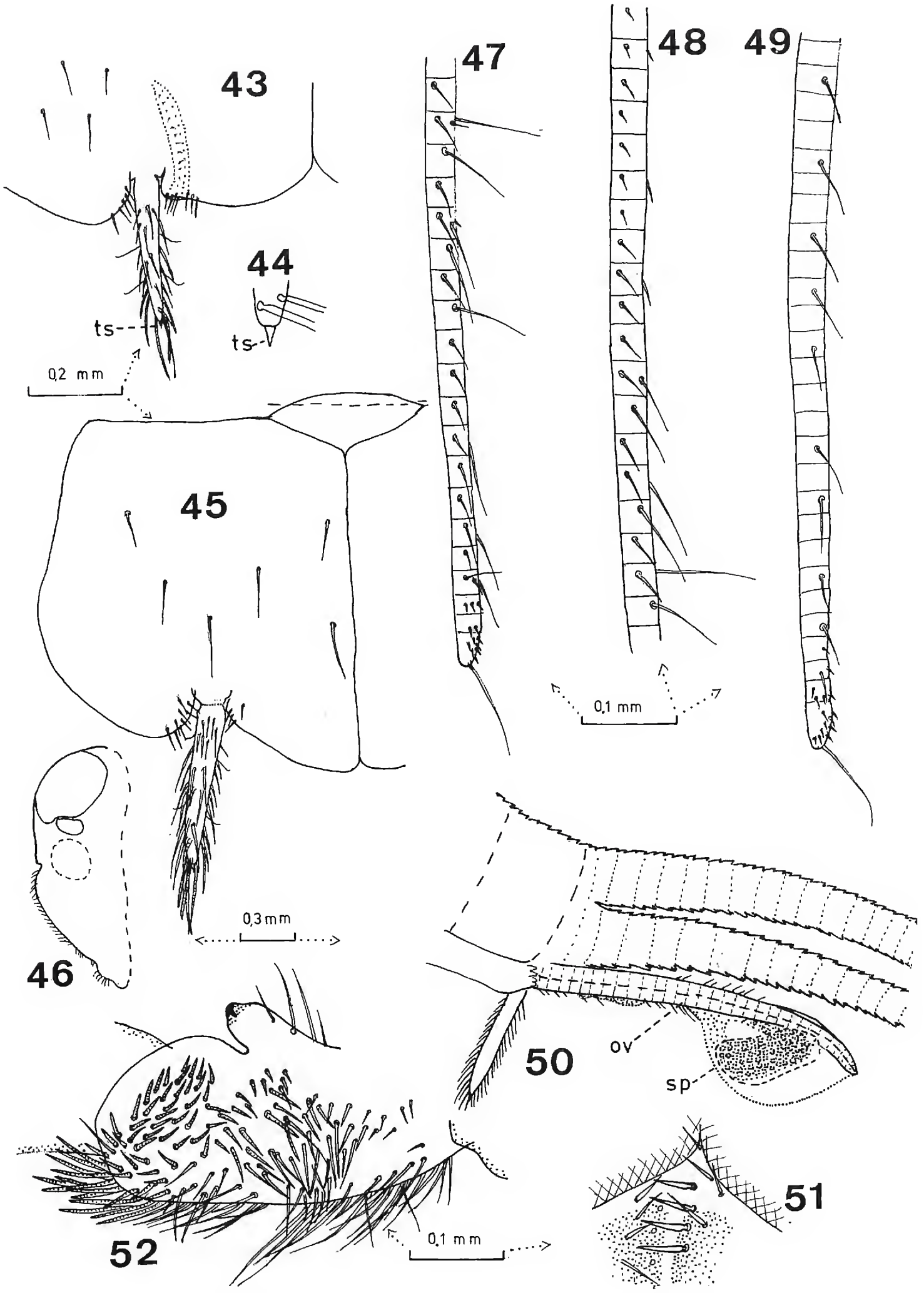
40. Distal portion of stylet. Figure 41. In part, with muscles for stylet (= ms) and coxal vesicle (= mc). Figure 42. Coxite IX with penis, ventral view.



Figures 43–52. Figures 43–50. *Machilinus* (*Nearctolinus*) *a. aurantiacus* (Schoett). Figures 43, 44. Stylet IV (female), partly, ventral view. Figure 43. Distal part of coxite with retractor muscle of reduced coxal vesicle, ts = terminal spine. Figure 44. Apex of stylet with reduced terminal spine (= ts). Figure 45. sternocoxite VIII (female), partly. Figure 46. Head (female), lateral view. Figures 47–49. Gonapophyses (female), ventral view. Figure 47. VIII, distal part. Figure 48. VIII, adjacent portion to Figure

Discussion.—The species *M. aurantiacus* was described by Schoett (1897) on the basis of specimens from the Sierra Nevada and Monterey, California. The description allows the genus to be recognized but mentions hardly any of the characteristics specific to the species, with the exception of the somewhat enigmatic details about coloration (pp. 188, 189): "The cerci are . . . dazzling white in color. . . . on each tergite are running 8–10 orange colored transverse lines." These statements could perhaps refer to alterations resulting from preservation. Silvestri (1911) used specimens from Shasta Springs, California and Boulder Canyon, Nevada for a redescription. In spite of many enquiries at American museums in an attempt to find the type material used by Schoett, it could not be found anywhere. It was probably deposited in the CASC-Museum and destroyed by a fire in 1911. There is no evidence of greater variations to be found in the extensive material which could justify the description of more than one species. The types of the second species described for North America, *M. nevadensis* Seetmann, 1937 could not be found either. The differences between *M. nevadensis* and *M. aurantiacus* mentioned by Sweetman result partly from the inadmissible comparison between color in living and fixed specimens, or from the the fact that Sweetman had only females at his disposal. Therefore, *M. nevadensis* must be regarded as a nomen nudum. The locality of the neotype lies between Monterey and Shasta Springs. Some light differences relating to the different length of specialized setae on article two of the male maxillary palp (Fig. 52) led to the description of a new subspecies.

A female from Sonora Pass had taken up a spermatophore (length 0.9 mm) that remained adhered to its ovipositor (Fig. 50). This reveals that in this genus there occurs a (probably indirect) transmission of spermatophores registered previously for *Machiloides tenuicornis* Stach, 1920 and *Neomachilellus scandens* Wygodzinsky, 1978, both from the same family (Sturm & Adis 1984, Sturm 1986). The spermatophore of *M. aurantiacus* shows a differentiated secret cover which is taken up together with the sperm and partially drawn out within the ovipositor. The formation of spermatophores by the males of *Machilinus* (*M.*) *rupestris gallicus* had already been assumed by Bitsch (1968) in the basis of studies on the inner sex organs.

The subgenus was collected only in the western part of North America. Fourteen of the 15 registered localities are in the USA (California [10], Nevada [2], Utah [1], Arizona [1]) and only one in Canada (British Columbia).

Material Examined.—ARIZONA. *COCHISE Co.:* Portal, 30 May 1967, C. Sabrocky, 5 females. CALIFORNIA. *CONTRA COSTA Co.:* 9.6 km (6 mi) W of Walnut Creek, 21 Oct 1967, L. N. Bell, 2 males, 1 female. *MARIN Co.:* Alpine Lake Valley, 24 Jun 1973, R. X. Schick, 1 female. *SONOMA Co.:* 3.2–4.8 km (2-3 mi) N of Sebastopol, 7–14 Jul 1963, P. Rubtzoff, 8 females. NEVADA. *NYE Co.:* Mercury, 6 Jul 1961–5 Aug 1962, 15 males, 43 females. CANADA. *BRITISH COLUMBIA.* Kamloops, 27 Oct 1929, O. Bryant, 1 female.

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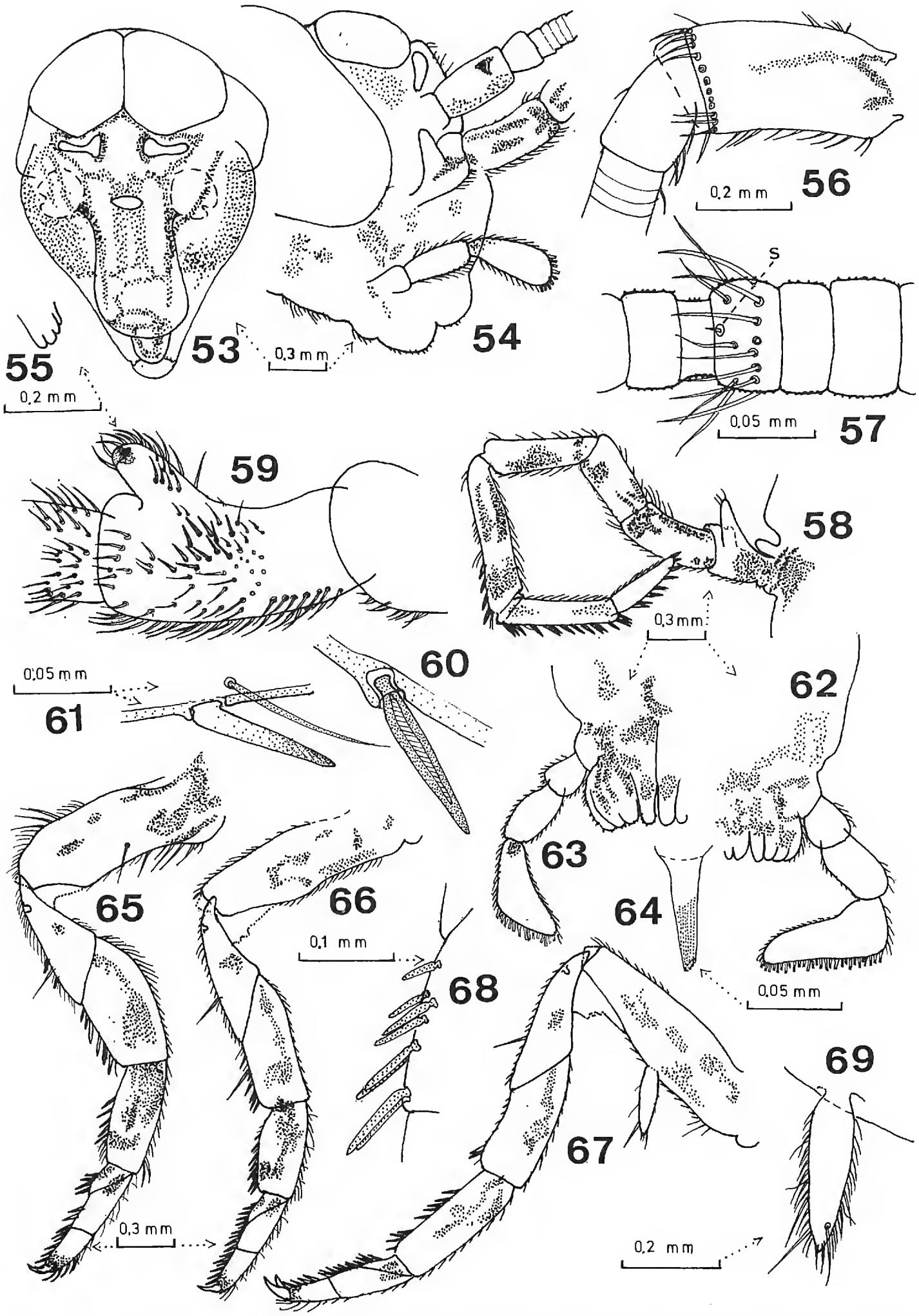
47. Figure 49. IX, distal part. Figure 50. Distal part of body (female), lateral view, ovipositor (= ov) with adhering spermatophore (= sp). Figures 51, 52. *Machilinus* (*Nearctolinus*) *aurantiacus setosus* NEW SUBSPECIES (male). Figure 51. Dorsal part of frons with spine-like setae, frontal view. Figure 52. Maxillary palp, lateral view, inner side.



Figures 53–69. Figures 53–60 and 62–69. *Praemachilellus rentzii* NEW SPECIES. Figure 53. Head (female), frontal view. Figure 54. Head (male) lateral view. Figure 55. Apex of mandible (female), frontal view. Figures 56, 57. Antenna (female). Figure 56. Base. Figure 57. Flagellum, apical article of a distal chain, s = sensory rod. Figures 58–60. Maxillary palp, lateral view. Figure 58. Survey (female). Figure 59. Article 2 (male), inner side. Figure 60. Spine-like seta on article V (female). Figure 61. *Machilinus* (*Neotropolinus*) *chilensis* NEW SPECIES, "spine" on article 5 (female). Figures 62–

Machilinus (*N.*) *aurantiacus setosus* Sturm & Bach, NEW SUBSPECIES (Figs. 51, 52)

Types.—Holotype: male; UTAH. 9 miles E of Oak City, Oak Camp. 1 Sep 1963, D. C. Rentz. Allotype: female; same data as holotype. Paratypes: 1 male, 1 female; CALIFORNIA. *TUOLUMNE Co.:* Chipmunk Flat near Sonora Pass, 19 Jul 1964, D. C. & K. A. Rentz. All types deposited in the California Academy of Sciences, San Francisco.

Description.—Spine-like setae on ventral-distal border of article two of male maxillary palp distinctly longer than in the nominate form, partly longer than one-third of median diameter of article (Fig. 52). Median part of frons in male with two rows of stout spine-like setae (Fig. 53). Hypodermal pigment of all coxae uniformly well developed on the surface. Area of short setae on labial palp article three of male more extended than in nominate form and reaching almost to outer margin.

Diagnosis.—The above differential characteristics of the subspecies are present only in the males. These show an obvious tendency towards an increased formation of long spine-like setae on article two of the male maxillary palps and of short ones on the median part of frons.

Discussion.—Because the chaetotaxy is not distinctly different from that of the nominate form, the form is ranked as a subspecies.

Etymology.—The subspecies is named after the big spine-like setae on maxillary palp article two and frons of male (setosus (latin) = bristly).

Material Examined.—See types.

Praemachilellus Sturm & Bach, NEW GENUS

Type Species.—*P. rentzii* Sturm & Bach, NEW SPECIES.

Description.—Head: dorsal part of frons distinctly protruded; eyes large, little longer than wide; lateral ocelli sole-shaped, inner distance smaller than width of one ocellus. Antennae: apparently shorter than body; distal articles of chains with scattered sensory rods. Mandible: apex distinctly four-toothed. Maxillary palps: longitudinal process on base well developed; triangular process on article one fairly digitate; articles five to seven with stout brown pigmented spine-like setae, typical spines absent, except for the terminal spine; article two of male with field of spine-like setae on inner side, with well developed hook on dorsal-distal margin. Labium: submentum near base of palps lateradly distinctly protruded; article one distinctly shorter than two; article three in female moderately, in male extremely widened. Legs: small coxal stylets on legs III only; femora I distinctly wider than II and III; ventral margin of all legs from femur distadly with dark spine-like setae. Urosternites: I–VII with one + one coxal vesicles, II–IX with stylets; terminal spines of stylets well developed, about one-fourth to one-third as long as stylets. Penis: shorter than one-half length of coxites IX; aperture triangular, inner border surrounded by small bulgy grooved setae. Ovipositor: of secondary type; relatively short, not extending beyond tips of coxites IX: distal articles of gonapophyses VIII each with transversal row of darkly pigmented strong setae, two distal articles of VIII with pigmented fossorial claws. Caudal appendages: typical hair-like scales absent; cerci with single terminal spine.

Diagnosis.—Besides the characteristic ovipositor the combination of the following characteristics can be used for the determination of the monotypic and well defined genus: Frons distinctly protruded; lateral ocelli sole-shaped, without

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64. Labium with palp, partly, ventral view. Figure 62. Male. Figure 63. Female. Figure 64. Sensory cone of labial palp article 3 (male). Figure 65. Leg I (female). Figure 66. Leg II (female). Figure 67. Leg III (female). Figure 68. Leg III (female), spine-like setae on tarsus 2. Figure 69. Leg III (female), coxal stylet.

obvious constriction in the median part; maxillary palps on articles five to seven with spine-like setae in the place of the usual spines; article one of labial palps distinctly shorter than article two; coxal stylets only on leg III; all legs with characteristic spine-like setae; aperture of penis with specialized grooved setae.

Etymology.—In some respects the genus is more primitive than the related genera *Machilellus* and especially *Neomachilellus*: prae (latin) = before.

Discussion.—Together with the genus *Kuschelochilis* Wygodzinsky, 1951 (Fig. 84), the new genus is the the only one within the Meinertellidae that has an ovipositor of secondary type. This shows that this feature, which is found extensively within the family Machilidae, either evolved separately in two different genus groups of Meinertellidae, or was not lost completely in the genotype of this family. The latter possibility seems more probable.

The presence of characteristic, straight and pigmented spine-like setae with a constriction near the base, on articles five to seven of the maxillary palps was apparently not described for Machiloidea up until now (Fig. 60). In other genera of Machiloidea these articles bear spines that are fastened with a broad base in the exocuticula. They are distinctly inclined on the basal part, surrounded at the base by a small cuticular ring and not clearly separated from the cuticula by a joint. Moreover, the spines are more securely attached to the exocuticula. Grooved setae around the aperture of penis are present in several genera of the Meinertellidae, highly specialized in *Neomachilellus* and *Meinertellus* (cf. Sturm 1984). A distinct feature of *Praemachilellus* is the much widened basal part of the setae and the fact that they are not arranged in distinct rows.

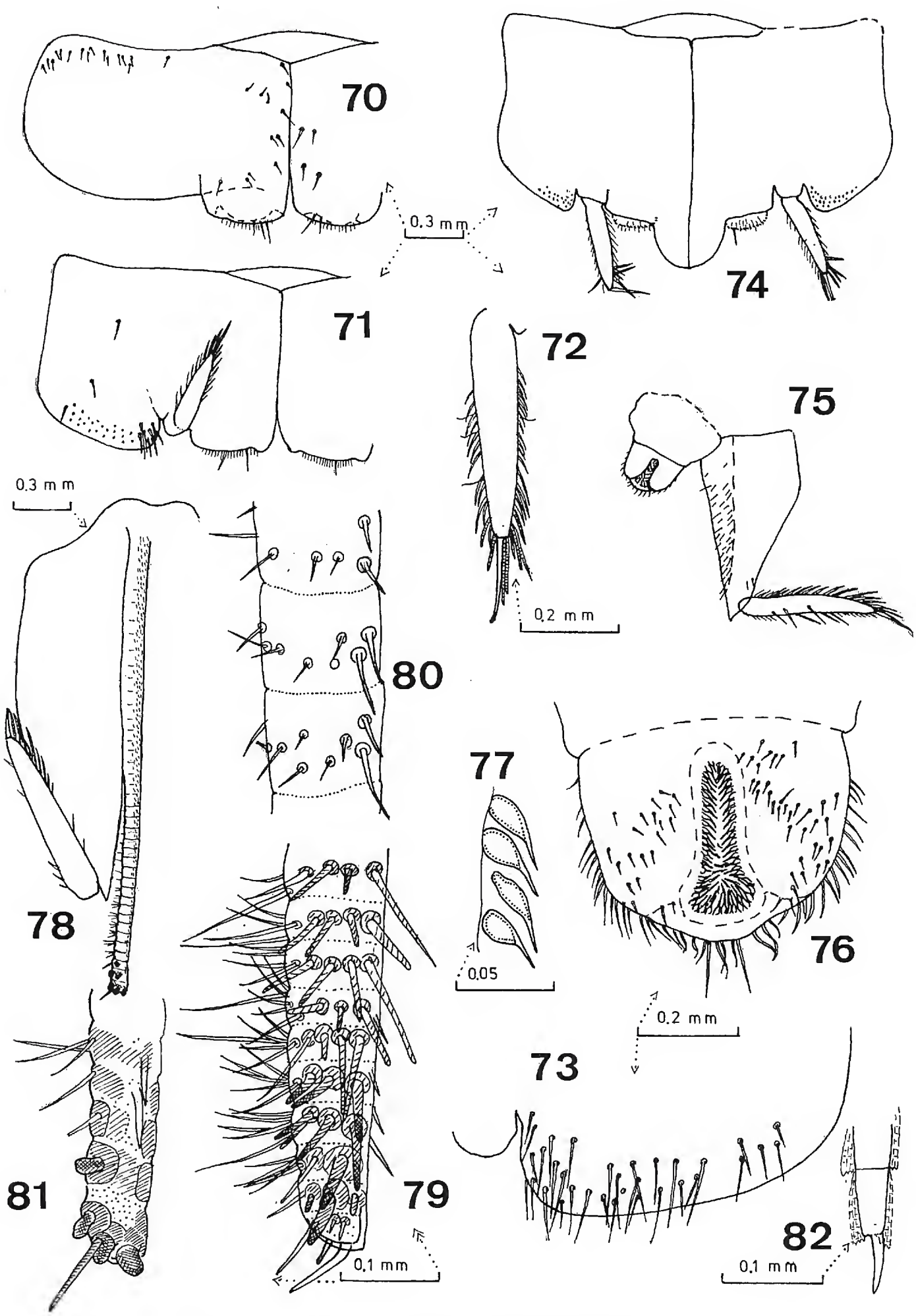
The presence of the ovipositor of secondary type and the presence of spine-like setae on the maxillary palps sets the genus apart within the Meinertellidae. The coxal stylets, only present on legs III, the pigmented spine-like setae on all legs, the obvious sexual dimorphism of the labial palps and the form and position of the lateral ocelli indicate that it is related to the genus *Hypomachiloides,* collected in Texas and Mexico. Distinct features of this genus are the ovipositor of primary type and the extreme sexual dimorphism of the labial palps (cf. Bach & Sturm 1988).

Material Examined.—See *P. rentzii.*

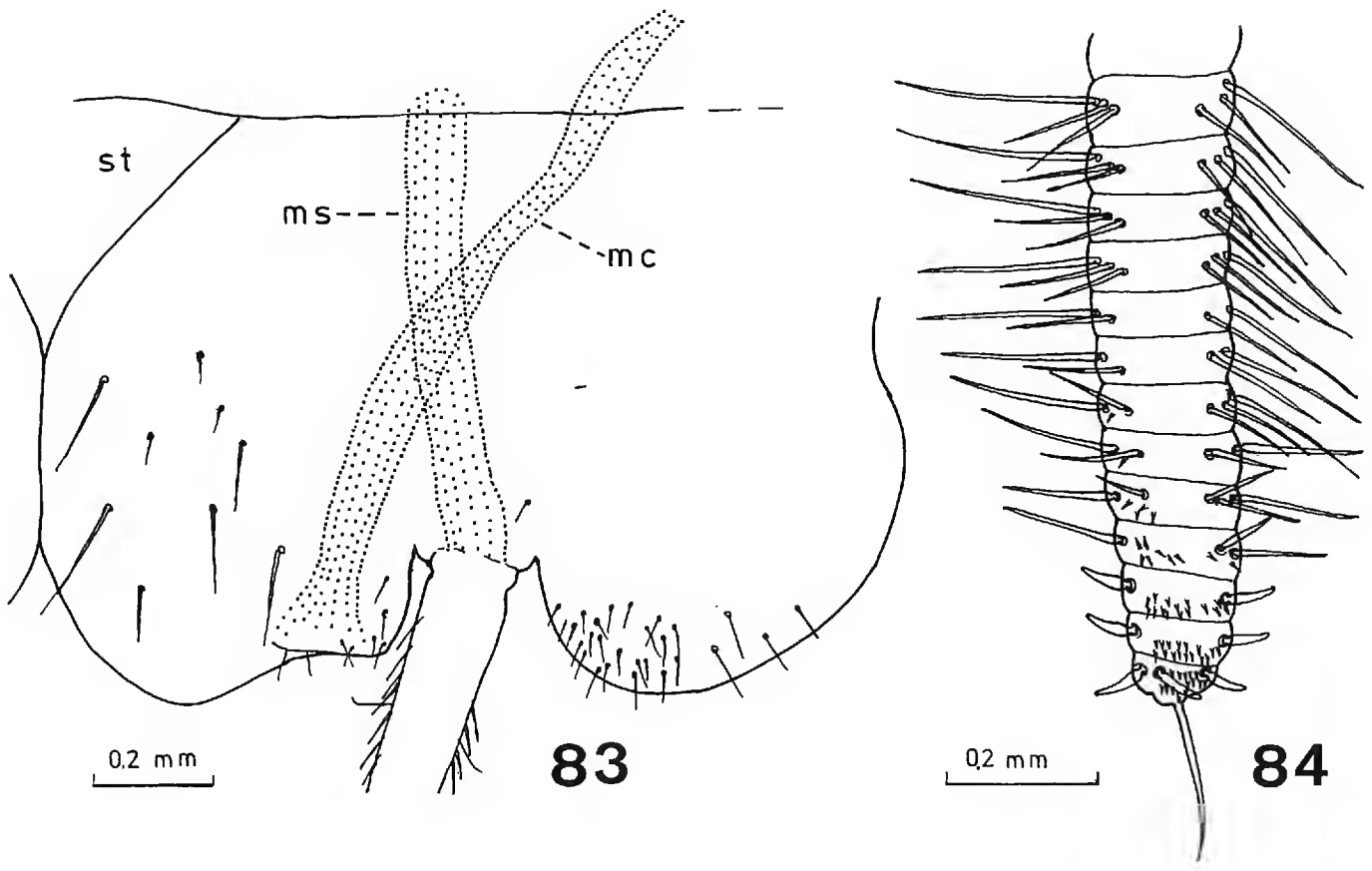
Praemachilellus rentzii Sturm & Bach, NEW SPECIES (Figs. 53–82)

Types.—Holotype: male; MEXICO. *CHIHUAHUA:* 21.8 km (13 mi) N of Camargo, 1340 m, ex *Larrea tridentata,* 4 Sep 1968, D. C. & K. A. Rentz. Allotype: female; same data as holotype. Paratypes: 3 males, same data as holotype; 1 female; MEXICO. *DURANGO:* 8.0 km (5 mi) W of Cucname, ex *Larrea tridentata,* 29 Aug 1964, D. C. & K. A. Rentz. All types deposited in the California Academy of Sciences, San Francisco.

Description.—Medium sized (adults 7.5–9.5 mm); well defined patches of dark violet to brown pigment on head, head appendages and legs; pigment on all tergites and on abdominal coxites more diffusely distributed. Head (Figs. 53, 54): dorsal part of frons distinctly protruded; eyes large (width: 0.75–0.85 × head width) somewhat wider than long (ratio length : width, 0.75–0.92; line of contact, 0.5–0.7 × eye length); lateral ocelli red brown, submedian to eyes, sole-shaped, distance between inner margins smaller than width of one ocellus; frons between lateral ocelli with some strong setae; clypeus with medium sized setae, pigment pattern see Figs. 53, 54. Mandibles (Fig. 55): distinctly four-toothed;



Figures 70–82. *Praemachilellus rentzii* NEW SPECIES. Figures 70–74. Urosternites (female), ventral view. Figure 70. I. Figure 71. V. Figure 72. Stylet V. Figure 73. V, distal-lateral part. Figure 74. VIII. Figure 75. Coxite IX (male) with penis, ventral view. Figure 76. Penis, ventral view. Figure 77. Grooved setae from inner margin of penis aperture. Figure 78. Coxite IX (female) with gonapophysis. Figures 79, 80. Gonapophysis VIII (female), ventral view. Figure 79. Distal part. Figure 80. Articles 21–23, counted from caudal. Figure 81. Gonapophysis IX (female), apex. Figure 82. Apex of cercus (male) with terminal spine.



Figures 83, 84. *Kuschelochilis ochagaviae* Wygodzinsky, 1951, paratypes. Figure 83. Detail of urosternite II (male), mc = muscle of coxal vesicle, ms = muscle of stylet, s = sternite. Figure 84. Apex of gonapophysis VIII (female).

nearly all of surface heavily pigmented. Antennae (Figs. 56, 57): shorter than body length (up to 6 mm); scape with small pigmented patches only, ratio length : width, 1.6–1.9; flagellum uniformly brown, distal chains with nine subarticles, distal subarticles of each chain with scattered sensory cones. Maxillary palps (Figs. 58–60): longitudinal process near dorsal base well developed; triangular process on article one long and fairly digitate; articles five to seven with straight pigmented spine-like setae instead of the usual spines (Figs. 60, 61); ratio length of articles seven/six/five/four = 0.65–0.8:1.0: 1.25–1.4:0.95–1.25 respectively; maximal number of spine-like setae on articles seven to five: 19, 23, 10 respectively; for pigment pattern see Fig. 58; article two of male with well developed process on the dorsal distal margin ending in heavily chitinized hook and with field of stronger setae on inner face. Labium (Figs. 62–64): submentum near base of palps lateradly distinctly protruded; ratio length of articles one : two of palps, 0.6–0.7, article three in female moderately in male extremely widened. Legs (Figs. 65–69): small coxal stylets present only on legs III, ratio length of stylet : length of femur, 0.4–0.5; femur I distinctly wider than II and III; ventral side of femur and more distal articles of all legs with brown spine-like setae, maximal number on femur, tibia, and tarsomeres: 10, 18, 9, 10, 7 respectively. Urosternites (Figs. 70–75): I–VII with one + one coxal vesicles; terminal spines of stylets hyaline and rounded by darkly pigmented shorter setae; median distal margin of coxites VI (female) strongly protruded; ratio length of coxite : length of stylet : length of terminal spine for II, 1.6–1.7:1.0: 0.3–0.4; for V, 2–2.3:1.0:0.35–0.45; for VIII = 1.5–1.7:1.0:0.3–0.4; for IX = 1.7–1.9:1.0:0.25–0.35 (male), 1.9–2.4:1.0:0.2–0.3 (female); coxites II–VIII with fairly well limited field of setae near lateral base of stylets extending for most part lateradly; coxites IX (male) with stripe of setae near distal-median margin; spine-like setae absent. Penis (Figs. 76, 77): shorter than one-half length of coxite IX; aperture ventral, subtriangular, inner side rounded by densely inserted grooved setae with bulgy basal part and thin hair-like end; external surface with unspecialized setae. Ovipositor (Figs. 78–81): relatively short, not extending beyond tips of stylets IX, with about 32 articles; of secondary type; gonapophyses VIII with short lateradly oriented terminal spine; five most distal articles each with one to three very strong and blunt dark setae, proximadly follow transversal rows of transitorial and normal setae (up to eight per article), number and size reduced on proximal half; two distal articles of gonapophyses IX each with one to three fossorial claws, typical transitional setae absent from more proximal articles. Caudal appendages (Fig. 82): typical hair-like scales absent; terminal filament broken; length of cerci up to 3.4 mm (about 0.4 × body length); cerci with single terminal spine.

Diagnosis.—This is the only species of the genus and it can be determined and characterized by the characteristics of the genus.

Etymology.—The species is named after the collectors D. C. & K. A. Rentz[1] who consequently collected interesting material on Machiloidea.

Material Examined.—See types.

Acknowledgment

We express our gratitude to the scientists who made it possible for us to examine this interesting material, especially to E. Tremblay (Instit. di Entomologia Agraria, Portici/Neapel), V. F. Lee (California Academy of Sciences, San Francisco), Mrs. K. Schmidt and R. T. Schuh (American Museum of Natural History, New York), A. Coddington and G. F. Hevel (U.S. National Museum, Washington) and W. Probst (Pädagogische Hochschule Flensburg). To Ms. F. Brady we are indebted for the revision of the English version.

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Received 1 July 1991; accepted 23 October 1991.

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PAN-PACIFIC ENTOMOLOGIST
68(3): 192–199, (1992)

FLOWER-BREEDING *DROSOPHILA* OF BOGOTA, COLOMBIA: NEW SPECIES (DIPTERA: DROSOPHILIDAE)

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Abstract.—There are two taxonomic groups of flower-breeding *Drosophila* in Bogota, Colombia and its environs, at altitudes of 2500 m and higher. The *onychophora* species group of the subgenus *Drosophila* is characterized by wide ovipositor plates studded with many stubby teeth. Thirteen species in this group are in the Bogota region: *D. bifurcada* NEW SPECIES, *D. choachi* NEW SPECIES, and *D. arane* NEW SPECIES are described here. A key for the 13 species is given. The *onychophora* group of flies breed in several genera of composites and other families, and some species are monophagous. Four species of the *flavopilosa* species group in the Bogota region breed in flowers of *Cestrum* (Solanaceae). This group in the subgenus *Drosophila* is characterized by a strongly spined ovipositor.

Key Words.—Insecta, Diptera, *Drosophila, onychophora, flavopilosa,* flower-breeding, Bogota

Over several years of collecting in the region around Bogota, Colombia, I found at least 50 different species of *Drosophila.* This is a considerable diversity for an altitude of 2500 m and higher and an average temperature of 15° C. For a majority of these, the breeding sites were not found. However, 17 were found breeding in live flowers. These *Drosophila* are largely in two main groups: the *flavopilosa* group (Wheeler et al. 1962) which breeds only in flowers of *Cestrum,* and the *onychophora* group (Vilela & Bachli 1990), with a characteristic toothed ovipositor, which breeds in flowers of several genera (Hunter 1979, 1988). In the Bogota region, there are at least 13 species in the *onychophora* group, 10 previously described (Hunter 1979, 1988) and three described in this paper. There are three other species in the *onychophora* group that are found in Bolivia and Peru and are described by Duda (1927). The Colombian species have eggs without filaments that are laid in the buds of their host flowers.

METHODS

Specimens have been deposited in the California Academy of Sciences. The hosts were identified by Enrique Forero of the Universidad Nacional de Bogota. The characters of the imagines given here are based largely on the holotype male; however, the body and wing lengths are average values for five live males and five live females. The wing indices are measured on slide preparations of five female and five male wings. The diagrams of genitalia are based on slide preparations of terminalia from several specimens.

TAXONOMY

Drosophila bifurcada Hunter, NEW SPECIES
(Fig. 1)

Types.—Holotype #15854: male; data: COLOMBIA, BOGOTA: aqueduct watershed of mountain Monserrate, 2600 m, 20 Aug 1980, A. S. Hunter; deposited:

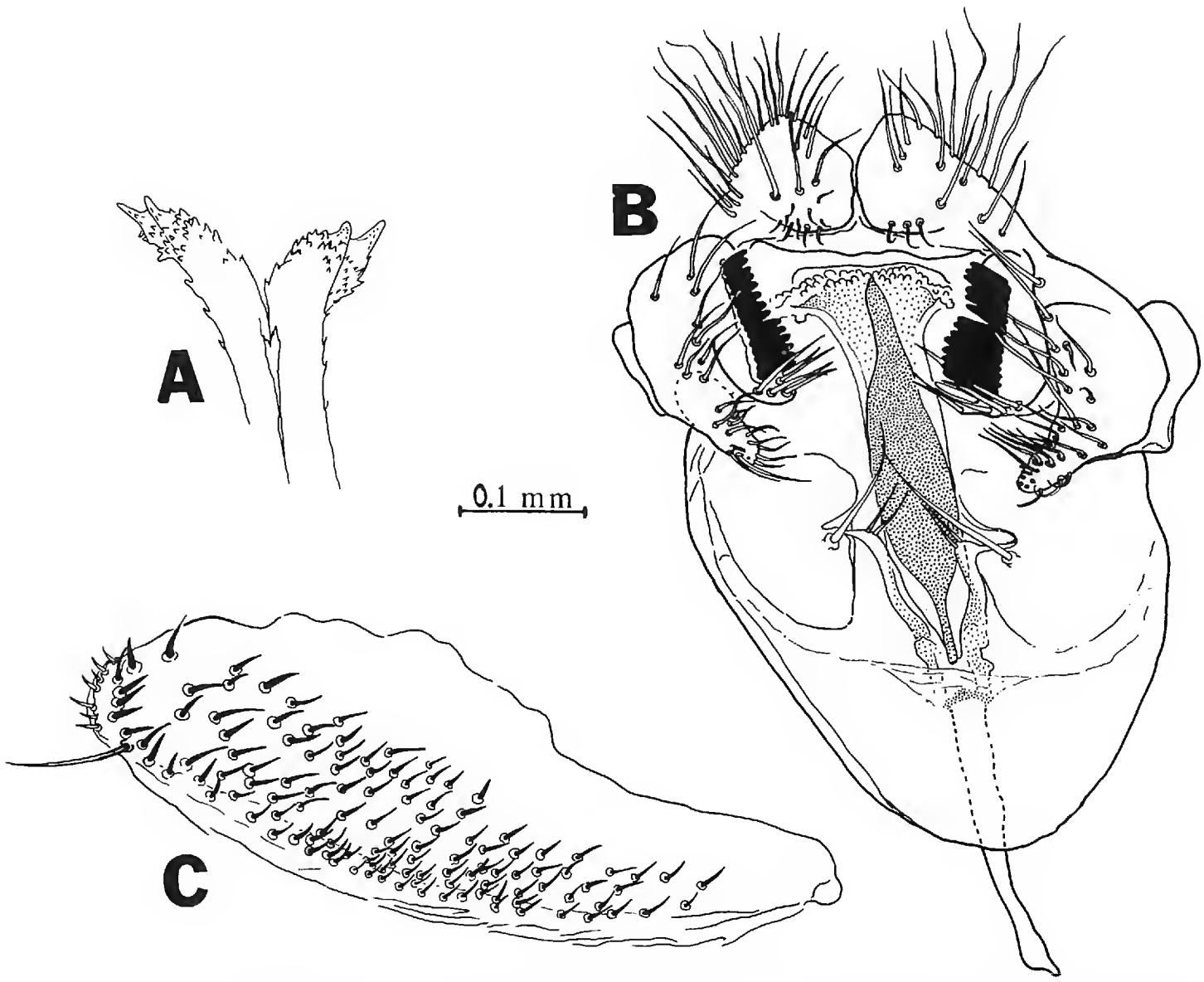

Figure 1. Genitalia of *Drosophila bifurcada,* A. tip of aedeagus, B. male terminalia, C. right ovipositor plate.

California Academy of Sciences, San Francisco. Paratypes: 3 females, 3 males; same data as holotype; deposited: California Academy of Sciences.

Description.—Male.—Arista with three dorsal, two ventral branches plus a terminal fork. Basal antennal segments tan; third segment brown; one medium and one short bristle on second segment. Frontal and ocellar triangles dark brown. Proclinate orbital bristle 0.75 × length of posterior reclinate; anterior reclinate one-third of posterior. Face brown; carina moderately high, narrow, slightly sulcate. Cheek tan; one long oral bristle. Distance from border of eye to base of first oral 0.2 × greatest diameter of eye. Eyes dark red; eye index 1.1. Palpus pale tan with one long, several medium length hairs. Acrostichal hairs in six rows between dorsocentrals; no prescutellars; anterior scutellars divergent. Thorax shiny brown with a pair of light stripes through dorsocentral bristles; scutellum and pleura shiny brown; halter pale tan. Anterior sternopleural bristle 0.66 × length of posterior; middle sternopleural 0.5 × length of anterior. Legs pale tan with darker terminal tarsal segment. Small apical and pre-apical bristles on first tibia; apical and pre-apical bristles on middle tibia; pre-apicals on third tibia; several thin bristles on front femur. Wing pale tan with slightly darker veins. Costal index 4.3, fourth vein index 1.5, 4c index 0.5, 5× index 1.2. Thicker hairs on anterior border to basal two-fifths of third section of costa. Abdomen brown, each tergite with narrow black band. Body length 2.9 mm; wing length 4.1 mm. Genitalia (Fig. 1): aedeagus pale tan, very slight dorsoventral curve; apex bifurcate, each tip secondarily bifurcate; tips serrate. Aedeagal apodeme thick, straight. Epandrium articulated with anal plate dorsoposteriorly; row of six bristles on medial surface projecting over surstyli; laterally, eight bristles; thick tuft of ten bristles on ventral lobe. Surstyli with 14 black primary teeth; fine, short black hairs all over surface; six short, tan bristles at anterior end. Surstyli united by wide, dorsal bridge (decasternum). Hypandrium with long, medioventral bristle on each side; finger-like gonapophyses with three yellow hairs.

Female.—Thorax slightly darker than that of male. Body length, 3.1 mm. Wing length, 4.1 mm. Spermatheca dark brown, spherical. Ovipositor plate brown, curved, many fine teeth (about 120) all over lateral surface; row of seven small teeth at rounded, dorsoposterior apex; one long bristle at ventroposterior apex.

Egg.—Pointed anteriorly; no filaments.

Larva.—First instar present in genital chamber of female has mandibular hook with bifurcate tip.

Diagnosis.—The many teeth on the ovipositor plates and the lack of egg filaments are characteristics of the *onychophora* group of *Drosophila* from Bogota. The bifurcate apex of the aedeagus distinguishes this species from others of the group.

Distribution.—*D. bifurcada* has been found along the river on mountain Monserrate, which is the watershed for the Bogota aqueduct.

Hosts.—Adult *D. bifurcada* emerge from pupae in the flowers of both *Liabum megacephalum* Schultze and *Bidens rubifolia* Humboldt (Asteraceae).

Material Examined.—See types.

Drosophila choachi Hunter, NEW SPECIES
(Fig. 2)

Types.—Holotype #15856: male; data: COLOMBIA, BOGOTA: road to Choachi on mountain Guadelupe, 2700 m, 13 Aug 1980, A. S. Hunter; deposited: California Academy of Sciences, San Francisco. Paratypes: 1 female, 2 males; same data as holotype; deposited: California Academy of Sciences.

Description.—*Male.*—Arista with two dorsal, one ventral branches plus a terminal fork. Basal antennal segments gray-brown; two bristles on second segment. Proclinate orbital bristle two-thirds length of posterior reclinate; anterior reclinate one-half length of posterior reclinate. Face gray-black; carina moderately high, not sulcate. Cheek black; one long oral bristle; palpus and proboscis tan-gray. Distance from border of eye to base of first oral bristle one-fifth of greatest diameter of eye. Eye bright red; eye index 1.1. Acrostichal hairs in 6 rows between dorsocentrals; no prescutellar bristles; anterior scutellars divergent. Thorax semi-shining black. Anterior sternopleural bristle 0.66 × length of posterior; middle sternopleural 0.5 × first, very thin. Legs yellow-tan, except coxa, proximal two-thirds of femur and last tarsal segment which are brown. Apical bristles on middle tibia and pre-apical bristles on all tibiae; five medium to long bristles on first femur. Wings pale gray with slightly darker veins. Costal index 4.8, fourth vein index 1.7, 4c index 0.5, 5× index 1.3. Thicker hairs along wing border to basal half of third section of costa. Abdomen yellow-tan, first two tergites with posterior black band wider in midline, fading out laterally. Body length, 2.6 mm. Wing length 2.7 mm. Genitalia (Fig. 2): aedeagus tan with brown tip; C-shaped curvature toward left; apex in shallow S-shaped curve; apodeme broadens at base. Epandrium articulated with posterior, lateral corners of hypandrium; row of seven long, tan hairs on medial border; group of four medium length hairs on anterior, medial apex. Surstyli with eight black, primary teeth; six small teeth on inner surface. Surstyli united by wide, dorsal bridge (decasternum). Hypandrium with long, medioventral bristle on each side; broad gonapophyses each with three medium length yellow bristles.

Female.—Abdomen brown-gray with black bands on posterior half of each tergite. Body length, 2.9 mm. Wing length, 3.0 mm. Spermatheca dark brown, ovoid. Curved ovipositor plate studded with about 140 short, stubby, black teeth; three long, one medium hairs on dorsal apex; four medium length hairs on ventral apex.

Egg.—Apex tapers to fine point; no filaments.

Diagnosis.—The many teeth on the ovipositor plate and lack of egg filaments are characteristic of the *onychophora* group of *Drosophila* from Bogota. The shape of the aedeagus (Fig. 2) and teeth of surstyli distinguish *D. choachi* from other species in this group.

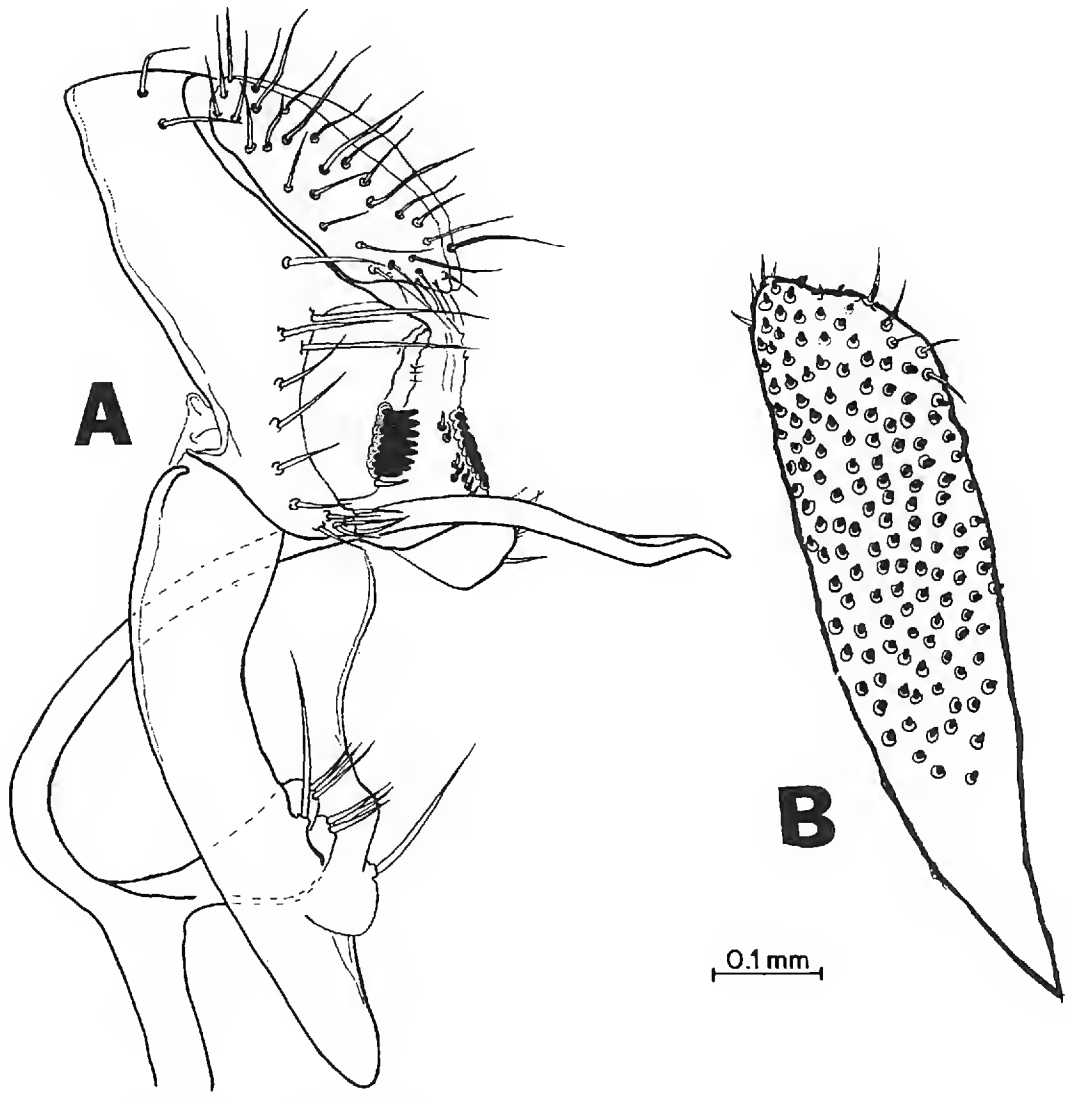

Figure 2. Genitalia of *Drosophila choachi,* A. male terminalia, B. right ovipositor plate.

Distribution.—*Drosophila choachi* has only been found in the paramo of Choachi on mountain Guadelupe.

Host.—Adults emerged from flowers of *Eupatorium vaccinaefolium* Benth (Asteraceae).

Material Examined.—See types.

Drosophila arane Hunter, NEW SPECIES
(Fig. 3)

Types.—Holotype #15853: male; data: COLOMBIA, BOGOTA: aqueduct watershed of mountain Monserrate, 2600 m, 12 Aug 1980, A. S. Hunter; deposited: California Academy of Sciences, San Francisco. Paratypes: 3 females, 3 males; same data as holotype; deposited: California Academy of Sciences.

Description.—*Male.*—Arista with three dorsal and one ventral branches plus terminal fork. Basal antennal segments dark brown; two medium hairs on second segment. Frontal and ocellar triangles light brown, bordered by dark brown. Proclinate orbital bristle two-thirds length of posterior reclinate; anterior reclinate one-half of posterior. Face brown; carina high, narrow, not sulcate. Cheek brown; one long oral bristle. Distance from border of eye to base of oral bristle one-fifth of greatest diameter of eye. Eye sepia; eye index 1.1. Palpus brown with many fine, medium length hairs. Acrostichal hairs pale yellow, in six rows between dorsocentrals; no prescutellars; anterior scutellars divergent; posterior dorsocentrals same length as scutellar bristles. Thorax brown-black. Halter pale tan. Anterior sternopleural bristle one-half length of posterior; middle sternopleural one-half length of anterior. Legs shaded from black femur to brown tibia to tan tarsus, excepting last tarsal segment which is brown.

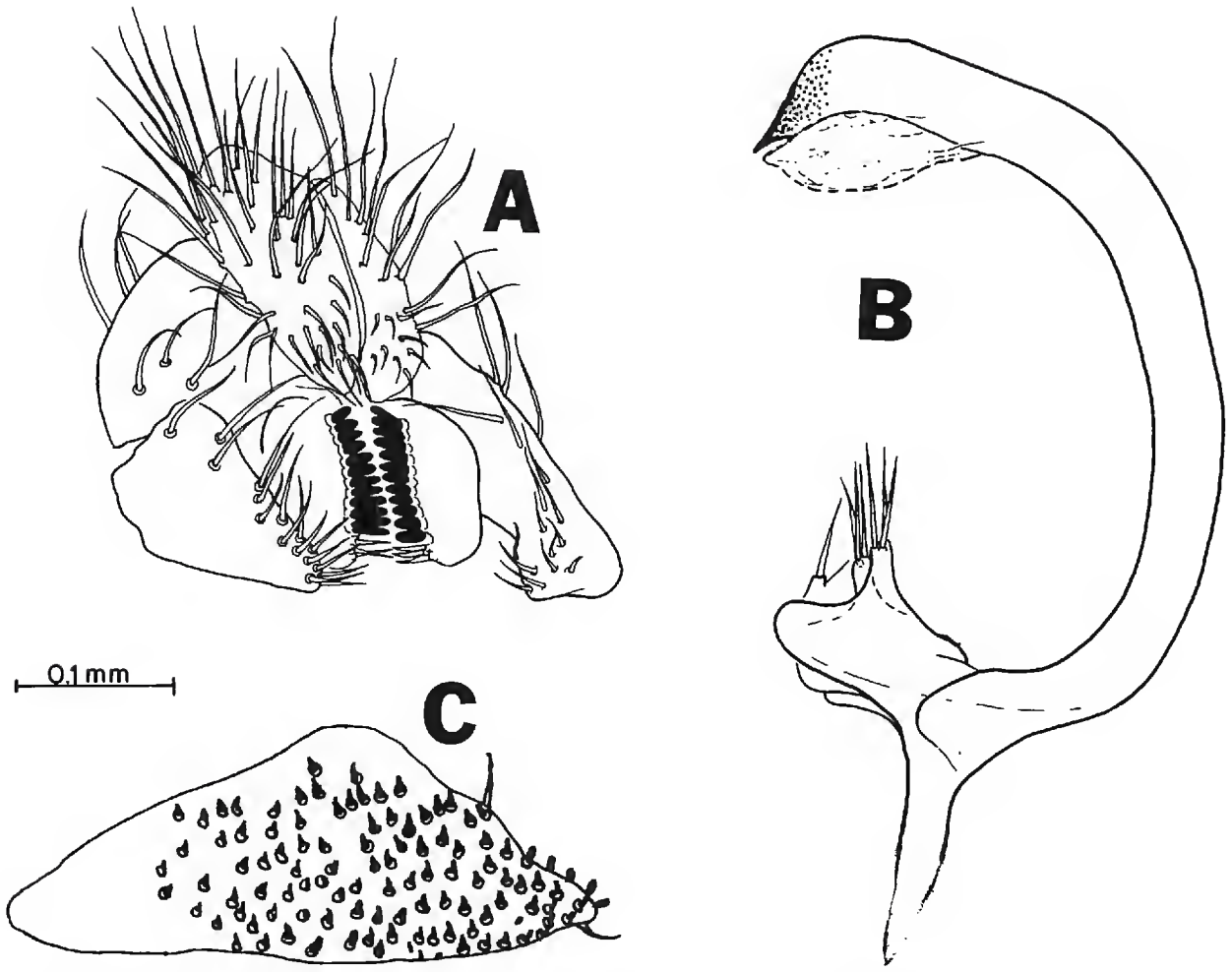

Figure 3. Genitalia of *Drosophila arane,* A. male terminalia, B. aedeagus, C. left ovipositor plate.

Apical and preapical bristles on middle legs, apical on first and pre-apical on third. Wings pale tan with slightly darker veins. Costal index 3.8, fourth vein index 1.6, 4c index 0.7, 5× index 1.1. Abdomen brown with darker band bordering posterior margin of each tergite. Body length 2.7 mm. Wing length, 3.6 mm. Genitalia (Fig. 3): aedeagus tan with sharply pointed black tip on scoop-shaped apex, apodeme thin, slightly curved. Epandrium articulates with anal plate dorsoposteriorly; row of five bristles extends from medial surface to overlap surstyli; tuft of six bristles on toe. Surstyli with 13 primary teeth; four stubby teeth on internal surface. Hypandrium with long, medioventral bristle on each side; finger-like gonapophyses, each with three to four long, yellow bristles.

Female.—Body length, 2.9 mm. Wing length, 3.7 mm. Spermatheca brown, spherical. Ovipositor with pointed apex; wide plates studded with about 100 short, stubby, black teeth; one long bristle dorsally; one yellow hair on ventral apex.

Egg.—Pointed anteriorly, no filaments.

Pupa.—Anterior spiracles have three long and five very short branches.

Diagnosis.—The many teeth on the ovipositor plate and lack of egg filaments are characteristic of the *onychophora* group of *Drosophila* from Bogota. The pointed tip of the ovipositor plates and the straight row of 13–14 primary teeth on the surstyli distinguish *D. arane* from other flies of this group.

Distribution.—*Drosophila arane* has been found along the river that is the aqueduct watershed from the mountain Monserrate in Bogota. The host flowers border the river just above the guard house.

Hosts.—Eggs, larvae and pupae of *D. arane* were found in flowers of *Siegesbeckia jorullensis* H.B.K. and *Liabum megacephalum* Schultze (Asteraceae).

Remarks.—Arane is the latin word for spider and refers to the appearance of this fly, which is that of a small spider with long, dark legs and compact body.

Material examined.—See types.

Key to *Drosophila* species of the *onychophora* group in Bogota and environs.

1a. Wings long (at least 4.4 mm); costal index (length of second costal section/third costal section) at least 5.0; arista with four upper and two lower branches + terminal fork: associated with flowers of *Bomarea* 2

1b. Wing length less than 4.4 mm; costal index <5.0; arista with only two to three upper branches; associated with flowers of genera other than *Bomarea* 3

2a. (1a). Cheeks white ..... *D. carablanca* Hunter

2b. Cheeks tan ..... *D. bomarea* Hunter

3a. (1a). Body narrow (like *Scaptomyza*), steel gray on live flies; associated with *Espeletia* flowers of paramo of Chisaca ..... *D. chisaca* Hunter

3b. Body form and color variable (distributed in Bogota and environs) ... 4

4a. (3b). Costal index from 4.2 to 4.9 5

4b. Costal index less than 4.2 8

5a. (4a). Eight rows acrostichal hairs, thorax brown, abdomen dark grey to black, wings smoky, associated with *Cleome* flowers .... *D. desbaratabaile* Hunter

5b. Six to eight rows acrostichal hairs, other traits variable, not associated with *Cleome* flowers 6

6a. (5b). Arista with two upper, one lower branches plus terminal fork; thorax semi-shining black; eyes bright red; associated with *Eupatorium* ..... *D. choachi* NEW SPECIES

6b. Arista with three upper, one to two lower branches + terminal fork; thorax brown; eyes dull red to burgundy color; associated with various different flowers 7

7a. (6b). Arista with three upper, two lower branches + terminal fork; thorax brown with lighter stripes through dorsocentrals; eyes burgundy; associated with *Liabum* and *Bidens* ..... *D. bifurcada* NEW SPECIES

7b. Arista with three upper, one lower branches + terminal fork; thorax unicolorous grey-brown; eyes dull red; associated with *Espeletia* ... . *D. freilejoni* Hunter

8a. (4b). Thorax tan to light brown 9

8b. Thorax dark brown to black 11

9a. (8a). Arista with two upper, three to two lower branches + terminal fork; six rows of acrostichals; abdomen tan with dark brown bands, wider on anterior segments and in midline; associated with *Liabum* and *Bidens* ..... *D. colmenares* Hunter

9b. Arista with three upper, one lower branches + terminal fork; seven to eight rows acrostichals; other traits variable 10

10a. (9b). Light brown thorax with central darker stripe; abdomen yellow-orange with tan bands more marked anteriorly and fading posteriorly and laterally; associated with *Liabum* and *Bidens* .... *D. franii* Hunter

10b. Thorax unicolorous light brown with green hue; abdomen tan with dark bands interrupted medially, thinning laterally; associated with *Montanoa* (crazy tree) ..... *D. arboloco* Hunter

11a. (8b). Small body, 2.0–2.3 mm long, wings less than 3 mm long; eight

rows of acrostichals; associated with *Chrysanthemum, Liabum* and *Bidens* ..... *D. margarita* Hunter

11b. Body length greater than 2.5 mm; wings 3 mm or longer; six to seven rows of acrostichals 12

12a. (11b). Arista with two upper, one lower branches + terminal fork; short, plump body shape; associated with *Liabum* ... *D. acuminanus* Hunter

12b. Arista with three upper, one lower branches + terminal fork; "spidery" body shape; associated with *Siegesbeckia* .... *D. arane* NEW SPECIES

Discussion

The best way to identify these species is by their genitalia (Figs. 1–3) (Hunter 1979: figs. 1–6; Hunter 1988: figs. 1–9). Drawings of the ovipositor plates show the differences in overall shape and distribution of teeth and hairs. Surstyli and aedeagi are distinctive for each species.

Drosophila of the *onychophora* group are not attracted to yeasted fruit or vegetable baits as most other drosophilids are. The flies rest on the host plant(s) and frequently occur inside the flower. A convenient way to obtain adults is to collect old flowers that are drying out, and allow the adults to emerge from the pupae within the flowers. In places where the host plants are abundant, adults may be swept with a net over the flowers. There is an area on the south bank of the river of the watershed on Monserrate mountain in Bogota (about 100 m above the guarded entrance) where five of the species occur. *Drosophila franii, D. arane, D. acuminanus, D. colmenares* and *D. bifurcada* occur on *Bidens, Liabum* and *Siegesbeckia* along this bank.

Both *D. bomarea* and *D. carablanca* were found only in the trumpet-shaped red blossoms of the *Bomarea* vine that occurs along the road to Choachi paramo in the region which overlooks the savanna of Bogota. On this same part of the road there are trees of *Montanoa ovalifolia* DC (Asteraceae) in which *D. arboloco* is found. Closer to the paramo, purple-flowered bushes of *Eupatorium* grow, and a few specimens of *D. choachi* emerged from these flowers. On the paramo of Choachi there are several different species of *Espeletia* in which *D. freilejoni* breeds. *Drosophila chisaca* is only collected in the paramo of Chisaca, about 50 km south of Bogota. Of the 13 species of the *onychophora* group found in Colombia, 11 breed in composite flowers and five appear to be monophagous.

These drosophilids were referred to as the "anthophilic group" in previous descriptions (Hunter 1979, 1988) because of their close association with flowers. Vilela & Bachli (1990) renamed the group based on the first species that had been described by Duda (1927), and also placed the group in the subgenus *Drosophila.* All of the 16 species of this group described to date were collected at 2500 m and higher in the Andes. Another undescribed species with genitalia typical of the group was collected at 3000 m in Ecuador (specimens in California Academy of Sciences). The wide ovipositor with many teeth on the lateral surface may be an adaptation for inserting eggs into the buds of flowers. The lack of egg filaments may be related to the type of substrate in which the eggs are laid. This characteristic is found in other flower-breeding *Drosophila* such as the *flavopilosa* group. Ovoviviparity was observed in *D. bifurcada, D. arane* and seven other species of this group (Hunter 1988). This has also been noted in other flower-breeding *Drosophila* and is perhaps of adaptive value in the flower niche. Although some of the

characteristics of these flies are suggestive of a relationship to the subgenus *Phloridosa,* Vilela & Bachli (1990) believe that they evolved independently.

The other major group of *Drosophila* of the Bogota environs that breeds in live flowers includes at least four species of the *flavopilosa* group (Wheeler et al. 1962). It is characterized by the distinctive ovipositor that has heavy black spines on the posterior edge. The eggs lack filaments or have very short ones. These flies breed in flowers of *Cestrum* species. They occur in the same locality where several species of the *onychopora* group are breeding in *Bidens, Liabum,* and *Siegesbeckia,* along the watershed between the mountains, Monserrate and Guadelupe. Several species of *Cestrum* grow there and are hosts to at least four species of the *flavopilosa* group. Although the two groups of plants are only a few meters apart, the flies of the *onychophora* and *flavopilosa* group occur on separate plants. The *Drosophila* of the *flavopilosa* group do not fly around much, but rest on the plants where they have to be aspirated or shaken off.

Drosophila acroria (Wheeler et al. 1962) is the most abundant of the *flavopilosa* species in the Bogota region. It occurs in several different sites, associated with *Cestrum parvifolium* Wild (Solanaceae). Two other species found in the watershed of Monserrate appear to have identical ovipositors with those described by Wheeler et al. (1962) as "unnamed species 3" and "unnamed species 6." The latter is distinctive, because it is tan and black, while other *flavopilosa* species are yellow. A fourth species that does not fit any published descriptions is found associated with *C. petiolare* and *C. tomentosum.*

Several species of unidentified *Drosophila* were found in the white flowers of *Datura* along with many *Zapriothrica.* Possibly these *Drosophila* feed on yeasts growing on decaying flowers, since no larvae occur in the intact live flowers on the bushes.

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Received 28 June 1991; accepted 15 November 1991.

PAN-PACIFIC ENTOMOLOGIST
68(3): 200–215, (1992)

KOREANURINA NEW GENUS, *LEENURINA* NEW GENUS AND *CAPUTANURINA* LEE, 1983 (COLLEMBOLA: NEANURIDAE) FROM NORTH KOREA

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Abstract.—Materials of Neanuridae, Collembola from North Korea were studied. *Koreanurina* NEW GENUS and *Leenurina* NEW GENUS are described, and their taxonomic positions are determined. The genus *Caputanurina* Lee, 1983 is redescribed. Several new species are also described: *Koreanurina szeptyckii* NEW SPECIES, *K. inexpectata* NEW SPECIES, *Leenurina jasii* NEW SPECIES, *Caputanurina intermedia* NEW SPECIES, *C. turbator* NEW SPECIES, *C. major* NEW SPECIES and *C. sexdentata* NEW SPECIES.

Key Words.—Collembola, *Koreanurina, Leenurina, Caputanurina,* North Korea, taxonomy

In 1983, Lee created the subfamily Caputanurinae for two South Korean species with extraordinary characters: the fusion of thorax I with the base of the head; the displacement of the head, anteriorly, and of the abdominal segments, posteriorly, resulting in a pronounced "cryptophthalmy" and distinct "cryptopygy." Also, the cuticule exhibits strong tegumental granulation.

According to Lee (1983), the subfamily contains only one genus, *Caputanurina* Lee, 1983; *C. serrata* Lee, 1983 and *C. nana* Lee, 1983 differ mainly in chaetotaxy, in the form of tegumental grains, as observed with a scanning electron microscope, and in the position of the eyes and the postantennal organ.

Our study, undertaken in 1985, is based on the materials collected in 1971, 1974 and 1981 by the expeditions of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. This material included species belonging to *Caputanurina* and to some related groups, and thus enabled us to taxonomically place these species more precisely in relation to the already known subfamilies of Neanuridae.

We also include *Koreanurina* NEW GENUS, related to a species of *Anurida* Laboulbène, 1865, although we consider *Leenurina* NEW GENUS to belong to the Caputanurinae. A discussion of each genus is presented below.

Abbreviations.—ISEA: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland; MNHN: Laboratoire d'Entomologie, Muséum national d'Histoire naturelle, Paris, France.

PSEUDACHORUTINAE SENSU MASSOUD, 1967

KOREANURINA NAJT & WEINER, NEW GENUS

Type Species.—*Koreanurina szeptyckii* NEW GENUS, NEW SPECIES.

Description.—Color light blue, dark blue, gray. Eyes and postantennal organ dorsal, latter with 9–11 vesicles in one row circle. Five-tooth mandibles. Maxillae type as in *Anurida,* with dentate maxillary

capitulum, free lamellae. Labium elongate, papillary L seta absent, labial organite (x) present. Labral chaetotaxy two/two, three, five, two. Antennae short. Antenna I with seven setae, antenna II with 11 setae. Antennae III and IV fused dorsally. Sensory organ of antennal segment III consisting of two microsensillae, two guard sensillae (the ventral one s-shaped) and one ventrolateral microsensilla. Antenna IV with six thick, subcylindrical sensillae and small dorsal external sensilla; subapical organite small but distinct; apical vesicle slightly bilobate; no sensory rasp. Ventral tube with four + four setae. Tibiotarsus with 18, 18, 17 setae; claw toothless. Furca vestigial, reduced to two small mamelons, each with one seta. Thorax I well separated. Abdomen VI ventral. No anal spines. Dorsal reticulation present on head, thorax II, III and abdomen I to V.

Diagnosis.—The presence of dorsal reticulation on head and thorax tergites II–III make it easy to discern *Koreanurina.* Table 2 presents the characters differentiating *Koreanurina* from *Leenurina* and *Caputanurina.*

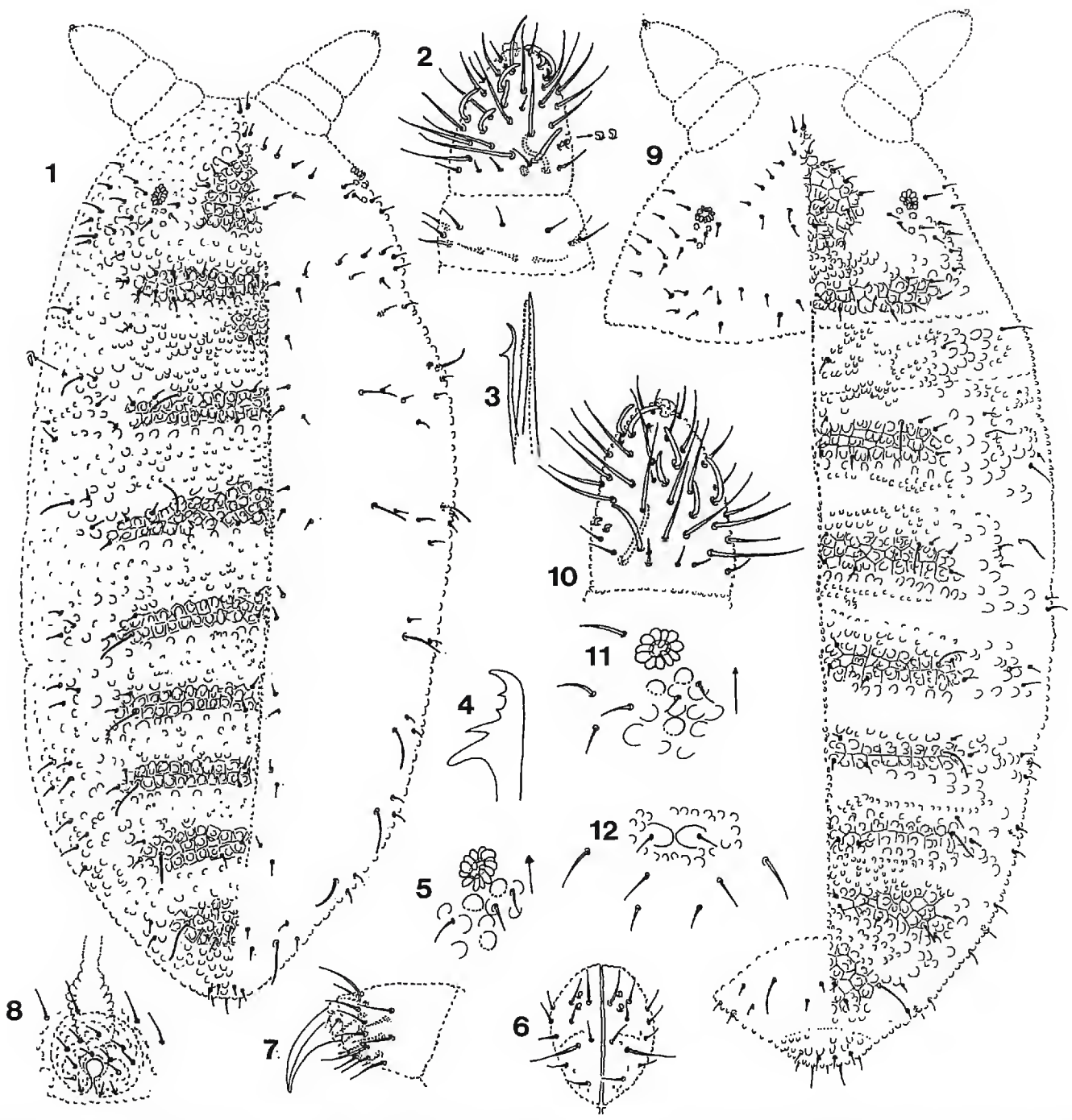
Discussion.—We included *Koreanurina* among the Pseudachorutinae because of the presence of six sensillae on antenna IV. The new genus has a well-separated thorax I, like in all other genera of the subfamily, which was divided by Massoud (1967) into two tribes. *Koreanurina* is, however, related to a single *Anurida* species (*A. hexophthalmica* Stach, 1949 of the Tatra Mts, Poland) in its habitus, buccal parts type, number and position of the eyes and the postantennal organ, the furca, "oligochaetosis," and abdomen segment VI, which is hidden under segment V.

Material Examined.—See *K. szeptyckii.*

Koreanurina szeptyckii Najt & Weiner, NEW SPECIES (Figs. 1–8)

Types.—Holotype: female; data: NORTH KOREA. *NORTH PYONGAN PROVINCE:* Myohyang-san Mts, nr Habiro waterfall, fresh litter in oak-maple-pine forest, 25 Jun 1981, A. Szeptycki & W. M. Weiner. Allotype, male, same data as holotype. Holotype and allotype deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. Paratypes, 9 specimens; 8 deposited in ISEA, 1 deposited in MNHN.

Description.—Female (holotype) length 0.44 mm, male (allotype) length 0.38 mm, paratypes length 0.42 and 0.46 mm. Color in alcohol spotted light blue for females, dark blue for males, ocular plate blue-black. Tegumental grain very strong. Dorsal reticulation hexagonal or square on head: a plate on vertex and two rows on seta c and p level; thorax II, III and abdomen I–V in two or three rows (Fig. 1). Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 11 setae. Antennae III and IV fused dorsally, ventral separation well-marked with very fine tegumental granulation. Sensory organ of antennal segment III consisting of: (a) two small sensillae bent in same direction without tegumental fold, (b) two subcylindrical guard sensillae (ventral s-shaped/bent in squashed specimens/very long compared with dorsal), (c) small ventrolateral sensilla in small groove. Antennal segment IV with six distinct subcylindrical thick sensillae, small dorsal external sensilla; subapical organite small, distinct; apical vesicle slightly bilobate, some ordinary setae with blunt apex (Fig. 2). Ocelli three + three. Postantennal organ 3.0–4.0× larger than ocellus, bearing 9–11 vesicles arranged in circle (Fig. 5). Labium elongate (Fig. 6), setae: L papillary and B absent, two + two labial organites (x) arranged one above the other on internal side of setae C and D. Labral chaetotaxy two/two, three, five, two. Mandibles with five teeth (Fig. 4), maxilla styliform with two lamellae, one styliform, the other with two teeth, and elongate maxillary capitulum with about 12 teeth (Fig. 3). Tibiotarsi I, II, III with 18, 18, 17 setae, with one pointed tenent hair and toothless claws (Fig. 7). Thorax sternites without setae. Ventral tube with four + four setae, one specimen with four + three; three + three in immature specimens. Vestigial furca reduced to two small mamelons, each with one seta. Male genital plate is presented in Fig. 8. Dorsal chaetotaxy (Fig. 1): short thin ordinary setae and thin long sensory setae with blunt apex, but setae on abdomen IV thicker, shorter than the others. Sensory chaetotaxy is "022/11111" per one-half tergite.



Figures 1–12. Figures 1–8. *Koreanurina szeptyckii* NEW GENUS, NEW SPECIES. Figure 1. Chaetotaxy and dorsal reticulation. Figure 2. Antennae III–IV. Figure 3. Maxillae. Figure 4. Mandible. Figure 5. Ocelli and postantennal organ. Figure 6. Labium. Figure 7. Leg II. Figure 8. Male genital plate. Figures 9–12. *Koreanurina inexspectata* NEW SPECIES. Figure 9. Chaetotaxy and dorsal reticulation. Figure 10. Antennae III–IV. Figure 11. Ocelli and postantennal organ. Figure 12. Vestigial furca.

Diagnosis.—*Koreanurina szeptyckii* can be distinguished by some morphological characters: the apical vesicle slightly bilobate, two + two setae between sensory setae on abdomen I to IV, the very long ventral guard sensilla of antenna III, short sensillae on antenna IV and the ratio of diameters of PAO to ocellus (Table 1).

Etymology.—Dedicated, as a token of friendship, to Andrzej Szeptycki.

Material Examined.—See types. In addition: NORTH KOREA. *NORTH PYONGAN PROVINCE:* Myohyang-san Mts, nr Sangwon waterfall, moss on granite in an oak-maple forest, 24 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen.

Koreanurina inexspectata Najt & Weiner, NEW SPECIES
(Figs. 9–13)

Types.—Holotype, female; data: NORTH KOREA. *KANGWON PROVINCE:*

Table 1. Characters differentiating *Koreanurina szeptyckii* NEW SPECIES from *K. inexspectata* NEW SPECIES.

Characters	*Koreanurina*	
	szeptyckii NEW SPECIES	*inexspectata* NEW SPECIES
Apical vesicle	slightly bilobate	distinctly trilobate
Number of setae between sensory setae on abd. I to IV	2 + 2	3 + 3
Guard sensillae of antenna III	differing in length, ventral one very long	almost equal
Antenna IV sensillae	short	long
PAO/ocellus ratio	3–4:1	2–2.5:1

Kumgang-san Mts, nr Kuryong waterfall, rock with bushes, herbs and mosses (litter and moss), 29 Jun 1981, A. Szeptycki & W. M. Weiner; deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. Paratypes, 2 specimens, same data as holotype: 1 immature female deposited in ISEA, 1 female deposited in MNHN.

Description.—Female (holotype) length 0.50 mm, female (paratype) length 0.54 mm. Color in alcohol light gray, ocular plate black. Very strong tegumental granulation. Dorsal reticulation present as in *Koreanurina szeptyckii* (Fig. 9). Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 11 setae. Sensory organ of antennal segment III consisting of: (a) two small sensillae slightly bent in same direction without tegumental fold, (b) two almost even, subcylindrical sensillae, (c) small ventrolateral sensilla in small groove. Antennal segment IV with six distinct subcylindrical long slender sensillae; small dorsal external microsensilla; subapical organite distinct; apical vesicle visibly trilobate (Fig. 10). Ocelli three + three. Postantennal organ, 2.0–2.5 × larger than ocellus diameter, bearing 11 vesicles arranged in circle (Fig. 11). Labrum, labium, maxillae and mandibles similar to those in *Koreanurina szeptyckii.* Tibiotarsi I, II, III with 18, 18, 17 setae including one pointed tenent hair, claw toothless. Thoraxic sternites without setae. Ventral tube with four + four setae. Abdominal sternites II and III without odd seta. Vestigial furca reduced to two small mamelons with one seta each (Figs. 12 and 13). Female genital plate is presented in Fig. 13. Dorsal chaetotaxy is presented in Fig. 9. Sensory chaetotaxy is "022/11111" per one-half tergite.

Diagnosis.—*Koreanurina inexspectata* is distinguished by three + three setae on the abdominal tergites I to IV and very long sensillae on the antennal segment IV. We present the differences between the two species of *Koreanurina* in Table 1.

Etymology.—The name comes from the Latin word for "unexpected."

Material Examined.—See types. In addition: NORTH KOREA. *KAESONG-SI PROVINCE:* Chonma-san Mts, nr Pakyon waterfall, maple-oak forest; litter, 15 Jul 1981, A. Szeptycki & W. M. Weiner, 1 specimen.

Caputanurinae Lee, 1983

In this subfamily, closely related to the Pseudachorutinae, we describe *Leenurina* NEW GENUS with two species; we redefine *Caputanurina* Lee, 1983, in which we include three new species.

This subfamily is mainly characterized by the absence of a well-defined thoraxic tergite I; it seems to be fused with the base of the head, where the two + two dorsolateral setae might be a remnant of prothorax chaetotaxy.

Leenurina Najt & Weiner, NEW GENUS

Type Species.—*Leenurina jasii* NEW GENUS, NEW SPECIES.

Table 2. Characters differentiating the genera: *Koreanurina* NEW GENUS, *Leenurina* NEW GENUS and *Caputanurina* Lee, 1983.

Characters	Pseudachorutinae	Caputanurinae	
	Koreanurina NEW GENUS	*Leenurina* NEW GENUS	*Caputanurina* Lee, 1983
Prothorax tergite	well defined	fused with head	fused with head
Eye position	dorsal	dorsal	dorsolateral or lateral
Postantennal organ	dorsal	dorsal	lateroventral or ventral
Head	normal	normal	with a V-like stitch along the whole vertex[a]
Abdomen V	normal	normal	inverted V-like
Habitus	normal	normal	dorsally flattened
Development of dorsal reticulation	+	++	+++
Antennal segment II setae	11	12	12–13
Dorsal setae present on thorax II–III	a1, p1, p2, p5 = s	a1, m1, p1, p5 = s	a1, p1, p2, p5 = s
Dorsal setae present on abdomen I–III	a1, p1, p5 = s or a1, p1, p2, p5 = s	a1, p1, p3, p5 = s	a1, p1, p2, p5 = s

[a] With one exception: *C. intermedia.*

Description.—Color blue or orange in live individuals. Eyes and postantennal organ dorsally. Ocelli two + two or three + three on well-defined plate with reticulation and strong granulation. Postantennal organ with 9–14 vesicles arranged in one row circle or oval. Mandibles with five teeth. Maxillae of the type *Anurida hexophthalmica* with two pointed styliform lamellae or tooth and maxillary capitulum with many small teeth. Labium short, papillary L seta absent, labial organite (x) present. Labral chaetotaxy: two/two, three, five, two. Antennae short. Antenna I with seven setae. Antenna II with 12 setae. Antennae III and IV fused dorsally. Sensory organ of antenna III built of two microsensillae, two almost even, subcylindrical guard sensillae and ventrolateral microsensilla. Antenna IV with six thick subcylindrical sensillae and a small dorsal external sensilla, subapical organite distinct, apical vesicle bi- or trilobate, sensory rasp absent. Ventral tube with four + four setae. Tibiotarsi with 18, 18, 17 setae, claws toothless. Vestigial furca reduced to two setae, with two mamelons or without protuberance (Lee, 1983). No anal spines. Head developed normally. Thoraxic tergite I fused at base of head, sternite developed normally. Abdomen VI in ventral position. No setae on thorax sternites, no odd setae on abdominal sternites II and III. Dorsal chaetotaxy consists of short and pointed ordinary setae and thin sensory setae. Very strong tegumental granulation. Reticulation on head, thorax II and III and abdomen I through V.

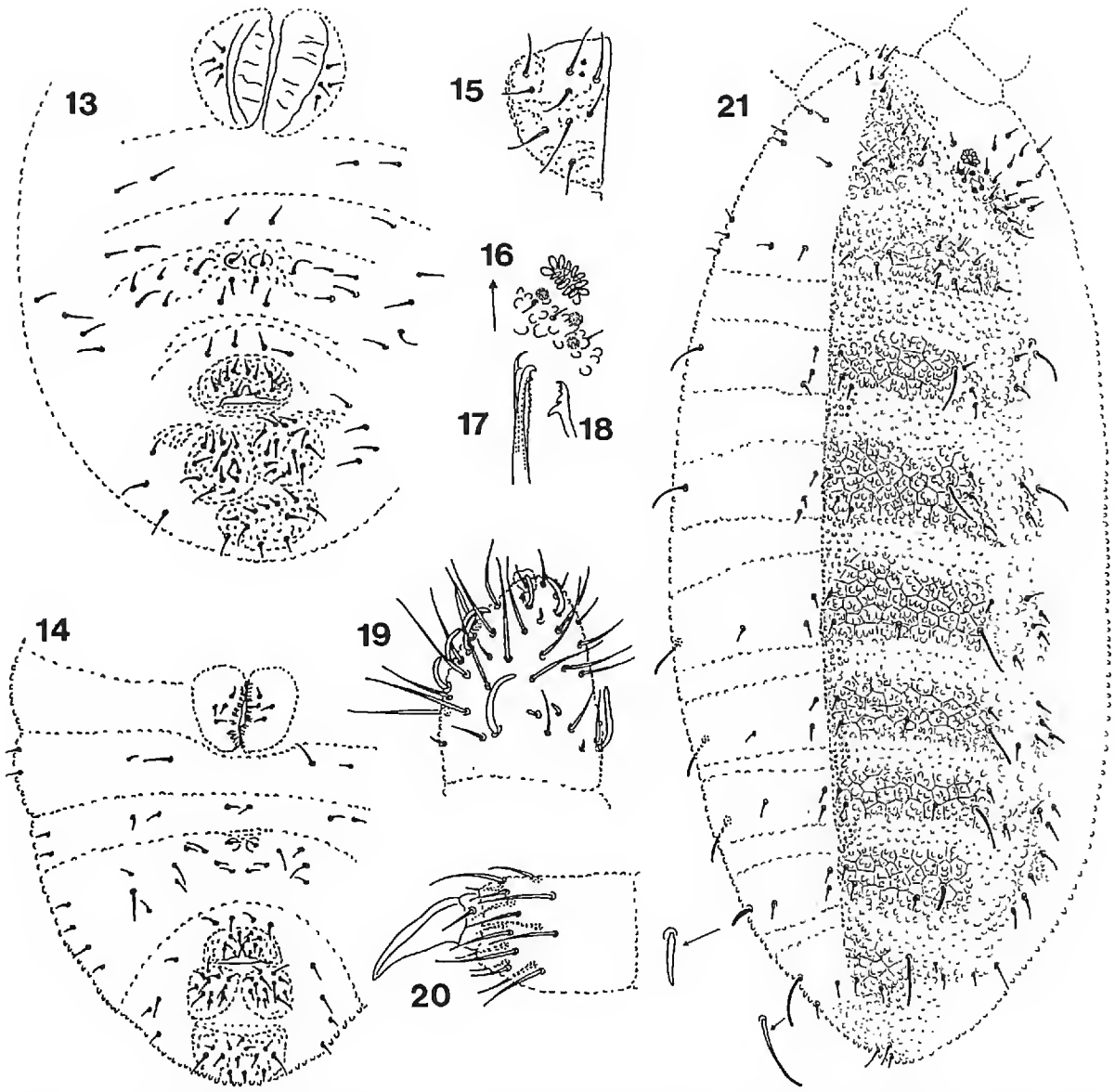
Diagnosis.—The new genus is close to *Koreanurina* and *Caputanurina.* We present their main differentiating characters in Table 2.

Etymology.—The new genus is dedicated to our Korean friend and colleague, B. H. Lee.

Material Examined.—See *L. jasii.*

Leenurina jasii Najt & Weiner, NEW SPECIES (Figs. 14–21)

Types.—Holotype, female; data: NORTH KOREA. *KANGWON PROVINCE:* Kumgang-san Mts, nr Kuryong waterfall, gorge of stream, with bushes, herbs and oak (litter), 1 Jul 1981, A. Szeptycki & W. M. Weiner; deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow,



Figures 13–21. Figure 13. *Koreanurina inexspectata* NEW SPECIES, abdominal segment I–VI. Figures 14–21. *Leenurina jasii* NEW GENUS, NEW SPECIES. Figure 14. Abdominal sternites I–VI. Figure 15. Labium. Figure 16. Ocelli and postantennal organ. Figure 17. Maxillae. Figure 18. Mandible. Figure 19. Antennae III–IV. Figure 20. Leg III. Figure 21. Chaetotaxy and dorsal reticulation.

Poland. Paratypes, 2 specimens, same data as holotype: 1 deposited in ISEA, 1 deposited in MNHN.

Description.—Female (holotype) length 0.56 mm, immature paratypes length 0.41–0.52 mm. Color in alcohol light blue. Ocular plate blue-black. Very strong tegumental granulation. Dorsal reticulation on head (central plate of vertex, dorsolateral plates, two plates in posterior part), thorax II and III and abdomen I through V. Prothorax tergite I unmarked (Fig. 21). Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 12 setae. Sensory organ on antennal segment III consisting of: (a) two small sensillae arranged in same direction without tegumental fold, (b) two long, almost even, subcylindrical guard sensillae, (c) small ventrolateral sensilla without groove. Antennal segment IV with six thick subcylindrical sensillae, small dorsal external sensilla; small subapical organite distinct, apical vesicles slightly bilobate, all ordinary setae with pointed apex (Fig. 19). Three + three ocelli with tegumental granulation of equal size. Postantennal organ oval, 4× longer and twice broader than ocellus, with 11–14 vesicles (Fig. 16). Labium short: no papillary L seta and B seta, labial organite (x) present as two + two small hyaline vesicles arranged one above the other (Fig. 15) between A and C setae (Fig. 18). Labral chaetotaxy: two/two, three, five, two. Mandible with five teeth, the basal one very strong (Fig. 18); maxillae with two lamellae, each with two apical teeth, and maxillary capitulum with 8–11 teeth (Fig. 17). Tibiotarsi I, II, III with 18, 18, 17 setae, including one pointed tenent hair, toothless claws, well-developed thorax sternites, without setae (Fig. 20). Ventral tube with four + four setae. Abdominal sternites II and III without odd setae. Vestigial furca reduced to two small mamelons, each with one seta (Fig. 14). Female genital plate is presented in Fig. 14. Dorsal chaetotaxy (Fig. 21): thin short pointed ordinary setae and long thin sensory setae with blunt

Table 3. Characters differentiating *Leenurina jasii* NEW SPECIES from *Leenurina nana* (Lee, 1983).

Characters	*Leenurina*	
	jasii NEW SPECIES	*nana* (Lee, 1983)
Color	light blue in alcohol	orange live
Number of ocelli	3 + 3	2 + 2
Number of vesicles and shape of postantennal organ	11–14, oval	11, in circle
Number of setae between abdomen IV sensory setae	a1, p1, p4,[a] p5 = s	a0, a1, a3, p1, p2, p5 = s
Vestigial furca	2 mamelons with 1 + 1 setae	without mamelon with 1 + 1 setae

[a] Variability of p4: cf. text.

apex, 4–5 × longer than ordinary setae except shorter thicker setae of abdomen IV. Sensory chaetotaxy is "022/11111" per one-half tergite. Number of setae between sensory ones of IVth abdominal segment varies from three + three to three + two to two + three.

Diagnosis.—*Leenurina jasii* can be distinguished particularly by chaetotaxic characters on the abdominal tergite IV, the color of the body and number of ocelli (Table 3).

Discussion.—At present the new genus contains two species: *Leenurina nana* (Lee, 1983) and *L. jasii.* Table 3 shows the main differentiating characters. It should be stressed that *L. nana* had been described as a species belonging to the genus *Caputanurina*; we are of the opinion that it fits well to *Leenurina.*

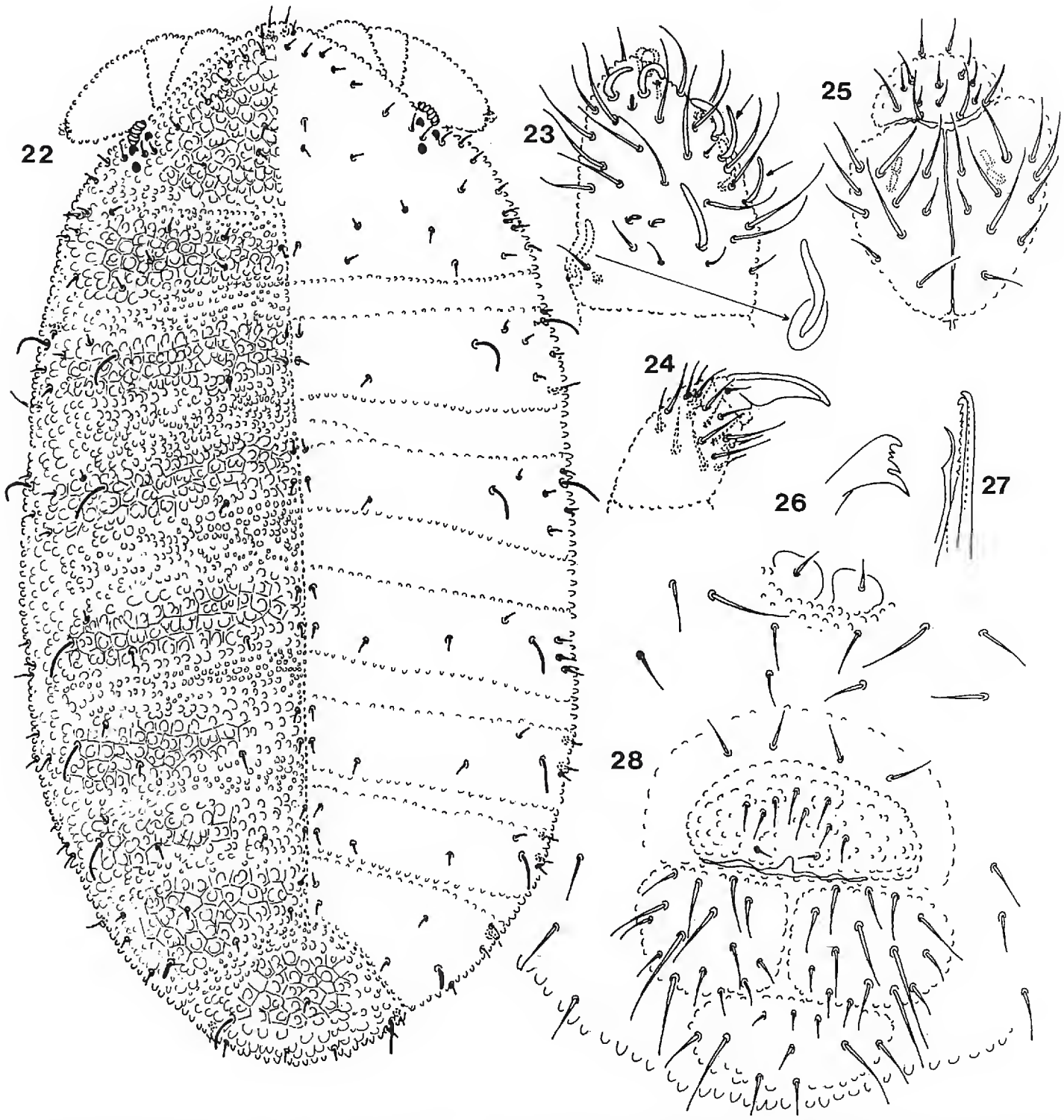
Etymology.—The species is tenderly dedicated to the son of one of us, Jaś—January M. Weiner.

Material Examined.—See types. In addition: NORTH KOREA. *KANGWON PROVINCE:* Kumgang-san Mts, Ou-Kumgang, oak-pine forest, litter on rock, 30 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen; Valley leading to Kuryong waterfall, groves with oak, pine and reed, litter, 1 Jul 1981, A. Szeptycki & W. M. Weiner, 1 specimen; Samil-pho lake, pine-oak groves, litter with mosses and decayed herbs, 3 Jul 1981, A. Szeptycki & W. M. Weiner, 1 specimen. *NORTH HAMGYONG PROVINCE:* Chuulonpho-ri, valley with oak-lime forest, under stone, 24 May 1974, A. Szeptycki, 1 specimen.

Caputanurina Lee, 1983

Type Species.—*Caputanurina serrata* Lee, 1983.

Description.—Color in alcohol blue, white or gray. Postantennal organ lateroventral or ventral with 11–14 vesicles arranged in one row circle. Eyes dorsal or laterodorsal, two + two or three + three ocelli. Mandibles with four to six teeth. Maxillae of the type of *Anurida hexophthalmica* with two free lamellae and clearly dentate maxillary capitulum. Labium short, no papillary L seta, labial organite (x) present. Labral chaetotaxy two/two, three, five, two. Antennae short. Antenna I with seven setae, antenna II with 12–13 setae. Antennae III and IV fused dorsally. Sensory organ on antenna III composed of two microsensillae, two subcylindrical, almost equal guard sensillae and one ventrolateral microsensilla. Antenna IV with six subcylindrical sensillae, small dorsal external sensilla, small subapical organite little- or well-distinct, apical vesicle bi- or trilobate without sensory rasp. Ventral tube with four + four setae. Tibiotarsi I, II, III with 18, 18, 17 or 19, 19, 18 setae, claws toothless or with one tooth. Vestigial furca reduced to one + one or two + two setae on two mamelons. No anal spines. Body oval, strongly flattened dorsoventrally. Thoraxic tergite I fused with base of head, distinct sternite of thorax I. Thoraxic sternites without setae. Head and abdomen V ogive- or V-like (abdomen V inverted V-like) except in *C. intermedia* NEW SPECIES. Position of abdomen VI completely ventral.



Figures 22–28. *Caputanurina intermedia* NEW SPECIES. Figure 22. Chaetotaxy and dorsal reticulation. Figure 23. Antennae III–IV. Figure 24. Leg III. Figure 25. Labrum and labium. 26. Mandible. Figure 27. Maxillae. Figure 28. Abdominal sternites I–VI.

Strong tegumental granulation. Dorsal reticulation present from head to abdomen V, except on intersegments.

Diagnosis.—*Caputanurina* is easy to discern by the head with a V-like stitch along whole vertex (with one exception), the abdomen V inverted V-like, eyes in the dorsolateral or lateral position, the postantennal organ in the lateroventral or ventral position, the habitus dorsally flattened and the very strong dorsal reticulation. The main differentiating characters of *Koreanurina, Leenurina* and *Caputanurina* are presented in Table 2.

Caputanurina intermedia Najt & Weiner, NEW SPECIES
(Figs. 22–28)

Types.—Holotype, female; data: NORTH KOREA. *NORTH HAMGYONG PROVINCE:* Susong-chon river bank, W of Chongjin, young pine forest with

small oaks and hazels, under stones, 22 May 1974, A. Szeptycki; deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. Paratypes, 3 specimens, same data as holotype; 2 deposited in ISEA, 1 deposited in MNHN.

Description.—Female (holotype) length 0.47 mm, paratypes length 0.40–0.54 mm. Color: dark blue. Very strong tegumental granulation. Dorsal reticulation (Fig. 22) arranged in areas as follows: median and dorsolateral areas on head; areas of two to three rows of reticulation from thorax II to abdomen IV, dorsomedian area on abdomen V; each hexagon exhibits one or two large secondary granulations on the surface (cuticule). No V-like stitch on head, frontal region elongate. Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 12 setae. Sensory organ on antennal segment III consisting of: (a) two small sensillae bent in same direction, (b) two guard sensillae of differing length (ventral one shorter and s-shaped), (c) small ventrolateral sensilla with large base, ordinary ventral internal setae short. Antennal segment IV with six sensillae: four thick, two long very thin; small dorsal external sensilla; subapical organite small, distinct; apical vesicle clearly trilobate (Fig. 23). Ocelli three + three situated dorsally, postantennal organ lateral with 14–15 vesicles in single row. Buccal cone short. Labium without L and B setae, labial organite (x) consists of two + two hyaline sensillae situated internally in comparison with C and D setae (Fig. 25). Mandibles with five teeth (Fig. 26). Maxillae of *Anurida*-type, maxillary capitulum with 8–11 teeth and two lamellae: one long with bent apex, other shorter, thin, with two teeth (Fig. 27). Tibiotarsi I, II, III with 18, 18, 17 setae. Claws toothless. Femur with very long ventral seta (Fig. 24). Ventral tube with four + four setae. Vestigial furca reduced to two small mamelons each with one seta (Fig. 28). Female genital plate is presented in Fig. 28. Dorsal chaetotaxy as in Fig. 22. Sensillary formula is "022/11111" per one-half tergite. Interestingly, sensillae on abdomen IV are shorter and thicker than elsewhere.

Diagnosis.—*Caputanurina intermedia* is very characteristic by the presence of three + three ocelli and by the absence of V-like stitch on the head. Table 4 shows the differentiating characters of the new species from the other species of the genus.

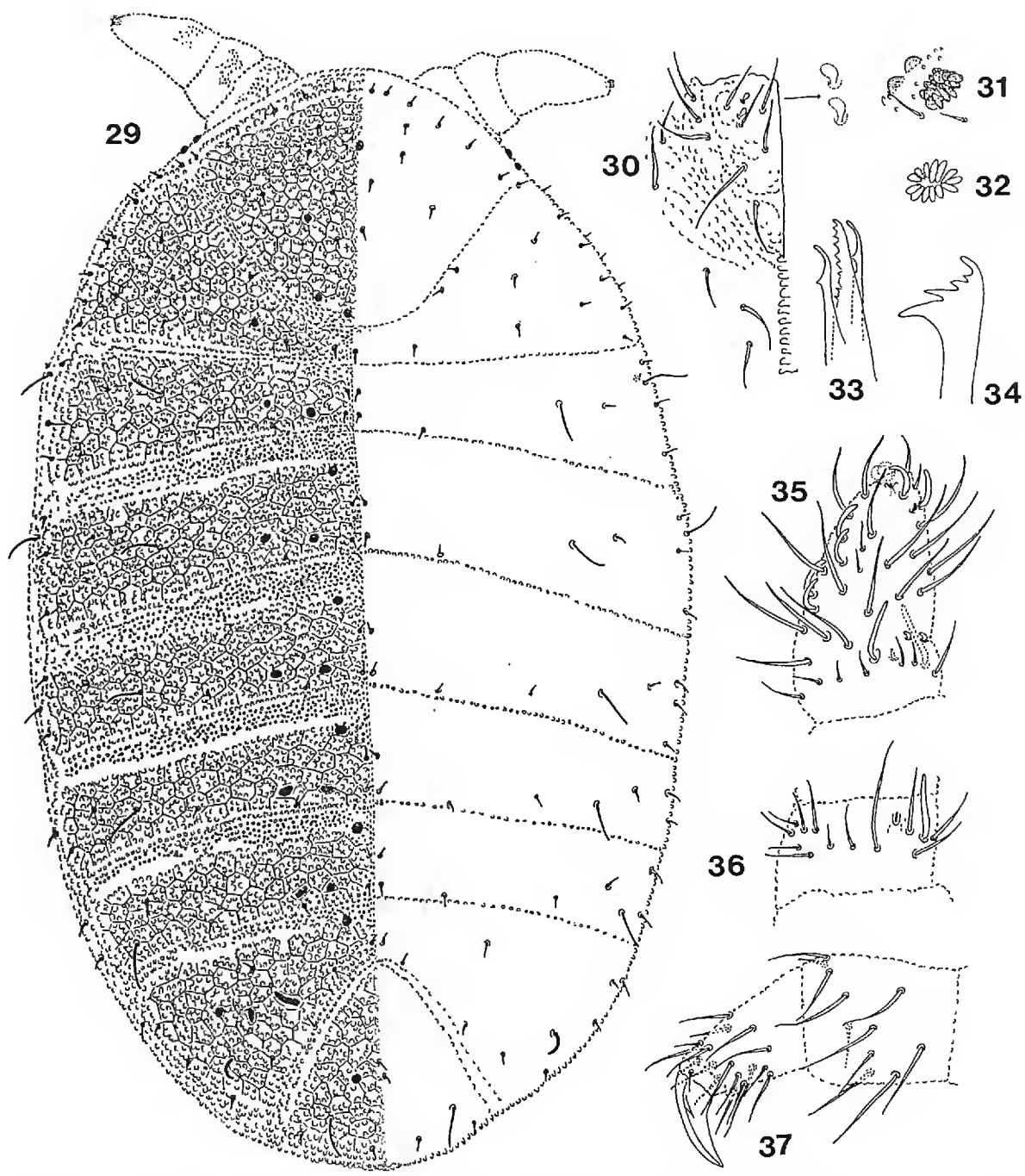
Etymology.—The name reflects the species' intermediate systematical position between *Leenurina* and *Caputanurina.*

Material Examined.—See types. In addition: NORTH KOREA. *SOUTH PYONGAN PROVINCE:* Paeksong-ri, forest with oaks, chestnuts, acacias, rhododendrons; litter with oak leaves and pine needles, 15 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen.

Caputanurina turbator Najt & Weiner, NEW SPECIES (Figs. 29–42)

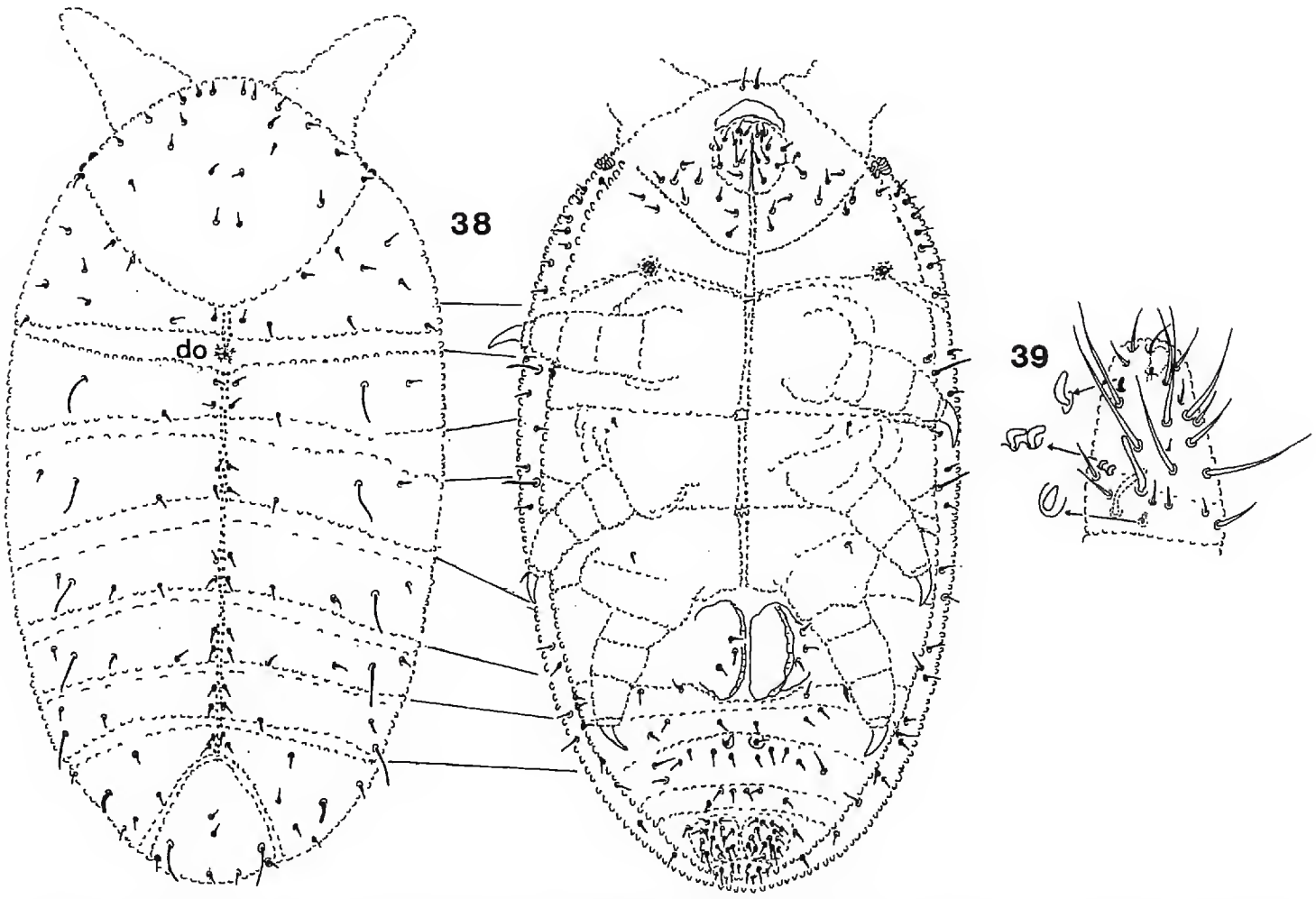
Types.—Holotype, male; data: NORTH KOREA. *NORTH PYONGAN PROVINCE:* Myohyang-san Mts, nr Habiro waterfall, oak-maple-pine forest, fresh litter, 25 Jun 1981, A. Szeptycki & W. M. Weiner. Allotype, female; same data as holotype. Holotype and allotype deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. Paratypes, 32 specimens, same data as holotype; 17 on slides and 10 in alcohol in ISEA, 5 in MNHN.

Description.—Male (holotype) length 0.68 mm, female (allotype) length 0.80 mm, adult paratypes, mean: 0.70 mm. Color in alcohol spotted blue. Strong tegumental granulation. Dorsal reticulation present from head to abdomen V, except for intersegments (Fig. 29). Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 12 setae. Sensory organ of antennal segment III consisting of: (a) two small sensillae bent in same direction, (b) two subcylindrical guard sensillae (ventral one slightly longer than dorsal one), (c) ventral microsensilla situated above base of



Figures 29–37. *Caputanurina turbator* NEW SPECIES. Figure 29. Chaetotaxy and dorsal reticulation. Figure 30. Labium. Figure 31. Ocelli and postantennal organ. Figure 32. Postantennal organ. Figure 33. Maxillae. Figure 34. Mandible. Figure 35. Antennae III–IV. Figure 36. Antennae III, ventral side. Figure 37. Leg III.

guard sensilla (Figs. 35 and 36). Antennal segment IV with six thick subcylindric sensillae, dorsal external microsensilla, very small distinct subapical organite, apical vesicle trilobate (Fig. 35). Ocelli two + two, situated laterally, postantennal organ lateroventral, covered by integument folding, with 13–14 vesicles in single row (Figs. 31 and 32). Buccal cone ventral, short. Labium short, no L and B setae, labial organite (x) consisting of two + two strong hyaline sensillae one above the other between A and C setae (Fig. 30). Mandibles with five teeth (Fig. 34). Maxillae thin, maxillary capitulum with about 10 teeth, internal lamella shorter and thinner with two distinct teeth, the external one with two teeth (Fig. 33). Tibiotarsi I, II, III with 18, 18, 17 setae. Claws with only one tooth on lateral internal lamella, without ventral tooth (Fig. 37). Femur with long ventral setae, including one particularly long. Ventral tube with four + four setae. Vestigial furca reduced to two small mamelons usually with one + one setae (Fig. 40); two + one and two + two setae were also observed there (Figs. 41 and 42). Abdomen VI completely hidden under abdomen V. Female and male genital plates are presented in Figs. 40 and 42. Pseudopore in front of the plates. Adult males exhibit secondary sexual features: sternite IV, V and anal valves with some ramified setae (excepting internal genital pointed setae). Dorsal chaetotaxy, very varied (especially on Vth abdominal segment) is presented in Fig. 29: short thin pointed ordinary setae and long thin sensory setae, excepting air of shorter thicker sensillae on abdomen IV. Sensory chaetotaxy is "022/11111" per one-half tergite.



Figures 38–39. *Caputanurina turbator* NEW SPECIES, first instar. Figure 38. Dorsal and ventral chaetotaxy, do = dorsal organ. Figure 39. Antennae III–IV.

First Instar.—Antennal segment IV with fewer ordinary setae than adult, setae longer than segment length; sensillary chaetotaxy reduced to dorsal external microsensilla only, subapical organite and simple apical vesicle (trilobate in adult specimens) present. Sensory organ of antennal segment III complete (Fig. 39). Buccal parts are slender. Dorsal chaetotaxy (ordinary and sensory setae) on head and body same number, position and variability as in adults especially on abdominal tergite V (Fig. 38).

Diagnosis.—*Caputanurina turbator* has one lateral internal tooth in the claw and two teeth in the external lamella of the maxillae. The differentiating characters of the new species are presented in Table 4.

Discussion.—Our observations of the first instar on *Caputanurina turbator* confirm those of Gruia (1974) on *Endonura tatricola* (Stach 1951), of Dallai & Martinozzi (1980) on *Thaumanura ruffoi* Dallai 1969, and of Deharveng (1983) on *Bilobella aurantiaca* (Caroli 1910), *Neanura muscorum* (Templeton 1835) and *Vitronura giselae* (Gisin 1950). However, in two species of *Mesaphorura* Börner 1901, studied by Rusek (1980), the first stage differs from the other ones, including adult specimens, by chaetotaxy reduced in comparison with the adult pattern. In *Mesaphorura sylvatica* (Rusek 1971) and *Mesaphorura yosii* (Rusek 1967), even the postantennal organ, the sensory organ of antennal III, and the number of setae as well as sensillae of antennal IV are reduced.

The first instar of *Caputanurina turbator* already exhibits dorsal reticulation along the whole length of head and body, but observation with an optical microscope yields only one secondary grain, surrounded by reticulation, just as in the adult specimen of *Caputanurina intermedia,* while four to seven secondary grains are found in adult *C. turbator.* Moreover, a dorsal organ was observed on thorax I in specimens at stages I and II. This organite is characteristic for Neanuridae

Table 4. Characters differentiating species of the genus *Caputanurina* Lee, 1983.

Characters	*Caputanurina*				
	intermedia NEW SPECIES	*serrata* Lee, 1983	*turbator* NEW SPECIES	*major* NEW SPECIES	*sexdentata* NEW SPECIES
Antenna II setae	12	?	12	12	13
Ventral guard sensilla—insertion type	without mamelon base large	?	without mamelon	on a mamelon	without mamelon
apical vesicle antenna IV	trilobate	trilobate	trilobate	trilobate	bilobate
Ocelli	3 + 3	2 + 2	2 + 2	2 + 2	2 + 2
Mandible teeth	5	4	5	5	6
Maxillae: maxillary capitulum teeth	8–11	9–10	10	11	10–12
External lamella	apex bent	?	long, 2 teeth	long, apex bent	7–10 teeth
Internal lamella	short, 2 teeth	?	short, 2 teeth	short, 2 teeth	long, thin apex pointed
Setae absent in labium	B	?	B	A	A
Setae in tibiotarsi I, II, III	18, 18, 17	?, ?, 17[a]	18, 18, 17	18, 18, 17	19, 19, 18
Tooth in claw	absent	absent	1 lateral internal	absent	absent
Setae in vestigial furca	1 + 1	2 + 2	1 + 1 (2 + 2, 2 + 1)	1 + 1	1 + 1 (2 + 1)
Length (mm)	0.40–0.54	0.6	0.68–0.80	0.88–0.93	0.67–0.70

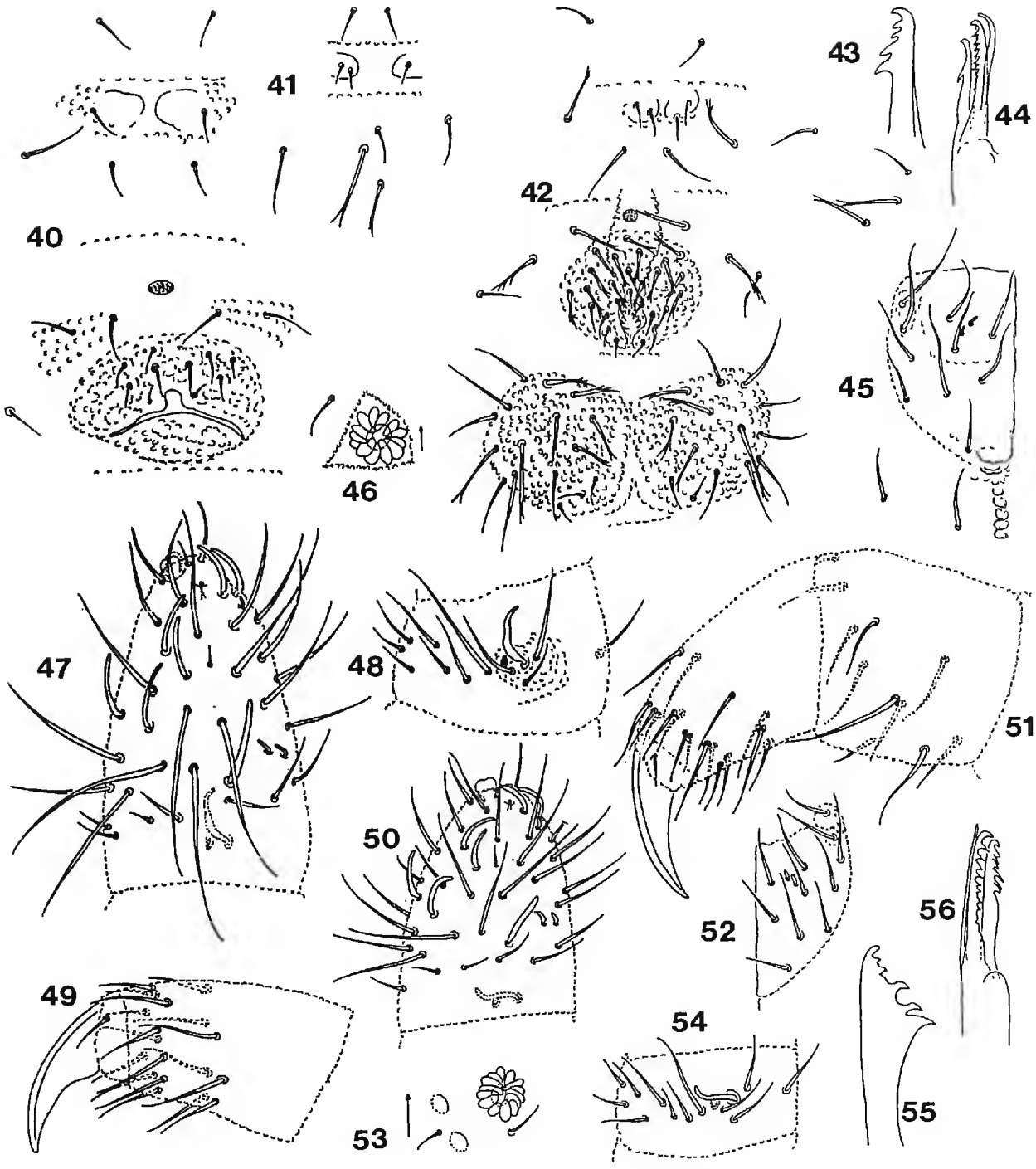
[a] After a figure by Lee (1983).

Neanurinae (Deharveng 1983) and Brachystomellinae (Najt, personal observation).

The odd dorsal organ is usually situated on the posterior limit of prothorax tergite. It is situated in the anterior intersegment of thorax II at its limit with posterior head margin (Fig. 38).

Etymology.—The name reflects the difficulties encountered while establishing the systematic position of the species.

Material Examined.—See types. In addition: NORTH KOREA. *NORTH PYONGAN PROVINCE:* Myohyang-san Mts, nr Yuson waterfall, forest with oak, maple, magnolia, pine, under rotting wood, 22 Jun 1981, A. Szeptycki & W. M. Weiner, 2 specimens; Hyangsan-chon river valley, at forest edge, under rotting wood, 23 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen; Hyangsan-chon river, oak-chestnut-pine forest, litter among granite rocks, 23 Jun 1981, A. Szeptycki & W. M. Weiner, 15 specimens on slides, 4 specimens in alcohol; Vicinity of Sanju waterfall, forest, moss on granite rocks, 24 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen. *SOUTH PYONGAN PROVINCE:* Paeksong-ri, forest with oak, chestnut, acacia, rhododendron, litter with oak leaves and pine needles, 15 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen; litter with mycelium, 11 Jul 1981, A. Szeptycki & W. M. Weiner, 4 specimens. *KAESONG-SI PROVINCE:* Vicinity of Kaesong, valley among hills covered with acacias, pines, maples, moss on humid stones, 13 Jul 1981, A. Szeptycki & W. M. Weiner, 1 specimen.



Figures 40–56. Figures 40–42. *Caputanurina turbator* NEW SPECIES. Figure 40. Vestigial furca and female genital plate. Figure 41. Vestigial furca. Figure 42. Vestigial furca, male genital plate and anal lobes. Figures 43–49. *Caputanurina major* NEW SPECIES. Figure 43. Mandible. Figure 44. Maxillae. Figure 45. Labial chaetotaxy. Figure 46. Postantennal organ. Figure 47. Antennae III–IV. Figure 48. Antennae III, ventral side. Figure 49. Leg III. Figures 50–56. *Caputanurina sexdentata* NEW SPECIES. Figure 50. Antennae III–IV. Figure 51. Leg III. Figure 52. Labial chaetotaxy. Figure 53. Ocelli and postantennal organ. Figure 54. Antennae III, ventral side. Figure 55. Mandible. Figure 56. Maxillae.

Caputanurina major Najt & Weiner, NEW SPECIES (Figs. 43–49)

Types.—Holotype, male; data: NORTH KOREA. *NORTH PYONGAN PROVINCE:* Myohyang-san Mts, nr Sanju waterfall, forest with oaks, maples, magnolias, pines, wet litter, 24 Jun 1981, A. Szeptycki & W. M. Weiner. Allotype, female, same data as holotype. Holotype and allotype deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. Paratype, 1 specimen, same data as holotype; deposited in MNHN.

Description.—Male (holotype) length 0.88 mm, female (allotype) 0.83 mm, paratype 0.90 mm. Color

spotted blue. Dorsal reticulation present from head to abdomen V. Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 12 setae. Sensory organ of antenna III consisting of: (a) two small tubular sensillae bent in the same direction, (b) two subcylindrical guard sensillae (ventral s-shaped and shorter than dorsal, situated on tegumental mamelon, with three ordinary setae), small ventral sensilla in groove at level of guard sensilla base; ordinary ventral internal setae long (Fig. 48). Antennal segment IV with six long thin sensillae, dorsal external microsensilla, subapical organite distinct, apical vesicle trilobate (Fig. 47). Two + two blue-black ocelli in lateral position. Postantennal organ in ventral position, clearly hidden under tegumental folds with 14–15 vesicles in circle (Fig. 46). Buccal cone ventral. Labium bigger and stouter than in *Caputanurina turbator,* without L and A setae; labial organite consists of two + two hyaline sensillae distributed internally between C, D and B setae (Fig. 45). Mandibles strong, with five teeth (Fig. 43). Maxillae stout, maxillary capitulum with 11 very pointed teeth, internal lamella shorter, with two teeth; thin external lamella, with bent apex, lies along the claw (Fig. 44). Tibiotarsi I, II, III with 18, 18, 17 setae, with some of ventral setae, pointed dorsal seta very long. Claw toothless (Fig. 49). Femur with a very long ventral seta. Ventral tube with four + four setae. Vestigial furca reduced to two mamelons, each with one seta. Male and female genital plates resembling *C. turbator.* Two pseudopores can be found in front of genital plate. Adult males exhibit secondary sexual characters in setae of abdominal sternites IV–V and anal valves; only four + four internal setae pointed in genital plate. Dorsal chaetotaxy (similar to *Caputanurina turbator*): short thin pointed ordinary setae, long slender sensory setae (excepting pair of sensillae shorter and thicker on abdomen IV). Sensory chaetotaxy is "022/11111" per one-half tergite.

Diagnosis.—This new species is large. The ventral guard sensilla of the sensory organ of antenna III is situated on an integumental mamelon. The maxillary capitulum has 11 teeth, and the external lamella is long with the bent apex. Table 4 shows characters differentiating *C. major* from the other species of the genus.

Note.—Numerous specimens of this species were used in a study of cuticule under a scanning and transmission electron microscope.

Etymology.—The name refers to its large size.

Material Examined.—See types.

Caputanurina sexdentata Najt & Weiner, NEW SPECIES (Figs. 50–56)

Type.—Holotype, male; data: NORTH KOREA. *PYONGYANG-SI PROVINCE:* Ryongak-san Hill, oak-acacia forest, litter, 13 Jun 1981, A. Szeptycki & W. M. Weiner; deposited in Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland. Paratype, same data as holotype, 1 male in ISEA.

Description.—Male (holotype) length 0.70 mm, paratype 0.67 mm. Color: very light blue from head to abdomen V in dorsomedian portion; spotted dark blue in dorsal external part; spotted light blue in antennae and legs; spotted blue in sternites; dark blue in ocular plate (females usually lighter). Strong tegumental reticulation from head to abdomen V. Antennae shorter than head. Antennal segment I with seven setae, antennal segment II with 13. Sensory organ of antennal segment III consisting of: (a) two small sensillae bent slightly in same direction, (b) two subcylindrical guard sensillae (ventral s-shaped), (c) one small ventral sensilla situated in small groove. Antennal segment IV with six subcylindrical sensillae, dorsal external microsensilla, subapical organite distinct; apical vesicle slightly bilobate (Fig. 50). Two + two ocelli in lateral position. Postantennal segment with 12–13 vesicles in circle in lateral position (Fig. 53). Buccal cone short. Labium as in *C. major,* without L and A setae, with labial organite (x) consisting of two hyaline sensillae between C, D and B setae (Fig. 52). Strong mandibles with six teeth (Fig. 55). Maxillae elongate; maxillary capitulum with 10–12 very pointed teeth; internal lamella, slightly shorter than claw, with 7–10 very pointed teeth; external lamella, of same length as claw, thin with pointed apex (Fig. 56). Tibiotarsi I, II, III with 19, 19, 18 setae, claws toothless (Fig. 51). Femur with very long ventral seta. Ventral tube with four + four setae. Vestigial

furca reduced to two mamelons, each with one seta. Adult males exhibit secondary sexual characters as in *Caputanurina major*. Dorsal chaetotaxy (similar to *C. turbator*) consists of short thin pointed ordinary setae, long slender sensory setae (excepting pair of sensillae, slightly shorter on abdomen IV). Sensory chaetotaxy is "022/11111" per one-half tergite.

Diagnosis.—The mandible of *C. sexdentata* has six teeth. Tibiotarsi with 19, 19, 18 setae. Table 4 shows differentiating characters.

Discussion.—Although all the species of the genus *Caputanurina* are similar, especially in color, habitat and dorsal reticulation, they differ in many features. The differences are summarized in Table 4.

Etymology.—The name refers to number of teeth in the mandible.

Material Examined.—See types. In addition: NORTH KOREA. *KAESONG-SI PROVINCE:* Chonma-san Mts, nr Pakjon waterfall, maple-oak forest, litter, 15 Jul 1981, A. Szeptycki & W. M. Weiner, 1 specimen in ISEA, 1 specimen in MNHN. *SOUTH PYONGAN PROVINCE:* Paeksong-ri, forest with oaks, chestnuts, acacias, rhododendrons, fairly dry litter, 15 Jun 1981, A. Szeptycki & W. M. Weiner, 1 specimen. *RYANGGANG PROVINCE:* Nampotae-san Mt, mixed forest with birch and larch, under (granite) stone, 8 Sep 1971, A. Szeptycki, 1 specimen.

Discussion and Conclusions

The subfamily Caputanurinae is unique among Neanuridae s. 1. and even among Poduromorpha in its exceptional characters: reduction of thorax tergite I and fusion with the base of the head.

As a result to the tendency towards "cryptophthalmy," the head has migrated ventrally and forward. The aperture of the buccal cone has also become ventral; the occipital part moved towards the vertex while thoracic tergite I became fused with each dorsolateral margin of the head. This tergite shows a reduction to two + two or three + three lateral setae. A tendency towards "cryptopygy" also appears: abdomen VI becomes invisible under abdomen V. Simultaneous emergence of the two tendencies results in a dorsal flattening of head and body. This character is found in *Leenurina*; it is very pronounced in *Caputanurina*.

We believe that environmental adaptation may have appeared in the past, and this the type of dorsally flattened body with its withdrawn fragile sensory organs (eyes, postantennal organ, antennae), might be the result of adaptation to a more sedentary and concealed life style.

Moreover, the group studied here exhibits dorsal reticulation, a trait that seems to be the result of ecological convergence and thus probably represents a homoplasy. This feature is also present in the Isotomidae, Onychiuridae, Hypogastruridae, and in other groups of Neanuridae. However, while dorsal reticulation appears only sporadically and independently in various genera of these families, it is a phylogenetically stable trait in the whole lineage of Caputanurinae.

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Received 1 August 1991; accepted 27 January 1992.

PAN-PACIFIC ENTOMOLOGIST
68(3): 216–221, (1992)

NEW GENERA OF NOTHOCHRYSINAE FROM SOUTH AMERICA (NEUROPTERA: CHRYSOPIDAE)

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Abstract.—*Hypochrysa viridula* Adams (SE Brazil) is the type of *Asthenochrysa* Adams & Penny, NEW GENUS. *Leptochrysa prisca,* Adams & Penny, NEW GENUS, NEW SPECIES (Peru) has microtrichia over the entire wing membrane, and extraordinarily narrow wings with rectangular gradate cells.

Key Words.—Insecta, Neuroptera, Chrysopidae, Nothochrysinae

This paper is Part 11b of the "Neuroptera of the Amazon Basin." We have dealt with Chrysopini (Adams & Penny, 1987); other parts are in preparation. Fossils of Nothochrysinae (= Dictyochrysinae) are known from the Miocene and Oligocene of the western United States, and mid-Tertiary of Denmark, France and Germany (Adams 1967, Séméria 1990). Members of this subfamily are united by several plesiomorphies: jugum and frenulum present, lack of alar tympanal organ, presence of archaic pseudomeida (usually strongly zig-zagged without overlap of branches of radial sector [except in *Nothochrysa californica* Banks and *Dyspetochrysa*]), a little-sclerotized prosternum. The only possibly synapomorphic character more or less definitive for this subfamily is the presence of five or six setal whorls on each flagellomere (Brooks & Barnard 1990). This character state is shared only by the Apochrysini; all other extant chrysopids have four whorls. We consider it highly probable that the Nothochrysinae are paraphyletic.

The seven previously known extant genera of Nothochrysinae were reviewed by Brooks & Barnard (1990). The few surviving members of this subfamily exhibit largely disjunct, apparently relictual, distributions. *Dictyochrysa* (3 species) and *Triplochrysa* (1 species) are Australian, *Kimochrysa* (3 species) and *Pamochrysa* (1 species) are South African. *Nothochrysa* (3 species) is found in western Europe and Pacific coastal states of the United States and Canada; *Pimachrysa* (5 species) occurs in California, Arizona and northwestern Mexico. *Hypochrysa* has 1 species in southern Europe.

In 1978, Adams described the first South American nothochrysine, *Hypochrysa viridula* Adams, from a single female specimen collected in northern Argentina. Since then, three additional specimens have come to light, all from Brazil. The presence among these of a male enables us to reconsider the generic affinities of this species. Also described here is a striking single female nothochrysine collected from the eastern slope of the Peruvian Andes, which is attributed to a new genus and species.

Biology.—Little is known of the biology of most nothochrysine species. Adults of *Pimachrysa* principally have been collected from November through April,

more frequently at molasses traps, along water flumes, and by sweeping, than by attraction to light. Seasonality of adult activity in some nothochrysines may be correlated with availability of preferred pollen sources. *Nothochrysa californica* individuals do not mate until after feeding on oak pollen (Toschi 1965). Tjeder (1966) found large amounts of Asteraceae pollen in the "colon" of *Pamochrysa stellata* Tjeder, and Adams (1967) identified the pollen in the digestive tract of *Pimachrysa intermedia* Adams as that of willow (*Salix*). Pollen was present in the guts of both genera described here. (In chrysopid abdomens that have been treated with potassium hydroxide, pollen grains, if present, are ordinarily found in both the foregut diverticulum and the hindgut.) Because Nothochrysinae lack the alar tympanal organ found in the more successful subfamily Chrysopinae, they may be more subject to nocturnal predation by bats (Miller & MacLeod 1966). Dispersion and oviposition commonly take place at night in most chrysopine species (Duelli 1984). High mortality of adults in flight might in part explain the paucity of living nothochrysine species.

Abbreviations.—Specimen depositories are represented as: CAS, California Academy of Science; NMNH, U. S. National Museum of Natural History; FSCA, Florida State Collection of Arthropods; MZSP, Museo de Zoología, Universidade de São Paulo.

Asthenochrysa Adams & Penny, NEW GENUS
Figures 1–9

Type Species.—*Hypochrysa viridula* Adams (1978). Holotype female: ARGENTINA. *MISSIONES:* Iguazu, 4–10 Oct 1927, R. C. and E. M. Shannon (NMNH); deposited U. S. National Museum of Natural History, Washington, D.C.

Description.—Flagellar segments slender (length 2.4 × width), five setal rows. Palpi slender, acute. Venation (Adams 1978: fig. 1) much as in *Hypochrysa*; forewing subcostal crossvein opposite basal third of cell M2; veins on sides of gradate cells nearly straight, not strongly undulating as in *Hypochrysa*; 2A and 3A approximated, connected by short crossvein, but terminating separately on wing margin (Fig. 8); microtrichia present over much of anal area. Hindwing subcosta and R not fused in middle. Tarsal claw with wide basal expansion and deep notch (Fig. 9). Body only lightly sclerotized, so that cuticle of pronotum and abdomen is shriveled and wrinkled in dried material.

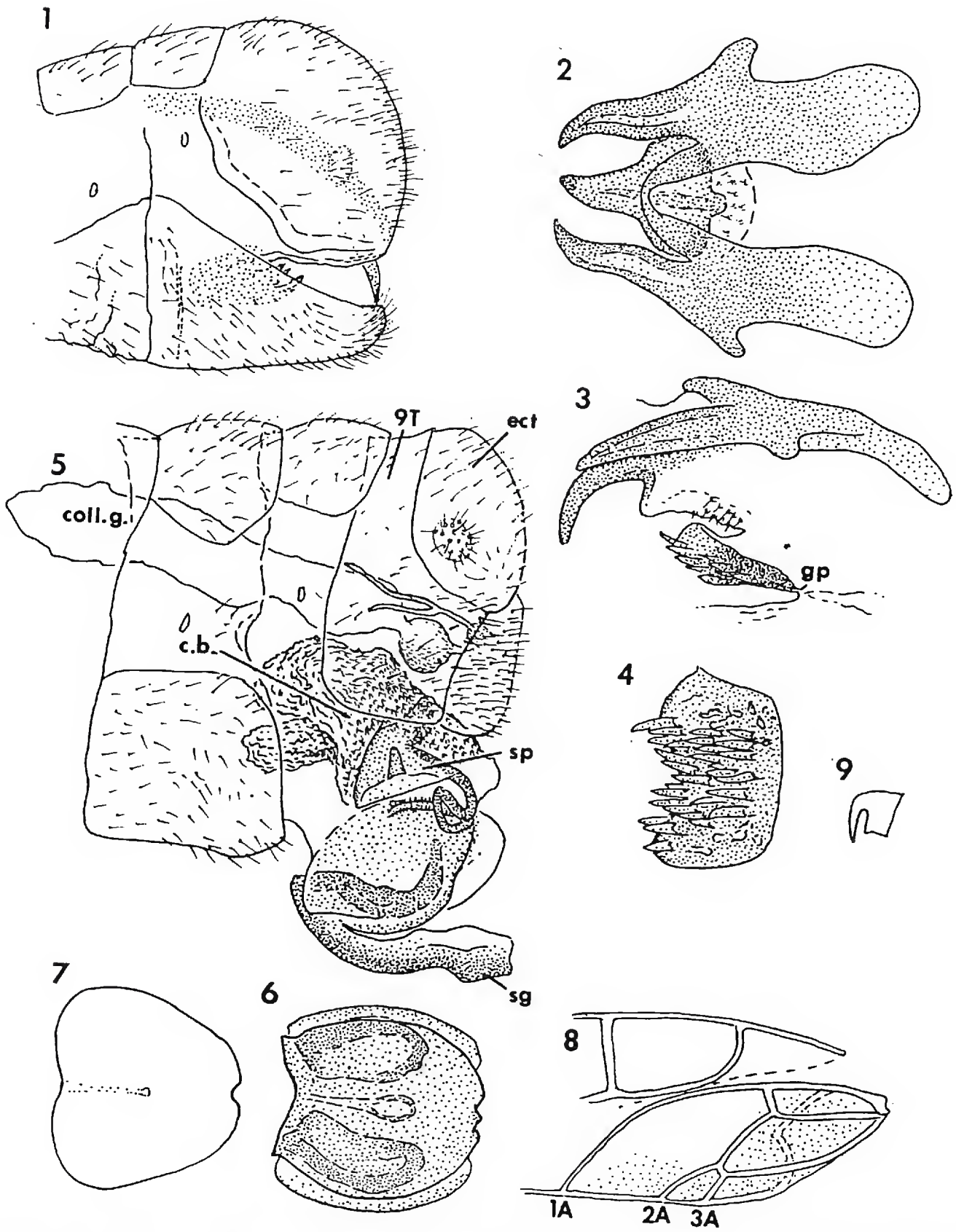
Male.—Genitalia massive; sternites eight and nine fused, suture vestigial; apex of ectoproct + 9T rounded (Fig. 1); microtholi absent. Gonarcus apodemes narrow, flattened dorsoventrally, continued posteriorly as sharp horns, bridge slender, upcurved; arcessus pointed and down-curved apically, broad basally (Fig. 2); gonosetae sparse, small; a heavily sclerotized plate bearing appressed, posteriorly directed spines lies between the gonosaccus and genital pore (Figs. 3 and 4).

Female.—Ninth tergite and ectoproct with weak demarcation suture; eighth abdominal spiracle on membrane; subgenitale a large flap hinged to massive secondary sclerites, the whole loosely attached and eversible (Fig. 5); spermatheca conical, bottom concave with slender ventral impression; duct short; bursa bearing triangular cristae internally, grading to smooth-walled anterolateral sacs (bursal glands?); colleterial gland sac smooth-walled; accessory gland slender, Y-shaped.

Diagnosis.—*Asthenochrysa* can be distinguished from other Nothochrysinae by the spinose plate between arcessus and gonopore in the male, the elaborate subgenitale in the female, and the lack of fusion of second and third anal veins of the forewing. It is the only small green nothochrysine in South America.

Etymology.—From the Greek *astheno*—weak, referring to the relatively lightly sclerotized thoracic cuticle, and to the fragility of the wings + *chrysa.*

Discussion.—*Hypochrysa, Kimochrysa,* and *Asthenochrysa* all have rather sim-



Figures 1–9. *Asthenochrysa viridula* (Adams). Figure 1. Male abdominal apex, lateral. Figure 2. Gonarcus-mediuncus complex, dorsal. Figure 3. Same, lateral, showing gonosaccal plate dorsal to genital pore. Figure 4. Gonosaccal plate, ventral. Figure 5. Female abdominal apex, lateral, showing everted subgenitale and internal structures (Espiritu Santo). Figure 6. Same, subgenitale, ventral. Figure 7. Subgenitale, ventral (Minas Gerais). Figure 8. Anal area of left forewing; microtrichia shown by stipple; jugal lobe folded under. Figure 9. Mesothoracic pretarsal claw. Abbreviations: c.b.—copulatory bursa; coll.g.—colleterial gland; ect—ectoproct; gp—gonopore; sg—subgenitale; sp—spermatheca; 1A, 2A, 3A—anal veins; 9T—ninth tergite.

ilar wing venation. The basal position of the subcostal crossvein, and the crossvein connecting 2A and 3A lying near the wing margin, are distinctive. Given the highly disjunct distributions of these relict genera, it is not surprising that their genitalia exhibit striking differences. Externally, in male *Hypochrysa,* the eighth

and ninth sternites are either separate (Adams 1967) or fused (Aspöck et al. 1980), and the ninth tergite and ectoproct are fused. In *Kimochrysa* these sternites are fused, but the ninth tergite and ectoproct are separate. In *Asthenochrysa,* both tergites and sternites are fused. The spinose plate between the mediuncus and gonopore is unique to *Asthenochrysa,* and this genus lacks the paddle-shaped entoprocessus of *Kimochrysa raphidioides* Tjeder and *K. impar* Tjeder, and the deeply bifid arcessus of *Hypochrysa.* In *Hypochrysa* and *Kimochrysa* females the subgenitale is normal-sized, not greatly enlarged as in *Asthenochrysa.*

There is some question as to whether the Brazilian and Argentinian material is conspecific. The subgenitale of the female from Minas Gerais is pyriform (Fig. 7), rather like that of the type of *A. viridula* Adams, while in the female from Espiritu Santo this structure is oval (Fig. 6).

Material Examined.—BRAZIL. *ESPIRITU SANTO:* Linhares, Parque Sooretam, Oct 1962, M. Alvarenga leg., 1 male 1 female (FSCA). *MINAS GERAIS:* Serra de Caraça, 4 Dec 1978, 1 female, Exp. Mus. Zool. (MZSP).

Leptochrysa Adams & Penny, NEW GENUS

Type Species.—*Leptochrysa prisca* Adams & Penny.

Description.—Flagellar segments slender (length 1.6 × width), with five complete and a partial sixth setal whorls; eyes small (Fig. 11); palpi elongate, tapered, galea narrow with conspicuous papilla. Claw without basal expansion. Wings elongate, forewing length 4.3 × width; entire membrane bearing microtrichia; gradate cells rectangular, not elongate-hexagonal; pseudomedia (Psm) with no contact between adjacent longitudinal undulating veins, its intervening crossveins all angled relative to longitudinals; basal subcostal crossvein opposite crossvein cu1; MP2 touching CuA, diverging to intersect crossvein mp3, then recurving to fuse with CuA; pseudocubitus well developed in both wings; second anal vein of forewing forked, posterior branch not reaching the margin; forewing with jugum, hindwing with frenulum. Hindwing with MP1 joined to Rs+MA by crossvein.

Diagnosis.—This genus is immediately distinguishable from all other extant Nothochrysinae by its uniquely narrow wings, rectangular gradate cells, and distinctive intramedian cell.

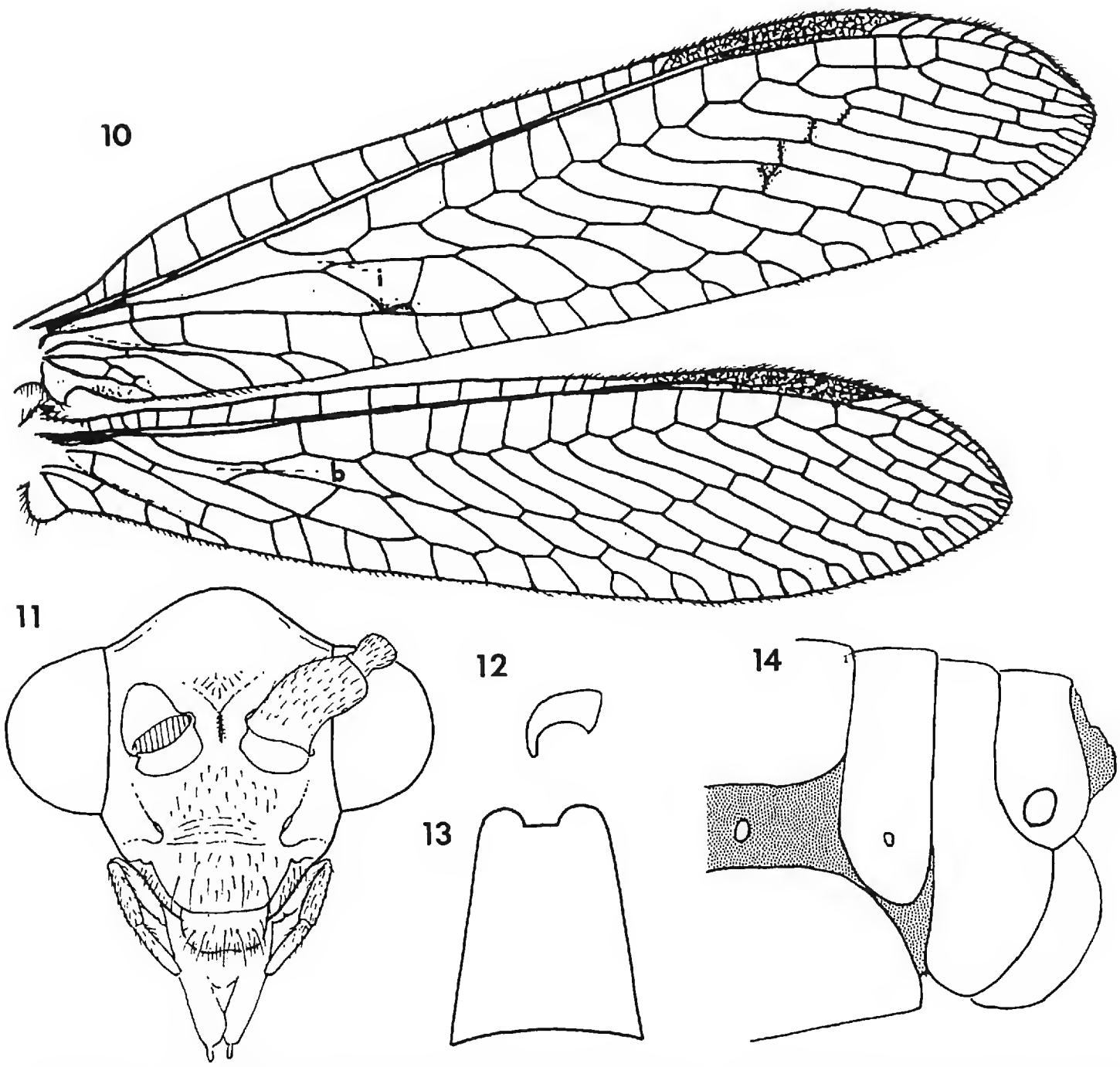
Etymology.—From Greek *lepto*—fine, slender, in reference to the wing shape + *chrysa.*

Material Examined.—*L. prisca* (see below).

Leptochrysa prisca Adams & Penny, NEW SPECIES
Figures 10–14

Type.—Unique holotype female, deposited: California Academy of Sciences. Label data: "PERU. *DEPT. AMAZONAS:* 18 km N of Puente Engenio, km 320, alt 1750 m, 9 Oct 1964, P. C. Hutchinson & J. K. Wright, collected on *Baccharis latifolia* #6380."

Description.—Head: frons, clypeus, gena, labrum, and vertex dark brown, without pale markings; maxillary and labial palpi dark brown; antennal scape about twice as long as broad, dark brown, curved laterally; more than 98 flagellomeres (apex broken off), basal 50 dark brown, apical segments pale brown. Pronotum short (width 0.85 × length at margin), pale brown with lateral black line expanded anteriorly and posteriorly, triangular dark spot medially; setae short, pale. Meso- and metanota dark brown with sparse pale setae. Legs entirely dark brown, with short golden pilosity. Forewing (Fig. 10) length 20.0 mm, width 4.7 mm; all veins dark brown, bearing short, pale brown setae aligned



Figures 10–14. *Leptochrysa prisca.* Figure 10. Wings. Figure 11. Head. Figure 12. Metatarsal claw. Figure 13. Subgenitale. Figure 14. Female abdomen. Abbreviations: b—banksian cell, i—intramedian cell.

with vein in a single row; pterostigma elongate, pale yellow with dark brown reticulations; forewing first MP-Cu cell short, second cell elongate due to absence of second mp-cu crossvein; membrane dark at junction of MP2 with CuA and bordering several inner gradates; 12–13 inner, 9–10 outer gradates (difficult to delimit gradates because of assimilation of gradate series into Psm and Psc). Hindwing color as in forewing, but no veins dark-margined; unusually large flap in jugal region. Abdomen dark brown, setation golden, short; tergite eight extending ventrally below upper margin of sternite seven; bearing spiracle (Fig. 14); ectoprocts distinctly delimited from tergite nine; callus cerci near anteroventral margin; subgenitale (Fig. 13) elongate, sclerotization apparently extending to margin of sternite seven. Spermatheca not seen. Gut contents: pollen.

Diagnosis.—*Leptochrysa prisca* is the only species in the genus.

Discussion.—This specimen is heavily infested with black fungal mycelium, clinging to the cuticle, and filling the abdominal cavity, making it impossible to trace internal reproductive structures. Spiracles, borders of sclerites, and location of the trichobothria were extremely difficult to locate. The resulting general black coloration, together with the peculiar venational pattern and wing conformation, conspire to make it appear unlike a chrysopid. The mycelium follows the wing

vein cavities, and forms a meshwork, especially visible on the base of the left forewing. The similarity of this mesh to that in the stigmatic areas suggests that these latter areas are also infiltrated by the mycelium. If this were the case, however, one would not expect such precisely equivalent development of the mesh in each of the four stigmatic areas. The elongate wings resemble those of certain Mesozoic genera, such as *Aristenymphes* Panfilov (1980), which formerly was considered to be a mesochrysopine, but now is thought to be more closely related to the Nymphidae (Martins-Neto, in litt.). The microtrichiose wing membrane is an archaic feature, typical of families such as Hemerobiidae, but restricted to the posterior forewing base in all other extant Chrysopidae. The configuration of the banksian cell of the hindwing (Fig. 10, "b") resembles that of the Miocene *Archaeochrysa* Adams (1967), but is not known to occur in other living chrysopids, in which MP contacts Rs+MA directly. The formation of the intramedian cell, wing elongation, and rectangular gradate cells are considered apomorphies.

Acknowledgment

Material has been made available through the kindness of Paul Arnaud (California Academy of Sciences), O. S. Flint (United States National Museum of Natural History), L. A. Stange (Florida State Collection of Arthropods) and N. Papavero (Museo de Zoología, Universidade de São Paulo). Their assistance is gratefully acknowledged.

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Received 19 September 1991; accepted 3 February 1992.

Errata and Restatement of Editorial Policy on Manuscript Revision and Acceptance

Recently, in a letter dated 9 June 1992, critical comments were brought to my attention concerning the scientific note: Martinez, M. J. 1992. A new ant introduction for North America: *Pheidole teneriffana* (Forel) (Hymenoptera: Formicidae). Pan-Pacif. Entomol., 68 (2): 153–154. Of these comments, the most critical, and those requiring address here, were that: (a) "T." Aguayo should be C. G. Aguayo; (b) Forel, as the taxonomic author of *P. teneriffana,* should have been unbracketed; (c) "*Iridomyrex*" should be spelled *Iridomyrmex*; (d) *Monomorium minimum* (Buckley) may not occur in California (see Univ. Kansas Sci. Bull., 53: 65–119.) and that the species referred to as such should have been listed as *I. ergatogyna* Wheeler; and (e) that for *Conomyrma bicolor* (Wheeler), *C. insana* (Buckley), *Tapinoma sessile* (Say) and *Iridomyrmex humilis* (Mayr), the taxonomic authors should have been in brackets, rather than unbracketed as in the article.

The situation reflects the dilemma of being an editor, and of a necessary dependence on the peer review process. The article was reviewed and significantly revised to reflect the concerns of two reviewer's recommending acceptance. A third reviewer (the commentor) belatedly recommended rejection for reasons that were largely addressed (were appropriate) in the revision of the manuscript; but he failed at that time to point out the corrections cited here.

It is, and has been, the policy of this journal to seek a third opinion on manuscript rejection, when reviewers, who ultimately determine the fate of a manuscript, disagree. Thus, a majority of referees, not the editor, determine whether a manuscript is ultimately accepted or rejected. The quality of this, and any other referred journal, therefore, necessarily depends on the timeliness and thoroughness of responses by its referees. The editor's job is to ensure that those corrective suggestions for manuscripts, which are listed by referees at the time of review and are objective and reasonable, are incorporated into, or are at least sufficiently addressed in, any required revision. This requires an editorial judgment on the appropriateness of a reviewer's comments, but also necessitates their presentation in their entirety in a timely fashion. The journal welcomes and solicits notifications of corrections after publication, but obviously would prefer that all problems be addressed during review.

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Ferrari, J. A. & K. S. Rai. 1989. Phenotypic correlates of genome size variation in *Aedes albopictus*. Evolution, 42: 895–899.

Sorensen, J. T. (in press). Three new species of *Essigella* (Homoptera: Aphididae). Pan-Pacif. Entomol.

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The PAN-PACIFIC ENTOMOLOGIST

Volume 68 October 1992 Number 4

Published by the PACIFIC COAST ENTOMOLOGICAL SOCIETY
in cooperation with THE CALIFORNIA ACADEMY OF SCIENCES
(ISSN 0031-0603)

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THE PAN-PACIFIC ENTOMOLOGIST (ISSN 0031-0603) is published quarterly by the Pacific Coast Entomological Society, c/o California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599. Second-class postage is paid at San Francisco, CA and additional mailing offices. Postmaster: Send address changes to the Pacific Coast Entomological Society, c/o California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599.

This issue mailed 30 November 1992

The Pan-Pacific Entomologist (ISSN 0031-0603)

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044, U.S.A.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PAN-PACIFIC ENTOMOLOGIST
68(4): 225–242, (1992)

ABRAHAM EZRA MICHELBACHER (1899-1991): THE BIBLIOGRAPHY OF ABRAHAM EZRA MICHELBACHER AND *SYMPHYLA* NAMED BY HIM

John A. Chemsak, E. G. Linsley, W. W. Allen,
and W. W. Middlekauff
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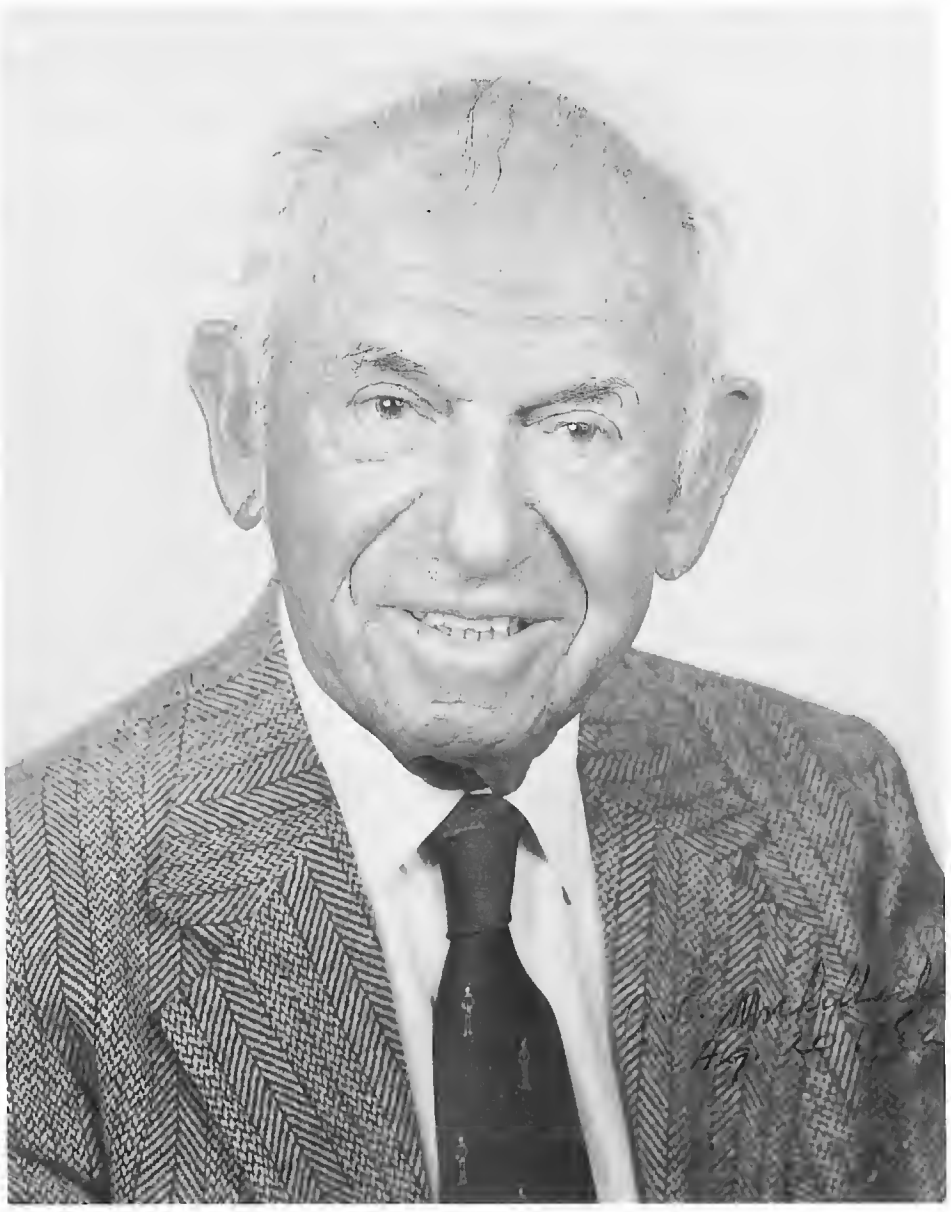
Abraham Ezra Michelbacher, better known to his friends as "Mickie," died in his home in Berkeley on 22 May 1991, at the age of 92. His vigor and memory had been rapidly declining for a few months.

Mickie was born on 12 Apr 1899, in Riverside, California, to Ezra and Ida Michelbacher. Most of his youth was spent at Riverside. He loved the beach and went to Newport Beach frequently throughout his life. During his younger years, he earned money by clamming, fishing, and working on dredges in the bay. During high school, he supplemented his income by picking oranges. He was always very competitive and later claimed that he was the fastest orange picker in the region (his working associates would never doubt this assertion). Although he worked for a while as a commercial albacore fisherman, he loved to fish as a recreation and continued to do so during vacation breaks throughout his life.



loved to fish as a recreation and continued to do so during vacation breaks throughout his life.

Before coming to Berkeley, he studied agronomy at the University of California, Riverside (then called the Citrus Experiment Station). In subsequent years he was to become well acquainted with Harry S. Smith ("Prof. Harry" to his devoted students and followers in the field of biological control at Riverside and elsewhere). Prof. Harry considered Michelbacher one of the few enlightened insecticide entomologists, and Mickie's appreciation of the value of biological control agents which grew out of their discussions was later reflected in the philosophical base of his approach to pest control.

At Berkeley, Mickie decided to major in economic entomology under the direction of Professor E. O. Essig. "Prof. Essig" became his mentor and very good friend and the two had a very strong, enduring, lifelong relationship. Essig's love of flowers and gardening was shared by Mickie, and the rose garden at his home became a showplace and source of flowers for numerous social events on the University campus.

Mickie earned a B.S. degree in 1927 and continued into the graduate program. On 30 Mar 1929, Martha Meyer became his beloved wife, friend and companion. His graduate study was completed with the awarding of the M.S. and Ph.D. degrees in 1930 and 1935.

While Michelbacher was a graduate student, Prof. Essig organized an informal student and faculty group called, "Fitchia." Both a social and entomological organization, participants met periodically in various homes including that of the Michelbachers. This pattern was extended by Mickie by means of what became a famous steak barbecue at the coastal town of Bolinas. One particularly memorable picnic took place on 7 Dec 1941, when, during the barbecuing activity the car radio announced the attack on Pearl Harbor.

Under the guidance of Prof. Essig, Michelbacher worked on the systematics of the garden centipede (*Symphyla*) for his doctoral dissertation. He ultimately became the world authority on this group.

Because Mickie was too old for military service during World War II, one of his most important contributions to the war effort consisted of helping to develop a research program for the Army Quartermaster Corps. This involved the testing of various food packaging materials for resistance to insect attack. Included in the program were entomologists on the Berkeley campus and food technologists at Davis. Research results were published in various scientific journals.

It would be difficult to detail Mickie's contributions to the field of entomology, but a resumé supplied by William W. Allen at a memorial service on 31 May 1991, touches on the highlights.

Over the past 50 years, much has been written and said about insect pest management, the pros and cons of biological control, and the use of insecticides. Books and articles abound by many authors; however, Mickie's research laid the foundation for present day insect control and he predicted its difficulties.

In his research on alfalfa, he clearly demonstrated the importance of *Apanteles* as a parasite of the alfalfa caterpillar and he stressed the general importance of fostering natural enemy suppression. He developed economic injury levels to preserve the activity of the parasite which is widely preached today and he advocated early cutting as a way to minimize the need for insecticides.

In his research with melons, tomatoes and walnuts, he clearly showed that non-selective insecticides would seriously increase aphids, scales and mites and he devised strategies and timing to alleviate these difficulties.

His work in the 1930s and 1940s really laid out all the principles of integrated pest management that have been researched, praticed, and preached over the past 50 years. His contributions are not widely recognized, because Mickie was more interested in his research than preaching about his work, and also he was a very modest person.

Graduate students who worked with Mickie included Bill Allen, Vern Stern, Hal Reynolds, Bob van den Bosh, and others. They learned field research methods from Smith (they all received Ph.D.s) and lots of practical entomology and philosophy from Mickie.

As a field researcher, and in his personal life, Mickie always ran a tight ship both in the use of his time and money. Field trips started at 4:00 in the morning, and if the work was well enough along, a milk shake was allowed for lunch. Successful graduate students that survived this regime then carried on the Michelbacher tradition. A few of the many outstanding included: Oscar G. Bacon, who became Chair of the Department of Entomology at Davis; Harold T. Reynolds, who became Chair of the Department of Entomology at Riverside; Ray F. Smith, who was a longtime Chair of the Department of Entomological Sciences at Berkeley; Minos Tzanakakis, Chair of the Department of Entomology at the University of Thessaloniki, Greece; and William W. Allen, Associate Dean for Research in the College of Natural Resources at Berkeley.

Michelbacher took an early retirement in 1960 and began a series of extended and shorter collecting trips during the next 27 years. Accompanied by Martha, Mickie travelled extensively in the Western Hemisphere in conjunction with the studies of P. D. Hurd and E. G. Linsley on the systematics and ecology of squash bees (*Peponapis* and *Xenoglossa*). The Michelbachers provided valuable data and specimens which were reported in a series of publications between 1964 and 1971.

In 1962, Michelbacher discovered an area near Gridley, California, containing large populations of squash bees. For the next several years he and Martha, with periodic assistance from others, made detailed records of flower and nest site activities of the bees. These included foraging periods and frequency, nest site requirements, including ground cover, and other new information about this bee. At the close of the study, burrows were excavated, and missing elements in the life history determined. This information led to an experimental transfer of bees from Gridley to the Oxford Research Tract at the University of California, Berkeley. Following successful establishment, the resulting populations were followed for several years. This raised the possibility of introducing them into other parts of the Old World (they are an exclusively New World group). Michelbacher discussed the matter at an International Congress of Entomology in Vienna and with colleagues in Moscow at a subsequent international congress. One attempt to introduce the bees into Hawaii failed for a variety of reasons.

In addition to work on squash bees, Mickie spent a substantial amount of time in the southwestern deserts collecting bees for the Essig Museum, with special emphasis on bee visitors to *Larrea,* sunflowers, and other plants of interest to his colleagues.

On 19 Aug 1965, the now famous "Nogales incident" occurred. The Michel-

bachers had parked their car on the shoulder of the highway about 50 miles south of Nogales, Mexico, in order to collect bees in the adjacent field. A drunken driver in a pick-up truck crashed into their car, resulting in the death of one of the truck's passengers. In accordance with Mexican law, Mickie was arrested for contributing to homicide and taken to jail in Nogales. By some deft maneuvering, he was able to arrange a transfer to a hospital room but remained under guard. (He was charged for both the room and the guard.) He was later permitted to move into a motel but could not leave Nogales without authorization. A long, drawn out procedure followed and he was finally permitted to leave after posting a $2400.00 bail. Intervention by the U.S. Department of State and officials of the University of California contributed to this release. On principle, Mickie refused to forfeit bail and continued his legal action. In February 1966, another hearing was held and he was more or less exonerated, paying a small fine, and, miraculously, having his bail returned. One condition of his release, however, was that he could not drive in Mexico for three years.

In 1967, the Michelbachers went on a collecting trip with John Chemsak to the Cape region of Baja California. This was the beginning of a close and congenial relationship as evidenced by 10 subsequent trips to Mexico, Costa Rica, Honduras and eastern California. Mickie loved to collect beetles and with the pressures of bee collecting removed, he once again became a very efficient beetle collector. He especially liked beating, a technique learned from Dr. E. C. Van Dyke, and was happiest when piles of cut slash were available nearby. Since beating is most effective during cool temperatures, Martha and Mickie went out at dawn. By the time their companion would rise for breakfast, they had collected dozens of cerambycids. Mickie also became adept at aerial net collecting but had little enthusiasm for light collecting.

The adventures and episodes during the field trips were numerous and varied, many humorous, and a few, serious. Mickie loved to recall incidents which had occurred during the early trips to Baja California and Chile with E. S. Ross. Subsequent trips provided a lifetime of memories.

The poverty encountered in Latin America was appalling to Mickie. On most of the trips to Mexico, the Michelbachers brought used clothing and bags of sweets which they distributed in the rural areas.

Michelbacher held active membership in many scientific societies and institutions. Included were the American Association of Economic Entomologists (member); American Association for the Advancement of Science (Fellow); Entomological Society of America (Fellow); California Academy of Sciences (Fellow); Pacific Coast Entomological Society (President and Honored Member); Northern California Entomology Club (President); the Western Society of Naturalists (member); the Commonwealth Club of San Francisco (member); and the scientific fraternities Alpha Zeta and Sigma Xi (member).

It would be easy to continue to enumerate the activities, attributes, accomplishments and virtues of Abraham Michelbacher. For our purpose, it is sufficient to recall that he was a great field ecologist who laid the foundation for modern ecological pest control. He was a superb teacher of first and second generation insect pest management researchers and practitioners. Mickie was one of the kindest and most generous people it has been our privilege to know. Several generations of students can attest to his assistance in times of need.

It has been an honor and privilege to have been associated with Mickie and he will be missed.

Mickie is survived by his wife, Martha, and daughter, Virginia Ingham.

New Taxa Described by Michelbacher

1. *Symphyllela subterranea* Michelbacher, 1939. Pan-Pac. Entomol., 15: 22.
2. *Symphylella essigi* Michelbacher, 1939. Pan-Pac. Entomol., 15: 23.
3. *Symphylella capitata* Michelbacher, 1939. Pan-Pac. Entomol., 15: 27.
4. *Symphylella oviceps* Michelbacher, 1939. Ann. Entomol. Soc. Am., 32: 748.
5. *Symphylella sierrae* Michelbacher, 1939. Ann. Entomol. Soc. Am., 32: 751.
6. *Hanseniella vandykei* Michelbacher, 1939. Ann. Entomol. Soc. Am., 32: 753.
7. *Symphyllelopsis alba* Michelbacher, 1941. Ann. Entomol. Soc. Am., 34: 142.
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Received 8 January 1992; accepted 1 February 1992.

PAN-PACIFIC ENTOMOLOGIST
68(4): 243–247, (1992)

A NEW SPECIES OF *TYDESSA* PEACOCK (COLEOPTERA: PYTHIDAE: PILIPALPINAE) FROM WESTERN NORTH AMERICA

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Abstract.—*Tydessa blaisdelli* Pollock, NEW SPECIES, is described on the basis of four specimens from California and Nevada. This species is compared to the other described species, *T. lewisi* (Pic), from Japan. The genus *Tydessa* is the only Holarctic representative of Pilipalpinae, and *T. blaisdelli* is the only known species of the subfamily in North America. A brief taxonomic history of the genus, and a key to adults are provided.

Key Words.—Insecta, Pythidae, Pilipalpinae, Holarctic, new species

The first described species now included in *Tydessa* Peacock was *Dasytes constrictus* Lewis (1895), a junior primary homonym of *Dasytes constrictus* Broun (1883). Pic (1937) provided the replacement name *Dasytes lewisi.* However, Peacock (1982) discovered that this species did not belong in *Dasytes,* and indeed, was actually a member of Tenebrionoidea rather than the Cleroidea. *Tydessa* was proposed by Peacock (1982) for the species *Dasytes lewisi* Pic, the genus being placed in Pyrochroidae, near *Incollogenius* Pic. The larva of *T. lewisi* was described by Nikitskiy (1986), who elevated Pilipalpinae to family rank, and proposed a new tribe, Tydessini, for reception of the single species *T. lewisi.*

Recently, I examined several specimens from California and Nevada also belonging to the genus *Tydessa*; these are members of an undescribed species. This new species is described below. Also, Sasaji (1986) and Watt (1987) mentioned an undescribed species of *Tydessa* from Taiwan; I have not yet been able to examine specimens of the Taiwanese species. This new U.S. species represents the first Nearctic record for Pilipalpinae; it is hoped that its description may lead to discovery of additional material and perhaps the larval stage, of this apparently rare beetle.

Adult specimens of *Tydessa* were borrowed from collections indicated by the following acronyms: ANP, Department of Entomology, The Academy of Natural Sciences of Philadelphia, Philadelphia; BMNH, Department of Entomology, British Museum (Natural History), London; CAS, Department of Entomology, California Academy of Sciences, San Francisco; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge.

TYDESSA PEACOCK 1982

Tydessa Peacock 1982: 362. Type species (by monotypy): *Dasytes constrictus* Lewis 1895 (= *D. lewisi* Pic); Nikitskiy 1986; Sasaji 1984, 1986; Watt 1987.

Key to adults of *Tydessa* Peacock

1. Antennomeres submoniliform (Fig. 3); hind angles of pronotum (Fig. 5) distinct, subrectangular; basolateral margins of pronotal disc subparallel

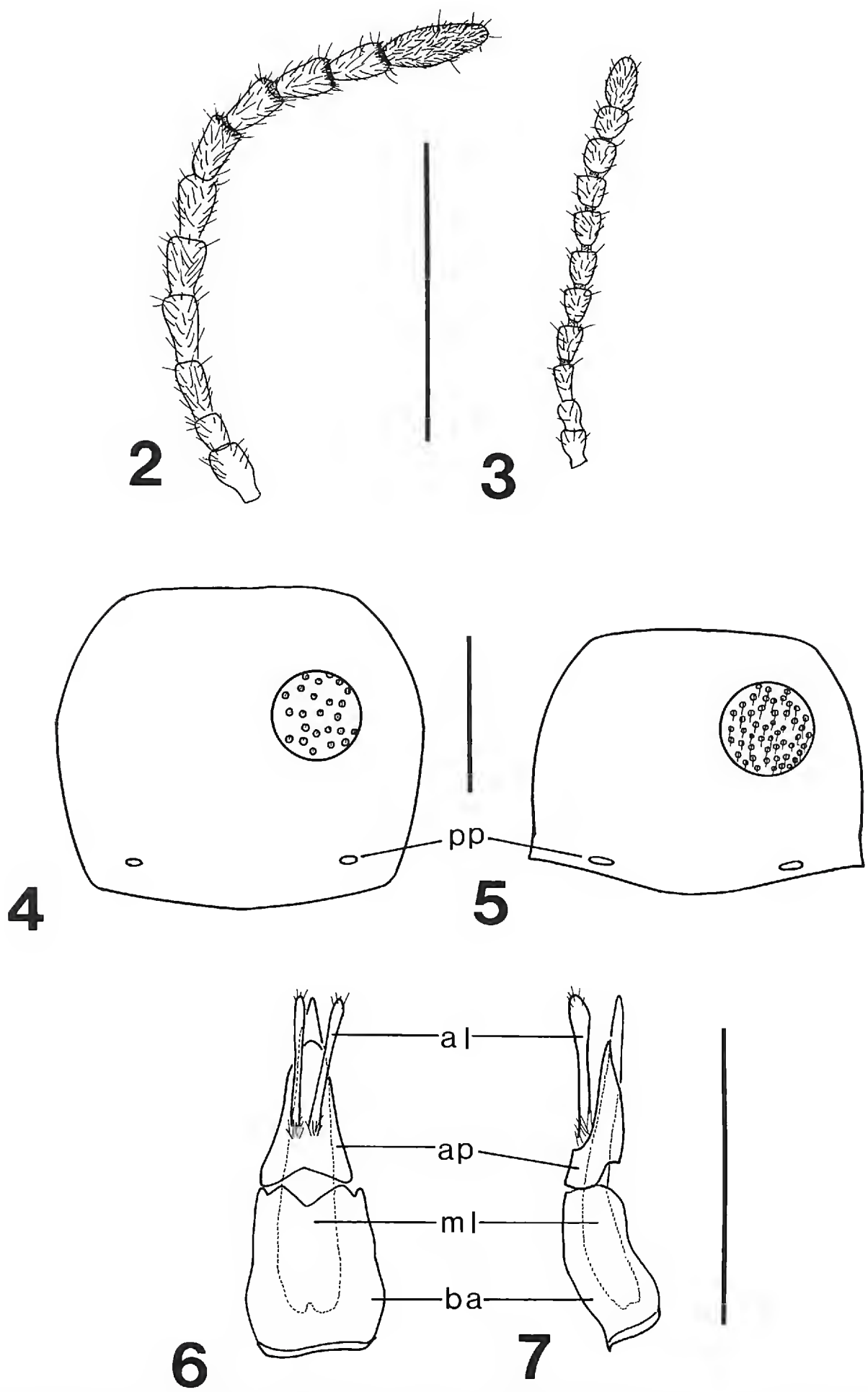
Figure 1. *Tydessa blaisdelli* Pollock, NEW SPECIES, female paratype [CAS]. Habitus, dorsal view. Length of specimen = 7.9 mm.

to slightly sinuate anterad hind angles; pubescence on pronotum and elytra distinct; color of head and pronotum dark piceous with blue metallic luster; distribution—Japan ..... *T. lewisi* (Pic)

– Antennomeres filiform (Fig. 2); hind angles of pronotum (Fig. 4) indistinct, rounded; basolateral margins of pronotal disc constricted anterad hind angles; pubescence on pronotum and elytra inconspicuous; color of head and pronotum piceous, non-metallic; distribution—western North America ..... *T. blaisdelli* Pollock, NEW SPECIES

Tydessa blaisdelli Pollock, NEW SPECIES

Types.—Holotype: male, labelled: "Adams Spgs, Lake Co. CAL. VI-18-11/F.E.



Figures 2–7. Figure 2. *Tydessa blaisdelli* Pollock, NEW SPECIES, male holotype [CAS]. Right antenna, dorsal view. Figure 3. *Tydessa lewisi* (Pic), female paralectotype [BMNH]. Right antenna. Scale bar for 2 and 3 = 1 mm. Figure 4. *Tydessa blaisdelli* Pollock, NEW SPECIES, male holotype [CAS]. Outline of pronotum showing sample of punctation and position of posterior pronotal pits. Figure 5. *Tydessa lewisi* (Pic), female paralectotype [BMNH]. Outline of pronotum showing sample of punctation and position of posterior pronotal pits. Scale bar 4 and 5 = 0.5 mm. Figure 6. *Tydessa blaisdelli* Pollock, NEW SPECIES, male holotype [CAS]. Aedeagus, ventral view. al = accessory lobe; ap = apicale; ba = basale; ml = median lobe. Figure 7. *Tydessa blaisdelli* Pollock, NEW SPECIES, male holotype [CAS]. Aedeagus, lateral view. Scale bar for 6 and 7 = 1 mm. al = accessory lobe; ap = apicale; ba = basale; ml = median lobe.

Blaisdell Collector/Blaisdell Collection/[pink disc]/HOLOTYPE ♂ Tydessa blaisdelli Pollock." Holotype deposited in the California Academy of Sciences. Paratypes: CALIFORNIA. *LASSEN CO.:* Lassen Peak, 30 Jun 1950 (P. S. Bartholomew Collection), P. S. Bartholomew, Calif. Acad. Sci. Accession 1967, 1 female [CAS]. NEVADA. *WASHOE CO:* Reno (Liebeck Collection), 1 female (disarticulated in alcohol) [MCZ]; no collection data (Horn Collection), 1 female [ANP].

Description [format follows Peacock (1982) for ease of comparison with *T. lewisi*].—*Color:* unmetallic brown to piceous; elytra slightly lighter in color than head and pronotum; basal three or four antennomeres and tarsi light brown. *Vestiture:* setae on inner margins of eyes conspicuous, slightly longer than diameters of punctures; setae on pronotum (Fig. 4) and elytra very short, barely visible, setae shorter than diameter of punctures; lateral margins of pronotal disc with scattered, short, erect setae; setae conspicuous on ventral surface, sparse on middle of metasternum; tibiae and tarsi with dense, long setae. *Punctation:* head with coarse, deep punctures, sparse on center of frons; punctures separated by approximately their own diameters; pronotal and elytral punctures shallow, small, separated by about 3.0× their own diameters; microsculpture absent among pronotal and elytral punctures, slightly granulate around inner margins of eyes; ventral surface variously punctate, more uniform on thorax, lighter on abdomen; mesepisternum impunctate along inner margin. *Form* (Fig. 1): head and pronotum subequal in width; elytra about 1.5× wider, approximately four × length of pronotum; lateral elytral margins subparallel, widened slightly about their midlengths. *Antennae* (Fig. 2): elongate, all antennomeres filiform; lengths of antennomeres 3–7 2.0 × widths; 8–11 slightly less elongated; antennomeres distinctly wider in females than in males. *Thorax:* pronotum (Fig. 4) subcircular, lateral margins of disc evenly arcuate from anterior to posterior margins; two small, deep pits near hind angles; hind angles poorly defined, rounded; lateral margins smooth, except for slightly raised carina extended anteriorly half the length of pronotum. *Male Genitalia* (Figs. 6 and 7): apicale slightly shorter than basale; apicale entire distally, not cleft between accessory lobes; accessory lobes elongate, slender, widened slightly distally. *Size:* length from 5.9–7.1 mm; maximum width (across elytra) from 1.7–2.4 mm.

Diagnosis.—Specimens of *T. blaisdelli* may be distinguished from those of *T. lewisi* on the basis of characters given in the key, above.

Etymology.—This species is named in honor of F. E. Blaisdell, Sr., who worked on Tenebrionoidea of western North America, and also who collected the holotype of the species.

Material Examined.—See types.

Comments

The genus *Tydessa* is the only Holarctic representative of Pilipalpinae, a subfamily otherwise represented only in Australia, Chile, New Zealand, and Madagascar. A phylogenetic and biogeographical analysis of the entire group is underway (unpublished data), using characters of both larval and adult stages.

The distribution pattern exhibited by members of *Tydessa* seems a possible candidate for an Asiamerican origin, as explained by Noonan (1986). Because nothing is known about the habitat requirements of the genus, it is difficult to speculate whether or not the disappearance of a transberingian dispersal corridor may have caused the vicariant event separating the Asian and North American stocks.

Acknowledgment

I am grateful to John Lawrence and Dan Young, for first bringing these specimens to my attention. Dave Kavanaugh provided much appreciated hospitality and support during a search for additional specimens of *Tydessa* at CAS. Ed Fuller

assisted in attempted field collection of specimens; his company was much appreciated. Thanks to R. E. Roughley for use of photographic equipment. G. E. Ball provided financial support for this study (NSERC A-1399). Valuable comments on the manuscript were provided by E. R. Fuller and two anonymous reviewers.

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Received 7 October 1991; accepted 28 January 1992.

PAN-PACIFIC ENTOMOLOGIST
68(4): 248–260, (1992)

POPULATION TRENDS AND BIOLOGICAL ASPECTS OF CEREAL APHIDS (HOMOPTERA: APHIDIDAE), AND THEIR NATURAL MORTALITY FACTORS ON WINTER WHEAT IN SOUTHWESTERN IDAHO

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ROBERT M. NOWIERSKI,[2] AND SUSAN E. HALBERT[3]

Abstract.—From 1986 to 1989, winter wheat grown under irrigation in southwestern Idaho was commonly infested by five species of cereal aphids, *Diuraphis noxia* (Mordvilko), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (L.), *Sitobion avenae* (Fabr.), and *Schizaphis graminum* (Rondani), although their population levels differed greatly from year to year. Autoecious *S. avenae* was found overwintering on the crop and usually initiated summer infestation earlier than the other species. Heteroecious *M. dirhodum* was rarely found during the autumn and initiated summer infestations later than *S. avenae,* possibly by immigrants from its primary hosts (*Rosa* spp.). Anholocyclic *D. noxia* survived the first winter after entering the region in June 1987 and achieved a dense summer population during 1988. However, colonies were not detected after mid-December during the unusually cold winter that followed and the aphid was scarce throughout 1989. The impact of cold weather may be reduced if a holocyclic population develops as may be possible as indicated by the discovery of oviparae in Idaho (Kiriak et al. 1990). This survey yielded no evidence that nymphs or adults of *R. padi* and *S. graminum* could overwinter on the crop. Both are typically holocyclic, overwintering on chokecherry, *Prunus virginiana* L., and grasses, respectively, but can sometimes overwinter anholocyclicly (Blackman et al. 1990). The summer population levels of the whole aphid complex usually remained relatively low. The highest population levels were typically observed late in the season and were reduced by entomophthoralean fungi and/or parasitoids, thus making the use of insecticides unnecessary in most years. The length and severity of freezing periods during the winter seemed to determine the timing of population recovery or immigration, and thus population sizes, during the summer. Mycoses occurred in the first two summers, causing mortalities of 46% and 90% for *M. dirhodum* and 17% and 7% for *S. avenae.* In contrast, aphidiid parasitoids killed more *S. avenae* (35%, 81%, 4%, and 59% at peak from 1986 to 1989, respectively) than *M. dirhodum* (about 5% at peak in 1986 and 1987 only). Mortalities attributable to mycoses or parasitoids were not consistently detected for other aphid species except *D. noxia,* which suffered 1–2% parasitism during the 1988 summer. Aphid-specific predators were not abundant on winter wheat throughout the survey.

Key Words.—Insecta, cereal aphids, population dynamics, Entomophthorales, Aphidiidae, winter wheat

Small grains grown under irrigation in southwestern Idaho are infested by most species of cereal aphids that occur in North America. English grain aphid, *Sitobion avenae* (Fabr.); rose-grass aphid, *Metopolophium dirhodum* (Walker); greenbug, *Schizaphis graminum* (Rondani); bird cherry-oat aphid, *Rhopalosiphum padi* (L.); and Russian wheat aphid, *Diuraphis noxia* (Mordvilko) were most common (Feng

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1990, Johnston & Bishop 1987). *Diuraphis noxia* was first found in the area during June 1987 (Feng 1990). These aphid species are all considered to be of economic importance. Few field studies have considered the whole complex of cereal aphids. Thus, little information is available concerning the population dynamics of these aphids and their natural enemies on winter wheat from planting through harvest in North America.

In this four year field study, we investigated the population trends and biological features of several aphid species, including *D. noxia,* their fungal pathogens and their hymenopterous parasitoids in irrigated winter wheat in southwestern Idaho. Data presented in this paper provide an overview of the cereal aphid complex and should be helpful in understanding the composition and population dynamics of local cereal aphid communities, their biology, and the roles of their natural enemies.

Materials and Methods

Field studies were conducted at or near the Southwestern Idaho Research and Extension Center in Parma, Canyon County, Idaho from 1986 to 1989. Each summer, commercial fields (5–15 ha each) were surveyed weekly from mid-May onwards; these fields were furrow-irrigated at intervals of approximately 10 days from late April or early May until crop maturity and were under regular management but with no insecticide application. Summer populations of various cereal aphids were monitored in one field in 1986, two in 1987 and 1989, and three in 1988. To observe the overwintering behavior of aphid populations on winter wheat, one early-planted (mid-September) field (about 5 ha) in Caldwell, about 30 km SE of Parma, was surveyed from the seedling stage through harvest during the 1987/88 growing season (weekly from late September through mid-November, biweekly the following month, monthly from January through mid-May, and then weekly until harvest). A second overwintering survey was conducted monthly at the same site starting in late October during the 1988/89 growing season.

Details about sample size and methods have been given elsewhere (Feng et al. 1991). Briefly, our sampling system ensured 600 tillers from 15 different locations in each field on each sampling occasion to be examined at low densities (≤ 5 aphids per tiller) and a minimum of 150 tillers at high densities (≥ 15 aphids per tiller), decreasing with increasing aphid density. Because aphid densities on winter wheat were usually low or intermediate, 300 tillers or more were sampled even at peak density.

Aphids in each sample were sorted to species and counted in situ. Records included the numbers of live aphids and those killed by mycoses (cadavers) and parasitoids (mummies). The number of tillers infested with aphids was recorded only during the last two growing seasons. Percent infestation was calculated as: infestation (%) = (number of tillers infested/number of tillers sampled) $\times$ 100. Percent mortality caused by mycoses or parasitoids was computed as: mortality (%) = [number of cadavers (or mummies)/(sum of live aphids, cadavers, and mummies)] $\times$ 100.

Temperature and precipitation data from a local weather station situated at the Research and Extension Center were used to interpret the population trends and the development of aphid mycoses and parasitoids in the field.

Results and Discussion

Aphid species commonly occurring on winter wheat during the survey were *D. noxia, M. dirhodum, R. padi, S. avenae* and *S. graminum*. Among these, *S. avenae* and *M. dirhodum* populations were more consistent than those of *S. graminum* and *R. padi* during the summers. *Diuraphis noxia* established dense populations on the 1987/88 crop, but became undetectable on winter wheat during summer 1989. Other aphid species, including *Rhopalosiphum maidis* (Fitch), *Diuraphis frequens* (Walker), and *Sipha elegans* del Guecio, were occasionally observed in small, isolated colonies and apparently were of minor economic importance.

Overwintering.—Autumn populations of *D. noxia, R. padi, S. avenae* and *S. graminum* in 1987 are shown in Fig. 1. Alatae of these four species from volunteer grain plants, corn or grasses near the field initiated infestation of winter wheat soon after seedlings emerged. No *M. dirhodum* colonies were found on winter wheat during the autumn because this heteroecious species is known to overwinter as eggs on *Rosa* spp. (Hand & Williams 1981). The densities of aphid populations and percentage of infestation both increased until mid-November. Thereafter, aphid populations were dramatically reduced (Figs. 1A, 1B) as cold temperatures ensued (Fig. 1C). Aphids became inactive or died after late December. During the following autumn and winter, only *D. noxia* and *S. graminum* were observed in the samples on 26 Oct (0.57 and 0.29 aphids per tiller, respectively) and 16 Dec (0.26 and 0.04 aphids per tiller, respectively). Thereafter, no live aphids except *D. noxia* (Fig. 1A) were detected until *S. avenae* colonies appeared in mid-May (Fig. 1B), though fundatrices of the latter species occasionally occur as early as March (S. E. Halbert, unpublished data). For convenience, the population dynamics observed in autumn and the overwintering potential of each aphid species are given separately and discussed below.

Diuraphis noxia was successful in surviving the first winter after it entered the region during the summer of 1987. The population density of this species was over one aphid per tiller during mid- to late November, with 27% of the tillers infested at peak, and remained detectable even during the coldest periods (Fig. 1A). Live aphids observed during the cold winter period consisted of older nymphs and apterae that appeared to be protected in the tightly rolled leaves. *Diuraphis noxia* dominated the complex on spring wheat during the following summer (Feng et al. 1991). However, live colonies were not found on winter wheat after late December during the colder 1988/89 winter and the aphid population did not fully recover during the following spring and summer. Live colonies were sporadic on regularly sown spring wheat (seeded in late March or early April), but were more common on late-sown spring wheat (seeded in late April or early May), after June of that year (Feng et al. 1991). There were 92 freezing days during the 1988/89 winter with a minimum daily temperature of −23° C. This contrasts to 54 freezing days with an extreme of −13° C during the 1987/88 winter and 59 freezing days with an extreme of −10° C during the 1986/87 winter (Fig. 1C). The longer duration of freezing and lower extreme temperatures appeared to contribute to the virtually undetectable levels in the *D. noxia* population on winter wheat in 1989.

Rhopalosiphum padi was one of the principal species infesting winter wheat during autumn 1987. Its population level reached 6.59 aphids per tiller (in contrast to only 1.27 for *D. noxia*) on 11 Nov and nearly half of all tillers sampled were

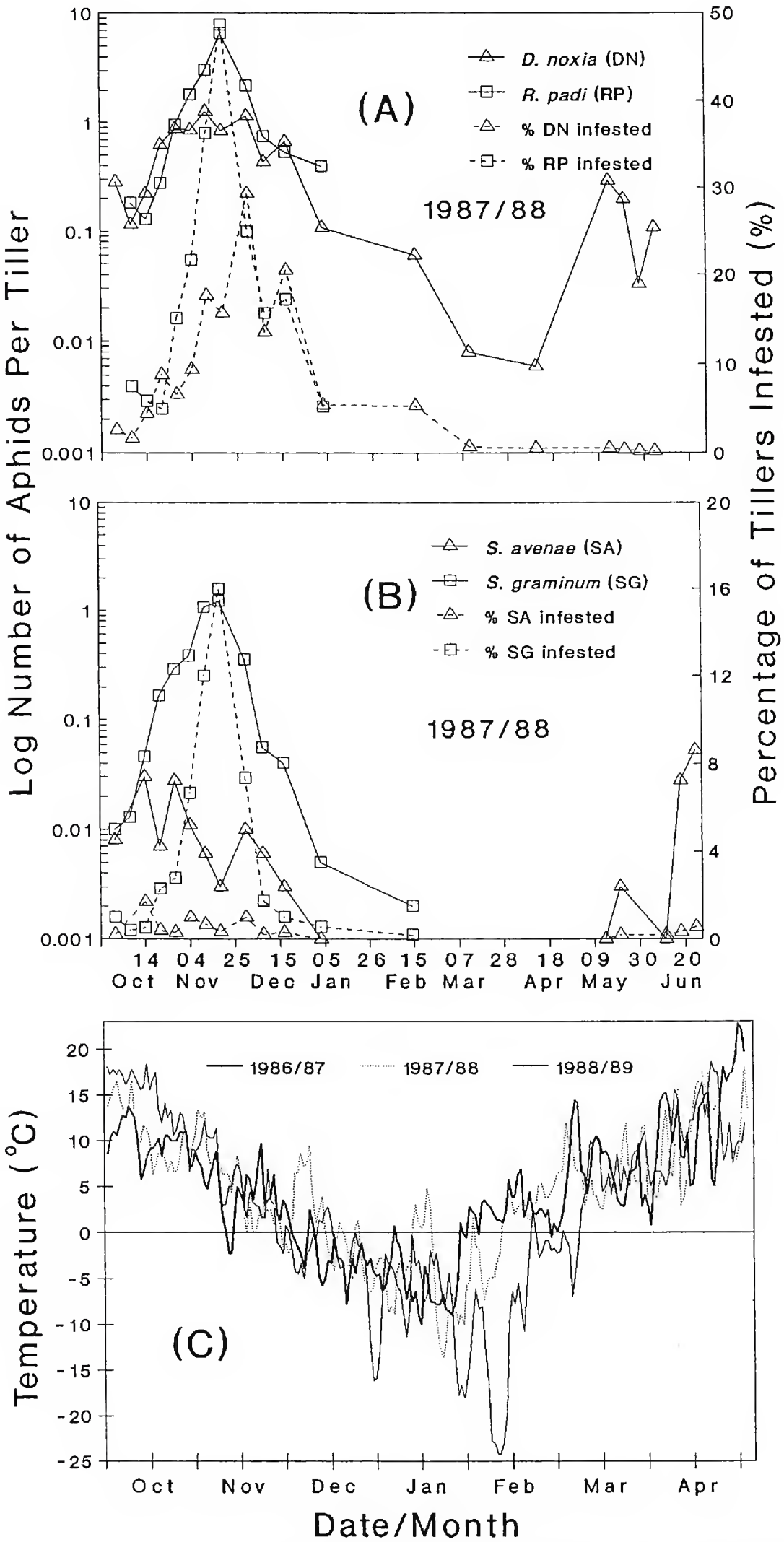

Figure 1. Autumn populations and overwintering of cereal aphids in winter wheat during the 1987/88 growing seasons. (A) *D. noxia* and *R. padi*. (B) *S. avenae* and *S. graminum*. (C) Daily mean temperature during the winter months.

infested with this species (Fig. 1A). Most colonies were found inhabiting the basal parts of plants (e.g., the undersurface of basal leaves and stems below the soil surface). Following this, *R. padi* populations rapidly decreased to 0.4 aphids per tiller (5% tillers infested) on 18 Dec. Thereafter, live aphids were not observed, though numerous dead ones (apparently having succumbed to freezing) remained visible in the field in January 1988. As a result, this species was not found during the following spring and summer. This suggests that there is little chance for *R. padi* to successfully overwinter in the parthenogenetic form on winter wheat in the study area because the 1987/88 winter was relatively mild (Fig. 1C).

As a heteroecious species, *R. padi* typically overwinters as eggs on its primary hosts, *Prunus padus* L. or related species (Robinson & Hsu 1963). Anholocyclic overwintering on winter grains or grasses is possible in mild or southern areas (Eastop 1981) (e.g., Lafayette, Indiana [Araya et al. 1987]). However, this life cycle does not occur for *R. padi* in Brookings, South Dakota (Kieckhefer et al. 1974), which is similar in latitude to southwestern Idaho. Early infestation of winter wheat followed by successful overwintering on the crop can increase losses in Washington (Pike & Schaffner 1985).

Sitobion avenae autumn populations were very small in 1987 (Fig. 1B) and undetectable in 1988. Its peak density was only 0.04 aphids per tiller, corresponding to an infestation level of less than 2% (Fig. 1B). A few oviparae were found during the autumn, but eggs were not detected. From 18 Dec onwards, live aphids were not found in the crop until mid-May of the following year.

Schizaphis graminum had a larger autumn population than *S. avenae* in 1987 (Fig. 1B). Its peak density was about one aphid per tiller (similar to the *D. noxia* population) on 18 Nov and resulted in an infestation of 16%. Thereafter, its population decreased but remained detectable until 17 Feb 1988. In contrast, during the following, colder winter, the population of *S. graminum* was detectable only until 16 Dec.

These two species are considered to be holocyclic in the northern United States (Blackman & Eastop 1984). In areas with spring and winter cereals, alatae from volunteer plants and grasses migrate to autumn-sown winter crops, on which they produce males and oviparae and then lay eggs to survive the winter months (Phillips 1916). Of the two aphid species, only *S. avenae* usually seems to fit this pattern in the study area because no sexuals of *S. graminum* were found during the survey. Although *S. graminum* survived all the periods of freezing during the 1987/88 winter (Figs. 1B, 1C), its population did not recover in the same field during the following spring and summer.

Summer Populations.—The population development of each aphid species and the mortalities caused by entomophthoralean fungi and/or aphidiid parasitoids are shown in Fig. 2 for the 1986 and 1987 summers and in Fig. 3 for the 1988 and 1989 summers. Data presented in Figs. 2 and 3 are mean estimates from two fields for 1987 and 1989 and three fields in 1988, respectively. The 1986 populations were estimated from only a single field. Aphid-specific predators such as coccinellids and syrphids were not common on winter wheat though they were sometimes abundant on spring, particularly late-sown, crops.

Initiation of Infestation.—As shown in Figs. 2 and 3, the populations of *S. avenae* were first detected on winter wheat in mid-May (1987, 1989) or late May (1986, 1988). The early colonies usually consisted of various nymphal instars and

fewer wingless adults. Thus, the starting population of this aphid species, though too small to be detected, started earlier and was possibly initiated by fundatrices that hatched from overwintered eggs, rather than by immigrants. Moreover, alatoid nymphs were well represented among the earliest observed nymphs, indicating a source of *S. avenae* for infesting local spring-planted grain crops. In contrast, *M. dirhodum* was found in the field one (1988), two (1986, 1987) or even three (1989) weeks later than *S. avenae.* The early colonies of *M. dirhodum,* found on plants each summer, commonly consisted of several early instars and one alate. Thus, it is postulated that the infestation of winter wheat by *M. dirhodum* was initiated by alate immigrants from its primary hosts because no colonies of this species were found during the preceding autumn.

Schizaphis graminum occurred on winter wheat at the same time as *M. dirhodum* in 1986 and 1988, but one week later in 1987 (Figs. 2 and 3). However, it was not found throughout the 1989 summer. Although *S. graminum* survived all the freezing periods during the 1987/88 winter (Figs. 1B, 1C), the population of this species was not detected until the end of the first week of June (Fig. 3A). The populations of *R. padi* were detected later than both of the above species in 1986 and a few days earlier in 1987, but were undetectable on the crop during the last two summers. Therefore, *R. padi* and *S. graminum* may have initiated their summer infestation primarily by their immigrants from other hosts or places, which is in agreement with observations from South Dakota (Kieckhefer et al. 1974).

The 1988 population level of *D. noxia* was relatively high (up to 0.16 aphids per tiller) at the first sampling time (17 May), two weeks before *S. avenae* populations were detected (Fig. 3A). Colonies of *D. noxia,* during this early period, consisted of nymphs and apterae. Therefore, it appears that 1988 summer populations of *D. noxia* on winter wheat were initiated by individuals that successfully overwintered in situ (Fig. 1A). Following the colder 1988/89 winter, initial infestation of the crop appeared to be largely due to immigration of alatae.

Population Development.—Summer populations of *S. avenae* and *M. dirhodum* were usually the highest among the aphid species found during this survey (Figs. 2 and 3). An exception occurred in 1988 when *D. noxia* populations were found to be more dense (2.99 aphids per tiller at peak) than the prior two aphid species (Fig. 3A). Though *M. dirhodum* infested the crop later than *S. avenae,* its populations peaked earlier, and were often larger, than those of *S. avenae.* The highest population densities of *M. dirhodum* and *S. avenae* were, respectively, 4.43 (25 Jun, early milky stage) and 3.73 (2 Jul, medium milky) aphids per tiller in 1986, 5.23 (3 Jul, hard dough) and 0.54 (3 Jul, hard dough) in 1987, 0.65 (21 Jun, soft dough) and 1.03 (7 Jul, nearly ripening) in 1988, and 0.46 (19 Jun, late milky) and 0.36 (26 Jun, soft dough) in 1989. Such population trends were similar to those reported by Ankersmit & Carter (1981).

The populations of *S. graminum* and, particularly, *R. padi* were relatively small and inconsistent in winter wheat during the summers. Peak densities of these two species were, respectively, 0.7 (2 Jul) and 0.03 (25 Jun) aphids per tiller in 1986, 0.6 (26 Jun) and 0.62 (3 Jul) in 1987, and 1.57 (21 Jun) in 1988 for *S. graminum* only.

These aphid species appeared to prefer different parts of the plants for feeding. *Sitobion avenae* preferred developing heads and upper leaves before heading,

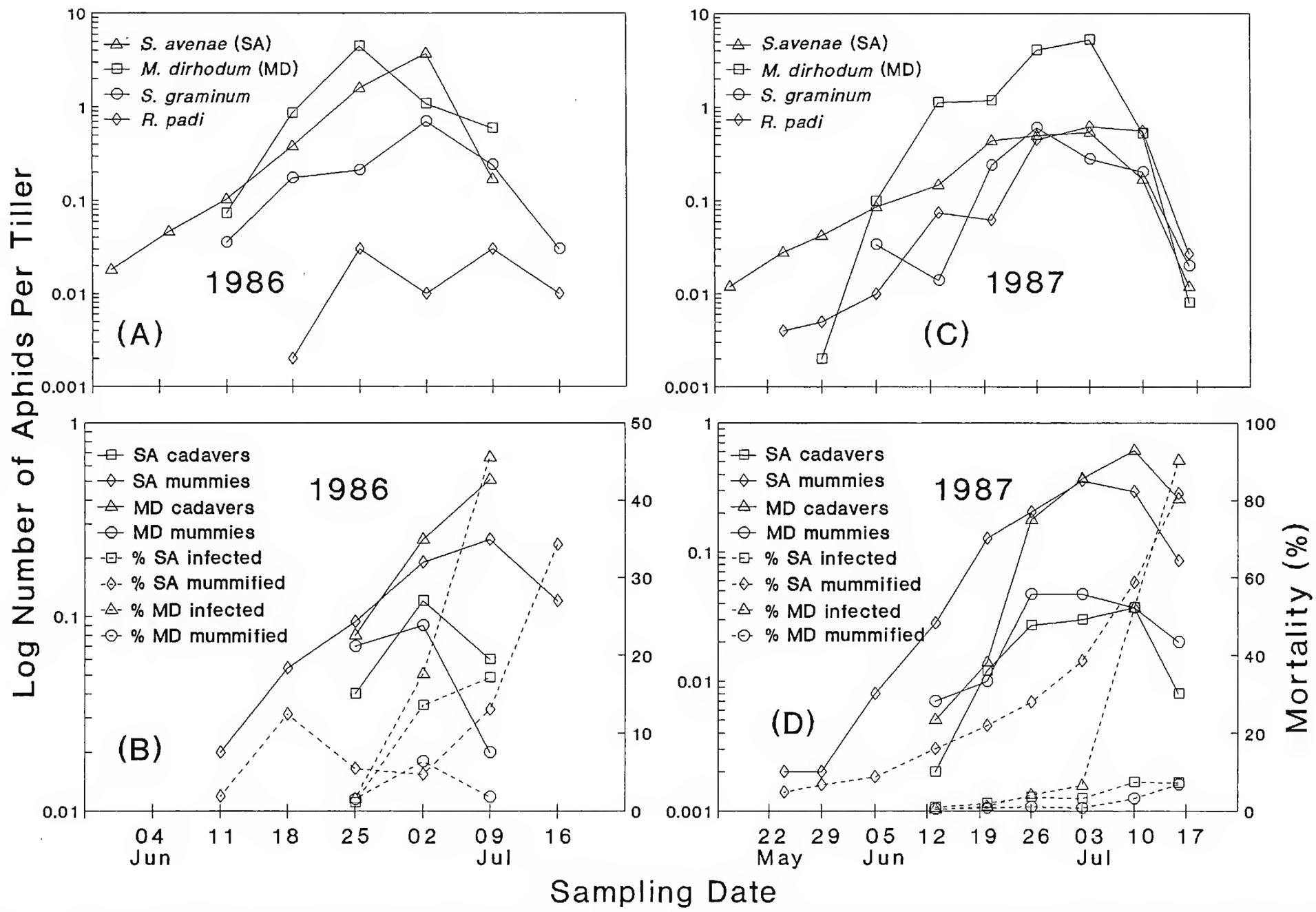

Figure 2. Summer populations of cereal aphids influenced by mycoses (cadavers) and parasitoids (mummies) in winter wheat during the 1986 (A & B) and 1987 (C & D) summers. Estimates were made from one and two fields in 1986 and 1987, respectively.

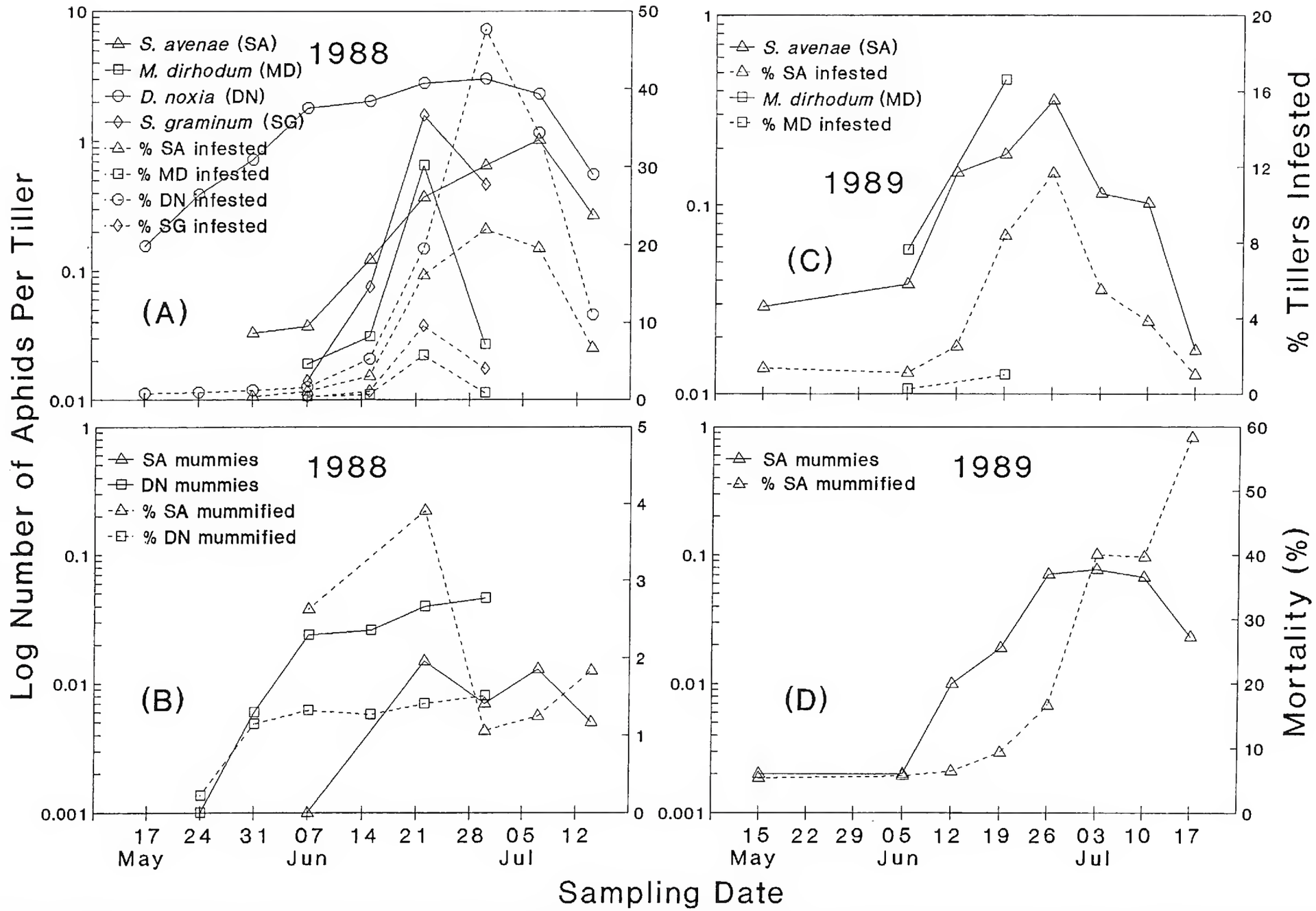

Figure 3. Summer populations of cereal aphids and their parasitoids (mummies) in winter wheat during the 1988 (A & B) and 1989 (C & D) summers. Estimates were made from three and two fields in 1988 and 1989, respectively.

whereas *M. dirhodum* tended to feed on the undersurfaces of older leaves and were rarely observed on heads. *Diuraphis noxia* preferred younger leaves, longitudinally rolled and striped when injured, at earlier stages of the crop but were also observed on heads and upper stems of more mature plants. *Schizaphis graminum* and *R. padi* were often found on leaves, on or inside the leaf sheaths and on the stems.

Mycoses.—Mycoses caused by entomophthoralean fungi appeared to significantly limit populations of *M. dirhodum* and *S. avenae* during the 1986 and 1987 summers (Fig. 2). Some cadavers of *S. graminum* and fewer of *R. padi* were also attributed to fungal infection in 1987. Few mycosed aphids of any species were found on winter wheat during the 1988 and 1989 summers (Fig. 3), although mycoses were still a principal factor reducing aphid populations in spring wheat during the same seasons (Feng et al. 1991). The highest mortalities of *M. dirhodum* and *S. avenae* in winter wheat due to fungal infection were, respectively, 46% and 17% in 1986, and 90% and 7% in 1987 (Figs. 2A, 2B). *Metopolophium dirhodum* was apparently far more susceptible to fungal infection than *S. avenae* in the field.

According to Feng et al. (1990a), the fungi capable of infecting cereal aphids on grain crops in southwestern Idaho during the 1986–1989 summers included 10 species, the most important of which was *Pandora neoaphidis* (Remaudire & Hennebert) Humber, followed by three *Conidiobolus* species. Among 2930 cadavers of six aphid species examined, 77% were killed by *P. neoaphidis* and 17.6% by *Conidiobolus* spp. Furthermore, *P. neoaphidis* and *Conidiobolus* spp. were responsible for 84% and 11% of 1417 *M. dirhodum* cadavers examined, and 24% and 68% of 217 *S. avenae* cadavers. The LC_{50} of *P. neoaphidis* for killing *M. dirhodum* was only 1.4–1.6 conidia/mm^2 (Feng & Johnson 1991). Thus, during the 1986–1987 summers, *P. neoaphidis* was a major pathogen associated with the mycoses of *M. dirhodum,* whereas *Conidiobolus* spp. were pathogens primarily associated with the mycoses of *S. avenae* (Feng 1991).

The patterns of aphid mycoses found in winter wheat during the survey may be interpreted as follows. First of all, having sufficient population levels of *M. dirhodum* which is more susceptible to fungal infection than some other aphid species (Feng & Johnson 1991, Feng et al. 1990b), appears to be a key factor. Mycoses occurred only during the two summers that experienced larger populations of *M. dirhodum* than *S. avenae* and other aphid species. When the *M. dirhodum* populations were small, as in 1988 and 1989, mycoses did not occur for *M. dirhodum* nor for any of the other aphid species, some of which occurred at high population levels (Fig. 3). For example, *D. noxia,* which had much higher population levels than *M. dirhodum* during the 1988 growing season, did not appear to be significantly affected by fungal infection. Second, temperature (influencing the development of both aphids and fungi) and precipitation (which increases the humidity within a crop and thus enhances conidial germination and infection) should also be considered. Cumulative precipitation and the timing of rainfall during the growing seasons greatly differed from year to year (Fig. 4B) and seemed to be more critical to the development of mycoses than temperature (Fig. 4A) (Feng et al. 1991). Frequent rainfalls throughout the 1987 summer and several small rainfalls during late June and early July in 1986 (Fig. 4B) coincided with the phase of the rapid development of mycoses in aphid populations during those summers (Fig. 2C, 2D). In contrast, there was little rain from early June

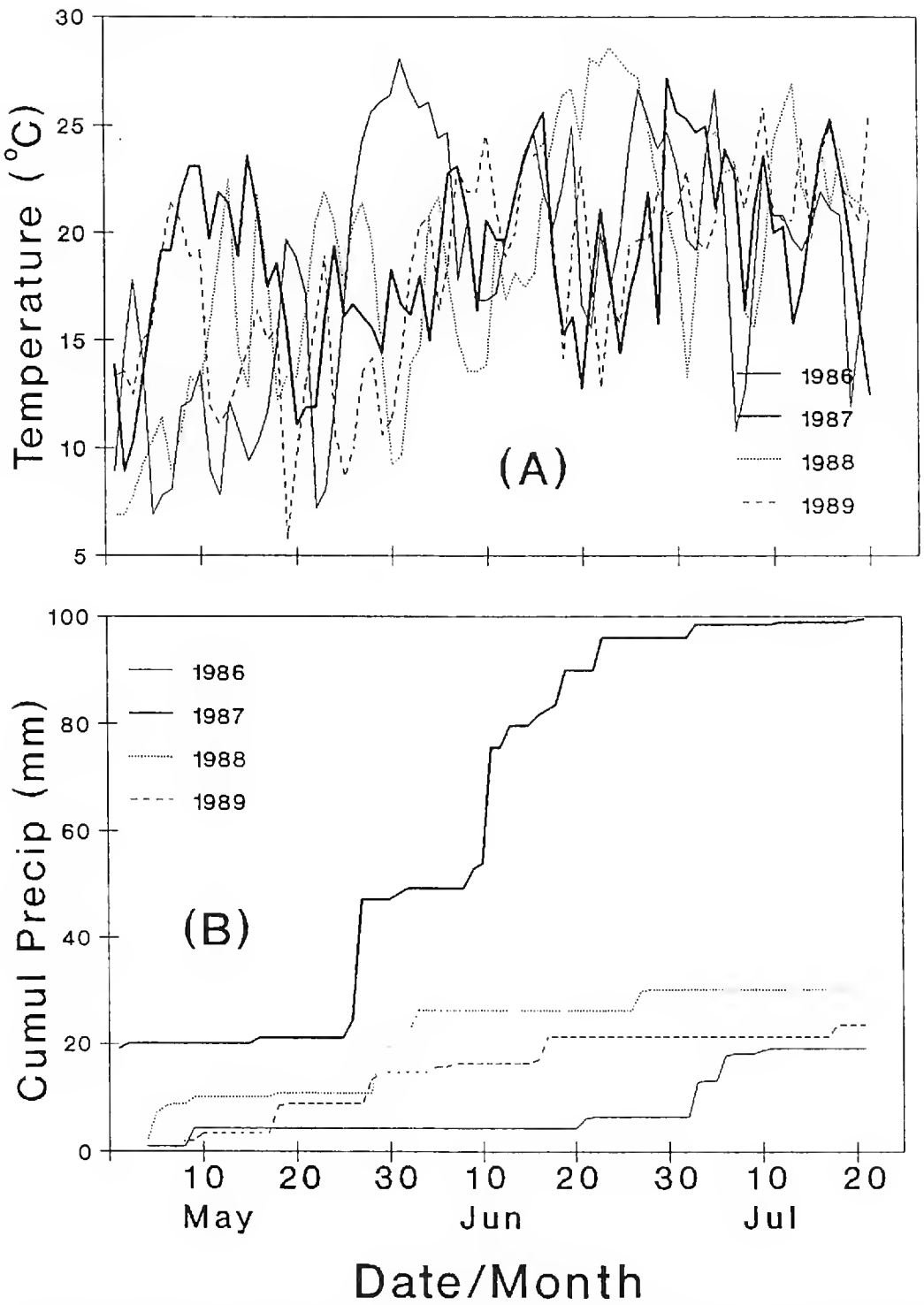

Figure 4. Weather patterns during the winter wheat growing season from 1986 to 1989. (A) Daily mean temperature (°C). (B) Cumulative precipitation (mm).

through July in 1988, and no rain during the last month of the crop season in 1989 (Fig. 4B). Also, irrigation was not supplied to winter wheat from late June onwards. Thus, low moisture under the crop canopy may have contributed to the undetectable level of fungal infection in aphid populations during the last two summers.

Parasitoids.—Primary parasitoids found to attack cereal aphids on winter wheat during the survey were all aphidiids, although an aphelinid species, *Aphelinus varipes* (Foerster), may attack *D. noxia* and *S. graminum* on spring wheat and barley and *R. padi* on corn (Feng 1990). The majority of *S. avenae* and *M. dirhodum* mummies were due to parasitism by *Aphidius ervi* Haliday, but *D. noxia* mummies were mostly attributable to attack by *Diaeretiella rapae* (McIntosh). *Praon* sp., possibly *P. gallicum* Stary, was found occasionally attacking all three aphid species. Mummies of *S. graminum* and *R. padi* were infrequently found on winter wheat because of their small or inconsistent populations.

Feng et al. (1991) found that parasitoids attacked cereal aphids, particularly *S. avenae,* earlier and at lower densities than fungal pathogens (Figs. 2 and 3). Parasitism was always higher for *S. avenae* than *M. dirhodum* and appeared to be a major factor suppressing the increase of *S. avenae* populations every summer. The highest mortality due to parasitism was 35% in 1986, 81% in 1987, 4% in 1988, and 59% in 1989. However, the mortality of *M. dirhodum* due to parasitism was always found to occur at low levels (about 5% at peak), and was not detected during the 1988 and 1989 summers (Figs. 2 and 3). This indicates that parasitoids were less important than mycoses in influencing the dynamics of *M. dirhodum* populations. Similarly, *D. noxia* suffered only 1–2% mortality due to parasitoids during the 1988 summer (Fig. 3B).

General Remarks.—Based on our four year field observations, the populations of cereal aphids in southwestern Idaho were much smaller on winter wheat than on spring wheat (Feng et al. 1991). The population level of *S. avenae,* the most injurious species to developing heads (Rabbinge et al. 1981, Vickerman & Wratten 1979), achieved only about one aphid per tiller at peak density on winter wheat during the summers from 1987 to 1989 and 3.73 aphids per tiller in 1986. The populations of the less injurious species, *M. dirhodum,* were larger in the first two summers but only about five aphids per tiller at peak. The economic threshold levels for the combined populations of *S. avenae* and *M. dirhodum* are 2–4 aphids per tiller at flowering, 6–10 aphids per tiller up to milky stage, and 10 or more aphids per tiller from the milky ripe to medium-dough stage (Johnston & Bishop 1987). Therefore, the population levels of the two species observed during the survey made insecticide application unnecessary. In fact, winter wheat received no insecticide application during the growing seasons.

The population stability of *S. avenae* and *M. dirhodum* may stem from their adaptation to local weather by successfully overwintering as eggs on winter wheat and roses, respectively. This contrasts to the inconsistent populations of other aphid species. *Rhopalosipum padi,* though not found on winter wheat during the 1988 and 1989 summers, did infest spring-planted wheat late in the seasons (from late June onwards; Feng 1990). Huge numbers of this species (up to thousands of aphids per plant) were commonly seen on corn in southwestern Idaho from late July through August or mid-September (Blackmer & Bishop 1991, Feng 1990). *Schizaphis graminum* also occurred on spring wheat after late June in 1989. These data suggest that infestation of local grain crops by *R. padi* and *S. graminum* was initiated by immigrants from other hosts. *Diuraphis noxia* appears to be able to survive local winter months with its anholocyclic life, at least in mild winters. The unusually cold 1988/89 winter was possibly a main reason that populations of *D. noxia, R. padi,* and *S. graminum* were undetected on winter wheat but found on other grain crops late in the following season. Therefore, the length and extremity of freezing time during winter months can apparently determine the timing of population recovery or immigration, and thus population sizes, of these aphid species during the summer.

From August through early October volunteer grains can be inhabited by numerous aphids of all the species except *M. dirhodum,* which was rarely observed after harvest (Feng 1990), and thus are sources of autumn aphid populations infesting winter wheat. However, for *R. padi* and *S. avenae,* field corn grown for

seed (plants left in the field until late September or even later after harvest) may be an even more important source of aphids to infest winter wheat (Feng 1990).

Mycoses and parasitoids are major biological mortality factors for *M. dirhodum* and *S. avenae* on winter wheat, although their influences differ from year to year. They apparently contributed to the collapse of *M. dirhodum* and *S. avenae* populations during the 1986 and 1987 summers. Even when *S. avenae* populations were small, as during the summer of 1989, there was a high level of parasitism. However, the life cycles of fungal pathogens and parasitoids associated with cereal aphids are not well understood. Cadavers were rarely found in autumn populations of cereal aphids on winter wheat. Mummies, though sometimes detected, were not common during the autumn. Their non-crop-feeding hosts are unknown in southwestern Idaho. Further study because this may help incorporate both mortality agents into a sound crop management program is warranted.

Acknowledgment

The authors wish to express their appreciation to K. W. Dorschner and D. J. Schotzko for critical review of this manuscript. This paper is published with the approval of the Director of the Idaho Agricultural Experiment Station as Research Paper 92703.

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Received 3 July 1991; accepted 1 April 1992.

PAN-PACIFIC ENTOMOLOGIST
68(4): 261–267, (1992)

COPULATORY COURTSHIP AND NOTES ON THE NATURAL HISTORY OF *OCHTHERA OCCIDENTALIS* CLAUSEN (DIPTERA: EPHYDRIDAE)

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Abstract.—Male *Ochthera occidentalis* court females both before and during copulation. The raptorial forelegs, which are relatively longer in males than in females, are used in aggressive displays.

Key Words.—*Ochthera occidentalis,* ephydrid fly, copulatory courtship, behavior, sexual selection

Male courtship behavior is generally thought to occur prior to genitalic coupling, and to function to induce the female to allow the male to copulate with her. Recent studies have shown, however, that courtship also frequently occurs *during* (and sometimes after) copulation ("copulatory courtship") (Eberhard 1991). The existence of copulatory courtship implies that selection has favored male abilities to induce females to perform post-intromission processes that increase their chances of fertilizing her eggs (Eberhard 1991; see also Otronen & Siva-Jothy 1991, von Helversen & von Helversen 1991). The existence of selection favoring copulatory courtship is of theoretical importance, in particular because a general theory of the evolution of animal genitalia (Eberhard 1985) is based on the premise that courtship after intromission has been achieved is common in animals with internal fertilization.

Thus the discovery of copulatory courtship in the ephydrid fly *Ochthera occidentalis* Clausen is of interest. The genus *Ochthera* is unusual in that both sexes have enlarged raptorial forelegs (Clausen 1977, 1980), which they use both as predatory and signalling devices (Deonier 1974, Simpson 1975). The adults are commonly found along mud or sand shores, or in swampy areas (Simpson 1975). This note describes the sexual behavior of *O. occidentalis* and other aspects of its natural history.

STUDY SITE AND METHODS

Observations were made on a cloudy day at the muddy edge of a shallow pool of brackish water on 8 Sep 1989 near Chamela, Jalisco, Mexico. I observed the flies by lying flat, so that my face was less than 18 cm from the surface of the mud and between 18 and 60 cm from the flies. All observations were in the approximately 0.5 m^2 area visible just in front of me as I lay still. There were generally 10–30 flies in this area at any given moment. This area was part of a small cove about 10 m across. Because major movements of my body disturbed the flies, some observations were recorded only after a behavioral sequence had ended, and approximate times of under 30 sec were estimated by counting off seconds; longer times were determined using a watch. Not all behavioral patterns were checked during each interaction, so sample sizes for different patterns differ.

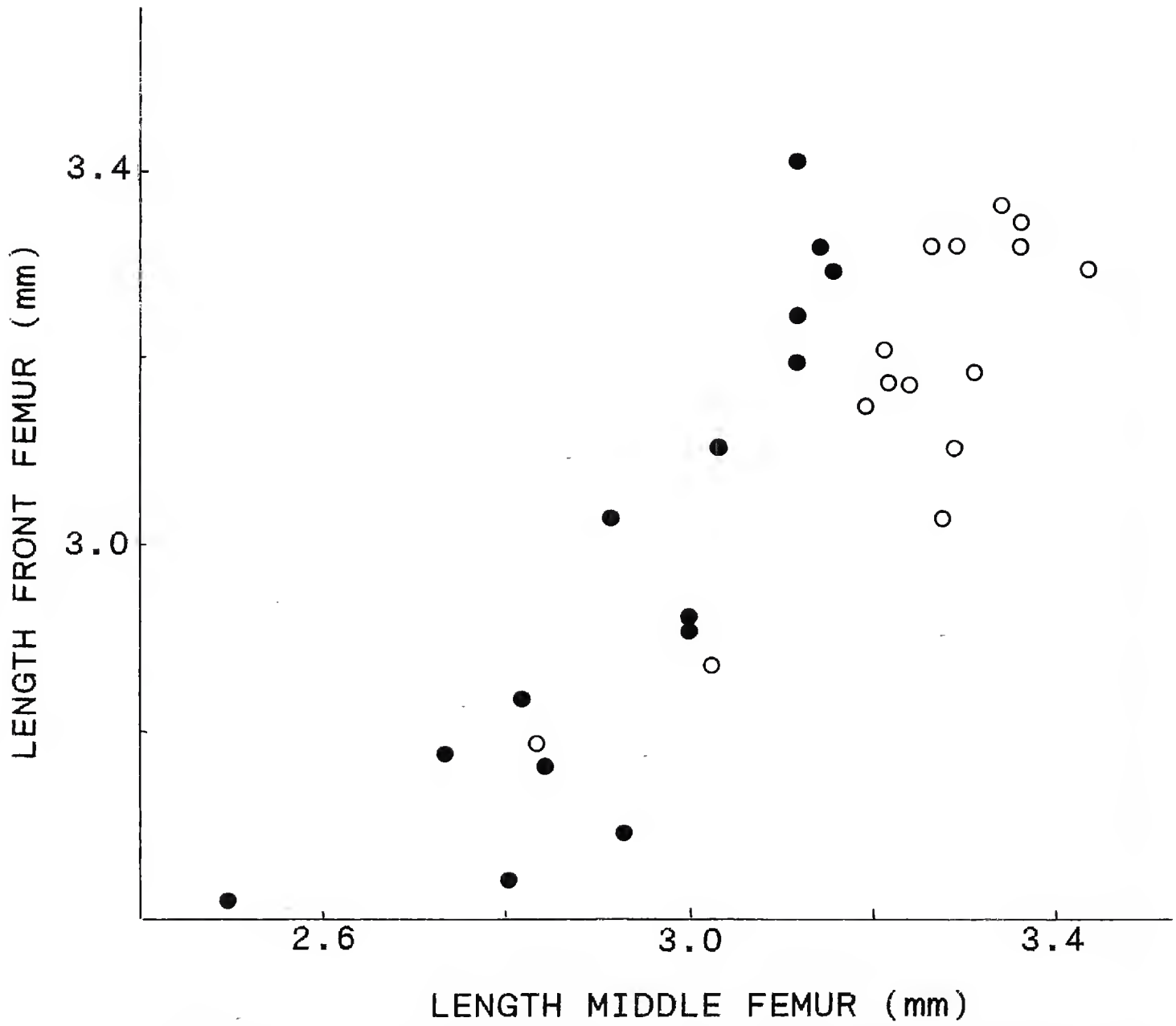

Figure 1. Relation between length of middle and front femur in 15 males (dark circles) and 15 females (open circles) of *O. occidentalis*. The males tended to be smaller, but had front femora of proportionally larger size.

Males and females could not be distinguished reliably in the field on the basis of their morphology. The sex of some individuals was established, however, on the basis of their behavior (males identified on the basis of having mounted another fly, females on the basis of having been mounted and copulated); by following the activity of these individuals it was possible to determine the sex of individuals performing some types of behavior.

Results

Sex Differences in Morphology.—Males at the study site differed from females in having a series of strong setae on the ventral surface of the hind femur. Males were somewhat smaller than females (mean head width was 2.71 ± 0.14 mm in males, and 2.89 ± 0.10 in females) ($P = 0.001$ with Kolmogorov-Smirnov Test). Male front femora were proportionally longer than those of females (Fig. 1) ($P = 0.028$ with Kolmogorov-Smirnov Test comparing ratios of front and middle femora of males vs. females). Both sexes had dense pads of hairs on their hind basitarsi.

General Activity.—Most flies were more or less continuously active, walking over the surface of the mud with their bodies held more or less horizontal, tapping

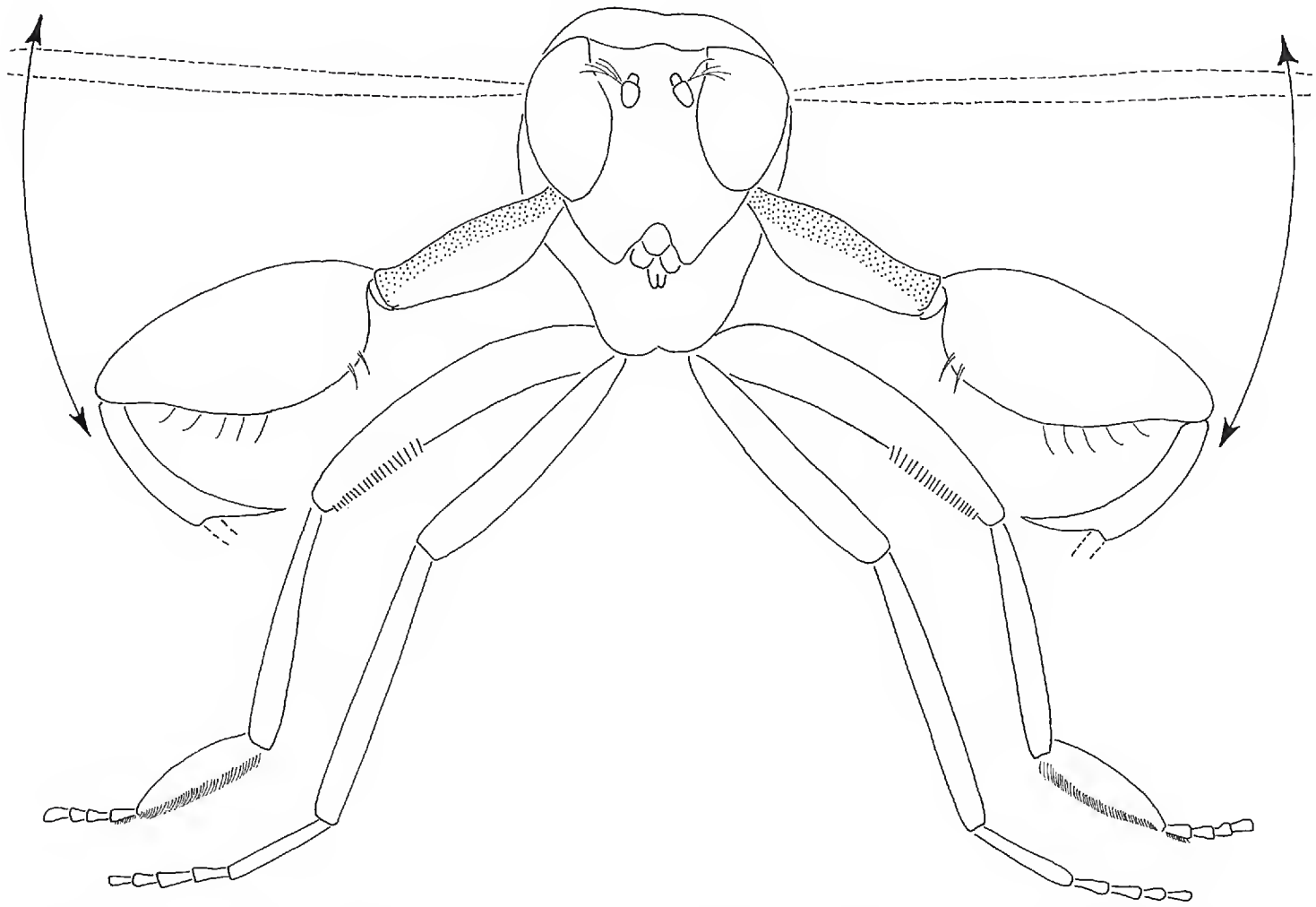

Figure 2. Stylized drawing of a male *O. occidentalis* with its forelegs spread to perform a vibration threat movement (arrows). Positions of front tarsi were not determined, and the tarsi are thus omitted. Stippled areas on front coxae are areas of silvery pile; in life the rest of the front coxae, femora, and tibiae are jet black. The wings (dashed lines) were sometimes vibrated during these displays.

rapidly up and down with their partially extended forelegs. A few paused immobile for several minutes at a time, with their bodies directed upward at about 30° with horizontal. Occasionally they flew, but usually only when frightened by my movements.

Aggressive Interactions.—Aggressive behavior began when one individual turned toward another nearby, and (usually) spread one or both wings. The forelegs were also spread horizontally so the shiny patch of white hairs at the base of the coxae and the flat, black prolateral surfaces of the expanded femur were directed toward the other individual (Fig. 2). The forelegs were waved up and down (Fig. 2), and also partially opened and closed. If the other individual moved away, the aggressor sometimes followed behind for a short distance. Threats of this sort were performed both to other *O. occidentalis* flies, and to much larger cicindellid beetles and saldid bugs.

Sometimes a threatened fly responded with a threat of its own. The two flies moved together until they stood head to head, each with its forelegs spread laterally. Both vibrated their forelegs up and down very rapidly, keeping them in the spread position. Often one or both also spread its wings and buzzed them. Sometimes the flies also pushed against each other with their heads. After no more than 1–2 sec, one of the flies walked or flew away, sometimes pursued briefly by the other.

Aggressive interactions were very common. Some males which were observed for 1–2 min seemed to be especially aggressive, either threatening or courting

every fly they encountered. Such males consistently caused other flies to withdraw. They did not, however, defend any specific site, but instead wandered slowly over the surface of the mud along with the rest of the flies. Quantitative data were not taken, but it appeared that females, at least just after copulating (when I was able to determine their sex), were less aggressive than males, although they also waved their forelegs aggressively.

Precopulatory Courtship.—Males sometimes jumped onto females' backs without any preliminary interaction. More often, however, a male followed behind a female for up to several seconds, keeping his body's long axis parallel to hers and his head about one to two head lengths behind the tip of her abdomen. His forelegs extended forward and vibrated rapidly up and down. The tips of the male's front tibiae or his front tarsi probably contacted the female's abdomen during these vibrations, but I was unable to confirm this. The male moved briskly to maintain his orientation and distance as the female moved and turned. Occasionally such a following male made an apparent attempt to stop the female by moving quickly in front of her, turning toward her and waving his front legs (females sometimes stopped moving forward when a male did this). The male then moved behind her again and resumed foreleg vibrations.

Mounting and Copulation.—In the next stage in courtship, the male jumped onto the female's back, always from the rear. Nearly always the female immediately swung her body violently from side to side in an apparent attempt to dislodge the male. There were additional rapid movements at this time, but the only one I was able to decipher was that the female usually (perhaps always) clawed at the fly on her back by reaching up and backward with her forelegs.

The female usually succeeded in displacing the male, and moved on, with the male either being left behind or following again at her rear, vibrating his forelegs. If the male was not dislodged within a second or two, the female became quiet. Other than brief turns toward approaching flies or other insects, and occasional waves of her forelegs, the female did not move during the rest of the time the male was mounted.

Once a female that had been mounted became quiet, the overall sequence of behavior was the same (19 cases observed carefully). The male immediately began rubbing her with his hind legs, using brief bursts of very rapid movements which lasted approximately 1 sec, interspersed with pauses which lasted on the order of one to several sec. The female's wings were slightly spread so that the tips of the male's hind tibiae and his hind tarsi touched the dorsal surface of her abdomen. Rubbing was performed on the dorsal and lateral portions of the posterior one quarter of the female's abdomen; contact was also made with the posterior margins of the female's wings. Each time the male began to rub, he raised his abdomen slightly, producing a small space between his abdomen and that of the female. The male's forelegs were folded against the anterior portion of his body, apparently out of contact with the female. Mounted males were never attacked or even threatened by other flies, although in a few cases another male vibrated his forelegs rapidly for less than a second at the rear of the female. A female with a mounted male was apparently less likely to flee when I moved than were other nearby flies, but females sometimes flew up to 2–3 m with a riding male when disturbed.

After 150–210 sec (n = 3), the mounted male always (19 of 19 cases) moved slightly posteriorly on the female and lowered the tip of his abdomen, and coupled his genitalia with hers. Genitalic coupling lasted an average of 23 ± 6 sec (n =

12). During this time the male always (15 of 15 cases checked for this detail) rubbed intermittently on the dorsal surfaces of the distal portions of the female's wings with his hind tarsi. The rubbing movements were similar to those of abdominal rubbing, but were less vigorous and perhaps also less rapid. In the latter part of copulation pauses between bursts of rubbing were shorter, with the male rubbing almost continuously.

During the last 2–4 sec of genitalic coupling, the female often (9 of 10 cases checked for this detail) waggled her abdomen. These movements were less energetic than those when a male first mounted. The male, perhaps in response to the waggling, dismounted by stepping backward. On several occasions, it was clear that his genitalia remained attached to hers after he stepped back, so that his abdomen was briefly bent forward under his body until uncoupling occurred. There were no further interactions, and the male immediately began moving his front legs and walked away. The female generally stood and groomed for several seconds, then also moved away.

A female that had just mated was often investigated by other flies which turned away immediately after brief contact with the tip of her abdomen. Occasionally, however, a male began following her, vibrated his forelegs and attempted to mount. None of the observed attempts was successful. It seems likely, however, that females do remate, and probably often, given the limited numbers of females present in the cove, the infrequency with which they flew away, and the substantial number of copulations I observed. One female that I followed for 5–10 min after a copulation ate three different prey, was approached and then immediately deserted by seven other flies, and was followed at least briefly with foreleg vibrations by seven others.

Feeding.—Flies moving across the mud tapping with their forelegs occasionally paused and touched the substrate with their mouthparts for approximately 1 sec. Usually I could not see that they obtained food in this way, but on two occasions a fly pulled a shining yellow cylindrical object (probably an insect larva) out of the mud as it raised its mouthparts. These larvae were approximately one quarter of the volume of the fly's head. These and four other food items were supported near the mouth by the prolateral surfaces of the front femora. None of the food items was identifiable, other than an adult ceratopogonid fly that I succeeded in collecting. In one case, a fly ate part of a yellow "larva" and then dropped it and moved away.

Oviposition.—At least five different flies performed what appeared to be oviposition. With the tip of the abdomen pressed to the mud, the fly vibrated its entire body forward and backward very rapidly for about 1–2 sec. Toward the end of this period the fly also rapidly scraped its hind tarsi on the mud, apparently pushing material toward the point where its abdomen touched the mud. Other flies passing near ovipositing individuals neither courted nor threatened them. After an oviposition, the fly moved away, and did not oviposit in the next few minutes.

Discussion

Female rejection of males was much more common than copulation, and overt rejection always occurred before, rather than after, the male began the prolonged and energetic precopulatory rubbing of her abdomen. Thus both this behavior and wing rubbing, which always occurred after the male had achieved intromis-

sion, apparently served to influence female behavior other than initial acceptance of intromission.

Copulatory courtship behavior is different in the other species of *Ochthera* that has been observed. Male *O. mantis* (DeGeer) push intermittently on the substrate with the hind legs during copulation, producing a rhythmic rocking motion of the pair (Simpson 1975), rather than rubbing the female's hind wings as in *O. occidentalis*. Duration of mating is also about ten times longer in *O. mantis* than in *O. occidentalis*. This apparently rapid divergence in copulatory courtship in closely related species is in accord with the hypothesis that it is under sexual selection (Eberhard 1991). Precopulatory courtship also differs between *Ochthera* species. The male of *O. mantis* rubs the female's genitalia for extended periods (Simpson 1975) rather than the dorsal and lateral portions of her abdomen, and prior to mounting males of both *O. mantis* and *O. exculpta* Loew face the female rather than trailing behind her (Simpson 1975).

The functional significance of two secondary sexual structures of males is suggested by the observations reported here. The row of setae on the male hind femur may rake across the posterior edge of the female's wing during precopulatory abdomen rubbing. The relatively longer front femora of males may be related to male–male aggressive displays, in particular the rapid up and down vibrations of front legs during frontal confrontations.

Several observations agree with previous accounts of other *Ochthera* species. In *O. mantis, O. tuberculata* Loew, and *O. exculpta* waving or semaphoring movements of front legs occur in both males and females, and are directed toward both conspecifics and other species (Deonier 1974, Simpson 1975). Waving exposes the fine, silver-colored pile on the inner surfaces of the front legs, including the UV reflective portion of the fore-coxae (Deonier 1974). This behavior has been taken to be courtship (Deonier 1974, Simpson 1975), but the displays by both male and female *O. occidentalis* to species such as cicindellid beetles support a second suggestion by Simpson (1975) that the movements represent threats. Female rejection of mounted males by swinging her body and pushing with her forelegs was similar in *O. exculpta* to that described here for *O. occidentalis*.

Simpson (1975) mentions that conspecific *O. mantis* males sometimes "batter" each other with their forelegs; this may correspond to the rapid up and down vibrations described here. The functional significance of the frequent threat behavior of *O. occidentalis* remains a mystery, since males did not defend either territories or females from other males.

Acknowledgment

I am grateful to Wayne N. Mathis for kindly identifying specimens, and help with literature. Mary Jane West-Eberhard commented on a preliminary version of the manuscript. My trip to Mexico was financed by the Centro de Ecología of the Universidad Nacional Autónoma de México, and my research was supported by the Smithsonian Tropical Research Institute and the Vicerrectoría de Investigación of the Universidad de Costa Rica.

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Received 19 September 1991; accepted 15 January 1992.

PAN-PACIFIC ENTOMOLOGIST
68(4): 268–278, (1992)

SEASONAL VARIATION IN ALLOPATRIC POPULATIONS OF *ISCHNURA DENTICOLLIS* (BURMEISTER) AND *ISCHNURA GEMINA* (KENNEDY) (ODONATA: COENAGRIONIDAE)

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Abstract.—We morphometrically evaluate the seasonal variation within two species of damselflies, *Ischnura gemina* (Kennedy) and *Ischnura denticollis* (Burmeister) in allopatry, in order to determine whether the same morphometric characters will be useful species discriminators in an *I. denticollis* and *I. gemina* hybrid zone. Canonical analysis of discriminance reveals that for both species, early emerging individuals are larger with wider heads than those that emerge later. In addition, each species displays other individual patterns of seasonal variation. Both damselfly species are phenetically distinct despite pronounced seasonal variation; this indicates that the morphometric characters used in this study are potentially suitable for use in diagnosis of hybrid zone individuals.

Key Words.—Insecta, Odonata, *Ischnura,* seasonal variation, morphometrics

Seasonal variation within insect species can produce individuals that are remarkably different in a number of morphological characteristics. The full extent of seasonal variation should be quantified, if morphological comparisons are made between two different species that are known or suspected to vary seasonally. Quantification of this variation is essential when the same morphological characteristics that vary seasonally are also potentially useful in the diagnosis of individuals from a hybrid zone. In this study, we morphometrically evaluate the seasonal variation within two species of damselflies, *Ischnura gemina* (Kennedy) and *Ischnura denticollis* (Burmeister) in allopatry, in order to determine whether the same morphometric characters will be useful species discriminators in an *I. denticollis* and *I. gemina* hybrid zone (Leong 1989).

Ischnura gemina is an uncommon damselfly restricted to the San Francisco Bay Area, California (Garrison & Hafernik 1981a) and is a candidate for listing as a threatened species. *Ischnura denticollis,* however, is widespread throughout the western United States (Pritchard & Smith 1956). A known hybrid zone extends along the eastern and southeastern areas of the San Francisco Bay region (Leong 1989) and a recently found sympatric population occurs near Suisun Marsh, Solano Co., California (Hafernik, unpublished data). In allopatry, both species are distinguishable by differences in secondary genitalic structure (the abdominal appendages of males and the prothorax of females) (Kennedy 1917, Garrison & Hafernik 1981a), but in the hybrid zone, these differences break down. Consequently, morphometric characters may be more useful species discriminators than traditional genitalic characters in the hybrid zone.

Both species inhabit small pools, creeks or drainage canals throughout their life cycle. Adults of both species exhibit similar color patterns and are sexually di-

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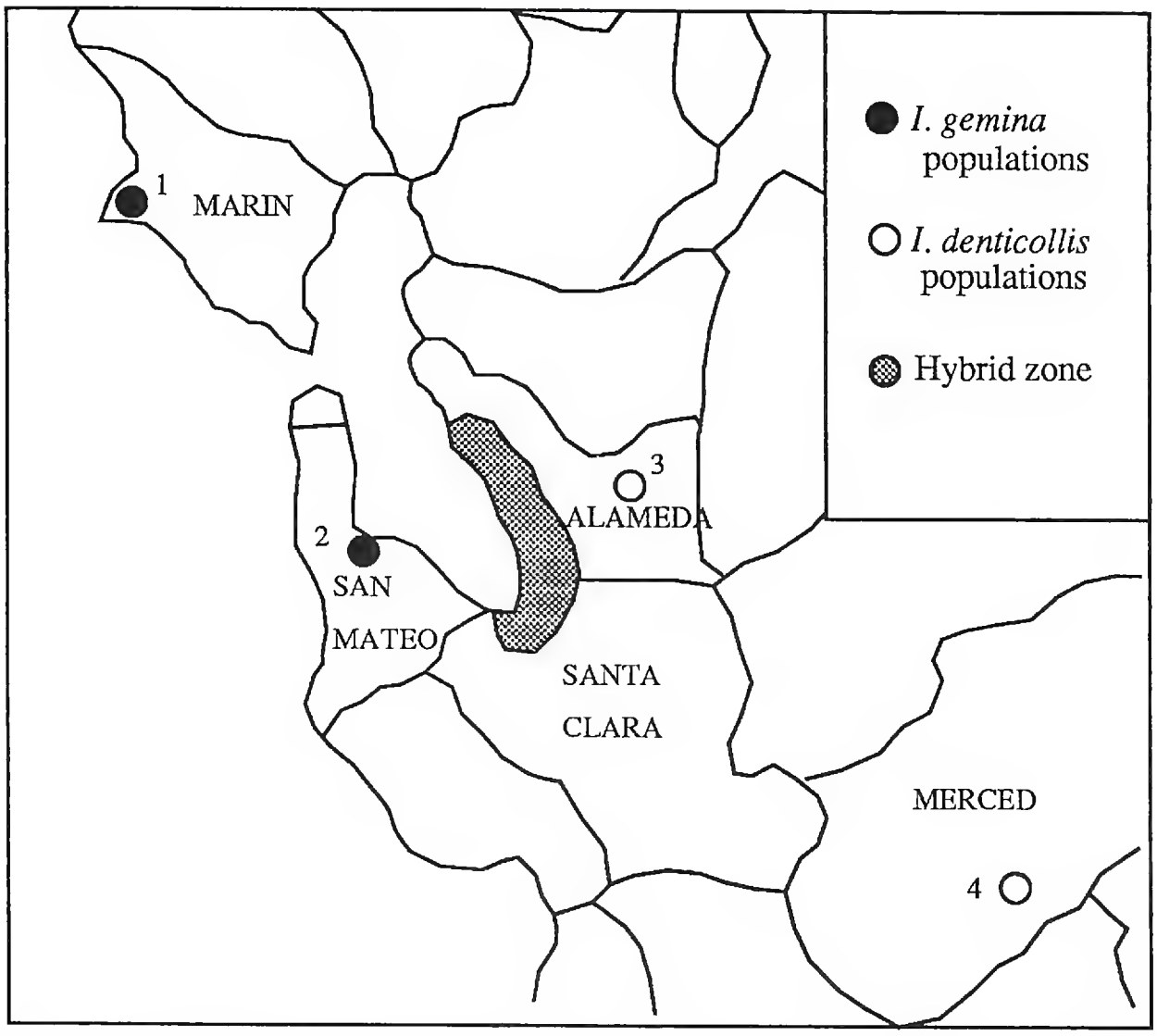


Figure 1. Location of populations sampled. Populations are numbered as follows: 1 = Point Reyes; 2 = Coyote Point; 3 = Livermore; 4 = Los Banos.

morphic; males are more brightly colored than females. Andromorph females, however, present an exception because they possess typical male color patterns. *Ischnura gemina* is slightly larger than *I. denticollis* and in both species, females are generally larger than males. Although some aspects of the life history, population structure (Garrison & Hafernik 1981b), and mating system of *I. gemina* (Hafernik & Garrison 1986; A. Balmy, unpublished data) are well known, the biology of *I. denticollis* is largely unknown.

Materials and Methods

We sampled two allopatric populations each of *I. gemina* and *I. denticollis* from August 1986 through October 1987 in the San Francisco Bay Area and in the Central Valley of California (Fig. 1 and Table 1). The Coyote Point population of *I. gemina* and the Livermore population of *I. denticollis* were chosen for two reasons: the known allopatric nature of these populations and their proximity to the hybrid zone. Three of the four populations were situated at the vegetated margins of lentic drainage canals and creeks, while the Point Reyes population was located along the edge of a coastal lagoon. We collected samples of 12–16 adult males and 7–17 adult females from each population per sampling period.

The Point Reyes population of *I. gemina* and the Los Banos population of *I. denticollis* were sampled as controls to determine whether or not the Coyote Point and Livermore populations represent typical *I. gemina* and *I. denticollis* popu-

Table 1. Populations of *Ischnura* studied.

Locality	Date	Season	Males	Females	Sample
I. gemina					
Marin Co.: Point Reyes Abbotts Lagoon	8 Sep 1987	Late 1987	14	12	PR
San Mateo Co.: Coyote Point channel along Airport Blvd.	11 Aug 1986	Middle 1986	12	10	CM86
	30 Apr 1987	Early 1987	12	7	CE87
	14 Jul 1987	Middle 1987	14	4	CM87
	3 Aug 1987	Middle 1987	2	4	CM87
I. denticollis	8 Aug 1986	Middle 1986	15	1	LM86
Alameda Co.: Livermore Las Positas Creek along Airway Blvd.	7 Sep 1986	Middle 1986	—	9	LM86
	24 Apr 1987	Early 1987	13	8	LE87
	16 Jul 1987	Middle 1987	12	10	LM87
	24 Sep 1987	Late 1987	16	17	LL87
Merced Co.: Los Banos channel near Billy Wright Rd.	4 Oct 1987	Late 1987	14	7	LB

lations. This comparison is important because a population morphologically deviant from the control probably lacks variation that is representative of the species, and would thereby serve as a poor reference group for defining the morphometric characteristics of each species.

We evaluated the importance of seasonal variation within populations by sampling the *I. gemina* Coyote Point and *I. denticollis* Livermore populations an additional two to three times (Table 1). In order to compare effectively temporal variation in these two populations, we collected the pairs of samples synchronously: in August and early September of 1986 and at six to nine week intervals during the 1987 flight season (March through October). Because the life span of *I. gemina* in the field, including maturation time, is as long as four to six weeks (Garrison & Hafernik 1981b; Hafernik & Garrison 1986), we chose a minimum six week sampling interval to insure that individuals that were sampled later in the season did not belong to the cohort sampled previously. Because the lifespan

Table 2. Characters used in multivariate analyses.

Character	Description
Thorax length (TH1)	Length along dorsal median ridge of thorax
Thorax width (TH2)	Greatest width across mesepimera
Thorax depth (TH3)	Distance from posterior corner of metacoxa to dorsal surface of thorax
Head width (H1)	Greatest width between inner margins of eyes along posterior edge of occiput
Head length (H5)	Length from anterior edge of frons to posterior edge of occiput
Wing length (L1)	Length from nodus to outer edge of pterostigma along the coastal margin of the right forewing
Wing width (W1)	Width from nodus to the distal edge of the second antenodal postquadrangular crossvein of the right forewing
Wing crossvein count (C1)	Number of postnodal crossveins on the right forewing between R1 and M1 excluding the nodus and the brace vein
Tibia length (T1)	Length from proximal process to distal end of the right protibia
Tibial spine count (C2)	Number of spines along the medial edge of the right protibia

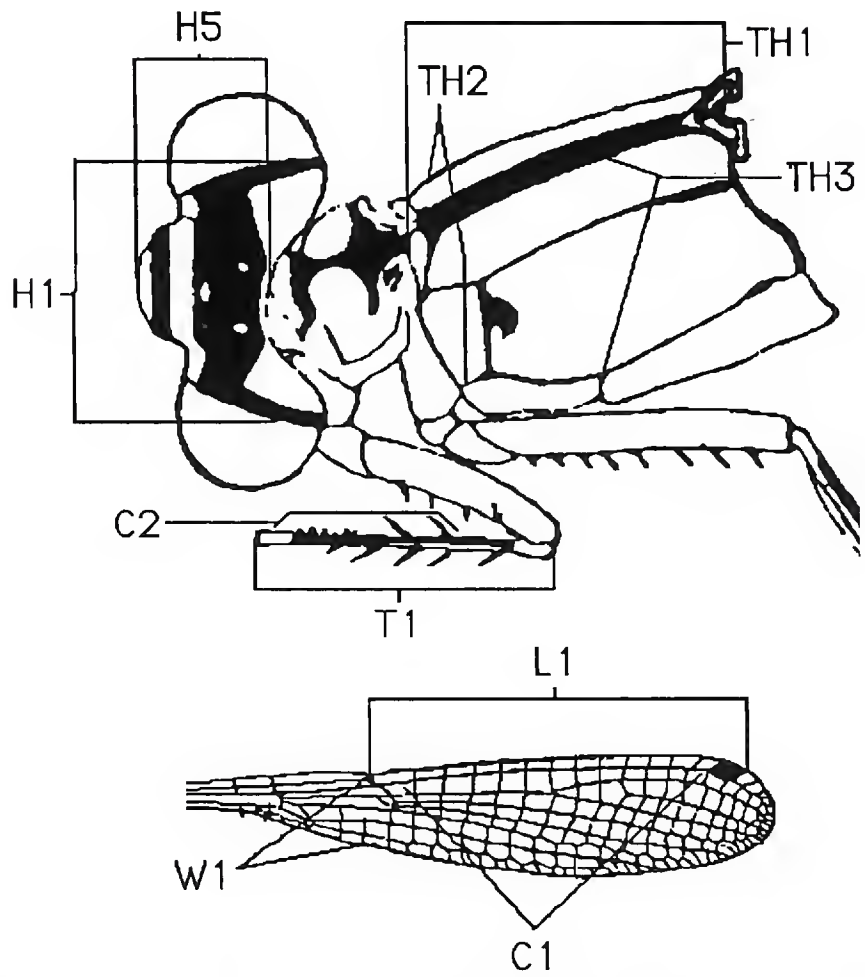


Figure 2. Characters measured. Top figure and bottom figure after Kennedy (1915) and Kennedy (1917), respectively.

of *I. denticollis* is unknown, we assumed that it is similar to *I. gemina.* Sampling dates were categorized as early, middle or late to facilitate comparisons. In two cases, the middle Coyote Point 1987 and the middle Livermore 1986 samples, two samples taken within the six week sampling interval were combined due to small sample sizes of one sex.

Eight continuous characters and two count characters were measured for all individuals (Table 2 and Fig. 2). We did not include body length in the multivariate analyses since it is highly correlated with thorax length ($r = 0.95$ for females; $r = 0.91$ for males). We selected these characters to represent the major shape and size attributes of the damselflies. We measured continuous characters to the nearest 0.03 mm using an ocular micrometer and high correlations between repeated measurements (see test-retest reliability, Kachigan 1986) confirmed the reliability of the eight continuous measurements ($0.96 < r < 0.99$; $P < 0.05$; $n = 66$).

A total of 89 females and 124 males were used in canonical analysis of discriminance, a type of discriminant analysis (Pimentel 1979). We analyzed sexes separately to control for sexual size dimorphism. However, we did not analyze andromorph females (those with male coloration) separately because they were not significantly different from heteromorph females in any of the measured characters. We used the Multigroup Discriminant Analysis program in BIOSTAT II (Pimentel & Smith 1986) to analyze the morphometric data. The standardized canonical analysis of discriminance of normal scores model (Pimentel 1979, Pimemtel & Smith 1986) was used to interpret the data because both continuous and count characters were included. Each sample listed in Table 1 was entered as a separate group for a total of nine groups.

Multivariate analysis of variance, classification and distance analysis were also

Table 3. Canonical vector coefficients and the percentage of variance explained by each canonical variate.

Character	Females		Males	
	CV 1	CV 2	CV 1	CV 2
TH1	1.379	0.884	−0.277	0.979
TH2	−0.548	0.486	−0.229	−0.95
TH3	0.523	0.780	0.031	−0.363
H1	−0.965	−0.267	1.160	−0.679
H5	−0.312	0.390	0.335	0.607
L1	0.079	−0.14	−0.074	0.764
W1	−0.512	−0.324	0.041	−0.121
C1	−0.438	−0.271	0.490	−0.363
T1	−0.299	−1.373	−0.290	−0.443
C2	−0.326	−0.006	0.259	−0.170
% Variance	75.5%	11.0%	85.7%	6.1%

performed on these groups. Tests of the equality of centroids were checked for significance ($P < 0.005$) before running the canonical analysis of discriminance. Because the results from the distance analysis yielded results similar to the classification of groups, only classification will be discussed. Only the first two canonical variates are discussed because the succeeding axes, in sum, explained less than 14% of the total variation and displayed no discernable patterns.

All specimens are deposited in the Entomology Museum, San Francisco State University, San Francisco, California.

Results

Canonical variate analysis readily distinguishes *I. denticollis* and *I. gemina.* In both sexes, the samples form discrete clusters along the first canonical variate only (Figs. 3A, 3B), although in males, one *I. gemina* male from Point Reyes is situated at the edge of the *I. denticollis* cluster (Fig. 3B). Characters that are most important in distinguishing between groups along this axis are those with high standardized canonical vector coefficients (Table 3). For females, thorax length, head width and to a lesser extent thorax width and wing width are most important; but for males, head width and the number of wing crossveins are important. The sign of a coefficient indicates the direction in which the character is increasing in magnitude; characters with positive coefficients increase as the axis increases and those with negative coefficients decrease. Thus, the position of both species along with first canonical variate reveals that *I. gemina* females are characterized by wider heads, thoraces and wings relative to thorax length (Fig. 3A). Similarly, *I. gemina* males are characterized by relatively wider heads and greater number of wing crossveins (Fig. 3B). Variation on the first canonical variate accounts for 75.5% of the total variation in females and 85.7% in males (Table 3). Additionally, all individuals were classified to the correct species, except for the *I. gemina* male mentioned above.

Vectors of mixed sign generally indicate that differences in shape rather than size define separation between groups. In both sexes, individuals along the first axis are not ordered by absolute size (Figs. 3A, 3B). Head, thorax and wing width, however, are moderately to highly correlated with thorax length ($0.76 < r < 0.95$)

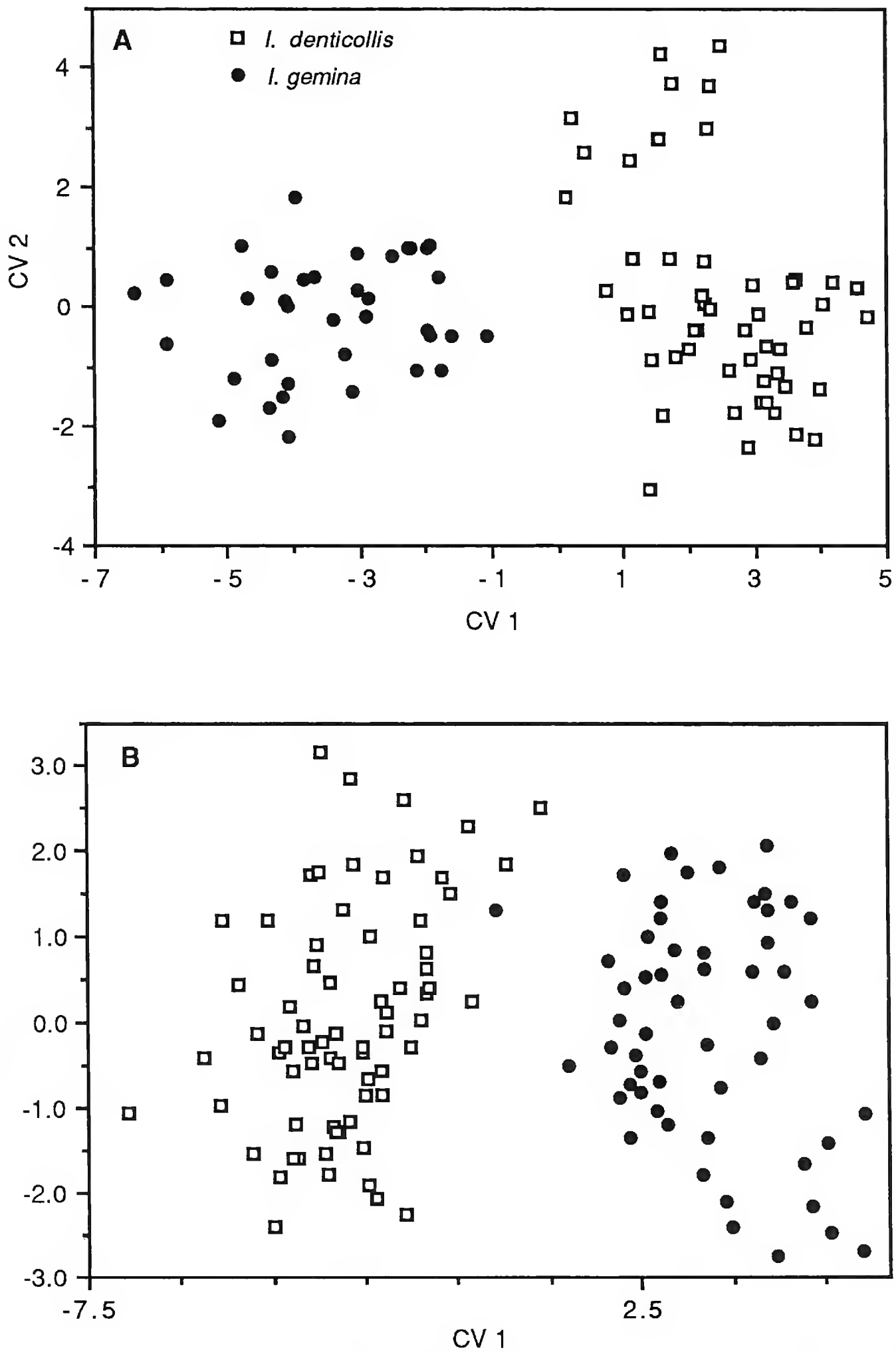


Figure 3. Plot of the first and second canonical variate scores of all individuals. A. Females. B. Males.

which, in turn, is highly correlated with body size. This suggests that the first axis represents a combination of size and shape differences (Table 3). Inspection of the coefficients for the second and third vectors indicates that these axes reflect size and shape differences as well.

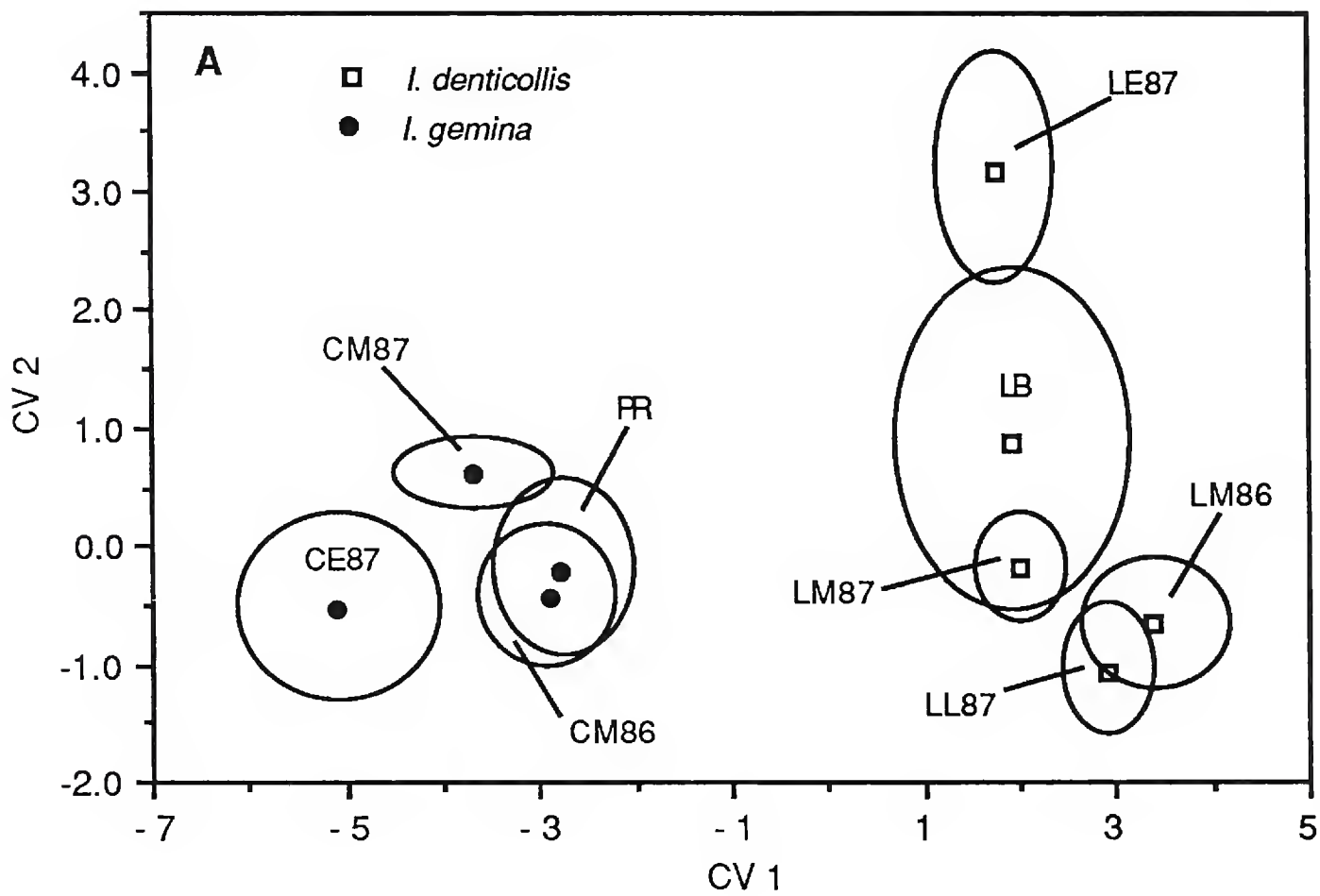
The *I. denticollis* Livermore and the *I. gemina* Coyote Point samples exhibit several pronounced patterns of seasonal variation. In *I. gemina* females and males of both species, the same characters that define interspecific differences also distinguish earlier emerging individuals from later ones within the same population. These seasonal changes are evident by the ordering of the Livermore and Coyote Point sample centroids and 95% confidence ellipses along the first axis (Figs. 4A, 4B). In particular, this axis distinguishes early emerging *I. gemina* females (Fig. 4A). All earlier emerging individuals possess proportionately wider heads; in addition, *I. gemina* females have proportionately wider thoraces and wings but earlier emerging males have a greater number of wing crossveins (Table 3). In *I. denticollis* females, however, the early, middle and late Livermore centroids are not clearly differentiated on the first canonical variate.

The second canonical variate also represents a pattern of seasonal variation that distinguishes earlier emerging individuals from later ones, but one that is more distinct than the previous pattern. The positions of the Livermore samples along the second canonical variate (Fig. 4A) reveal that earlier emerging *I. denticollis* females are differentiated from later seasonal samples by longer, wider and deeper thoraces and relatively shorter tibiae (Table 3). However, females from the *I. gemina* Coyote Point samples do not show this second seasonal pattern, and characters which discriminate early emerging *I. gemina* females from later ones are clearly different from those for *I. denticollis* females. In males, the positions of the Livermore and Coyote Point samples on the second axis indicate that the *I. denticollis* and *I. gemina* populations exhibit reversed seasonal patterns (Fig. 4B). Earlier emerging *I. gemina* individuals tend to possess proportionately shorter thoraces, heads and wings while earlier emerging *I. denticollis* males have proportionately longer thoraces, heads and wings (Table 3). The seasonal pattern represented by the second canonical variate explains 11.0% and 6.1% of the total variation in females and males respectively.

The classification of individuals to the correct seasonal population sample provides another measure of the seasonal differentiation within the *I. denticollis* Livermore and *I. gemina* Coyote Point populations. Most females were classified correctly (84%) as were males (70%). Classification of females suggests that the *I. gemina* Coyote Point samples are more differentiated seasonally than the *I. denticollis* Livermore samples. Of the Coyote Point samples, only two individuals from the CE87 sample were misclassified whereas three of the four Livermore samples had two individuals misclassified each. Only one female from the LE87 sample was misclassified, and *I. denticollis* females from other samples were never misclassified as LE87.

Classification of males reveals that they are less seasonally differentiated than females. The Coyote Point samples had four to five misclassifications each except for CE87, which had only one misclassification. Similarly, the Livermore samples had four to seven misclassifications each except for LE87, which had only one misclassification.

The morphometric characterization of the *I. gemina* Point Reyes and *I. den-*



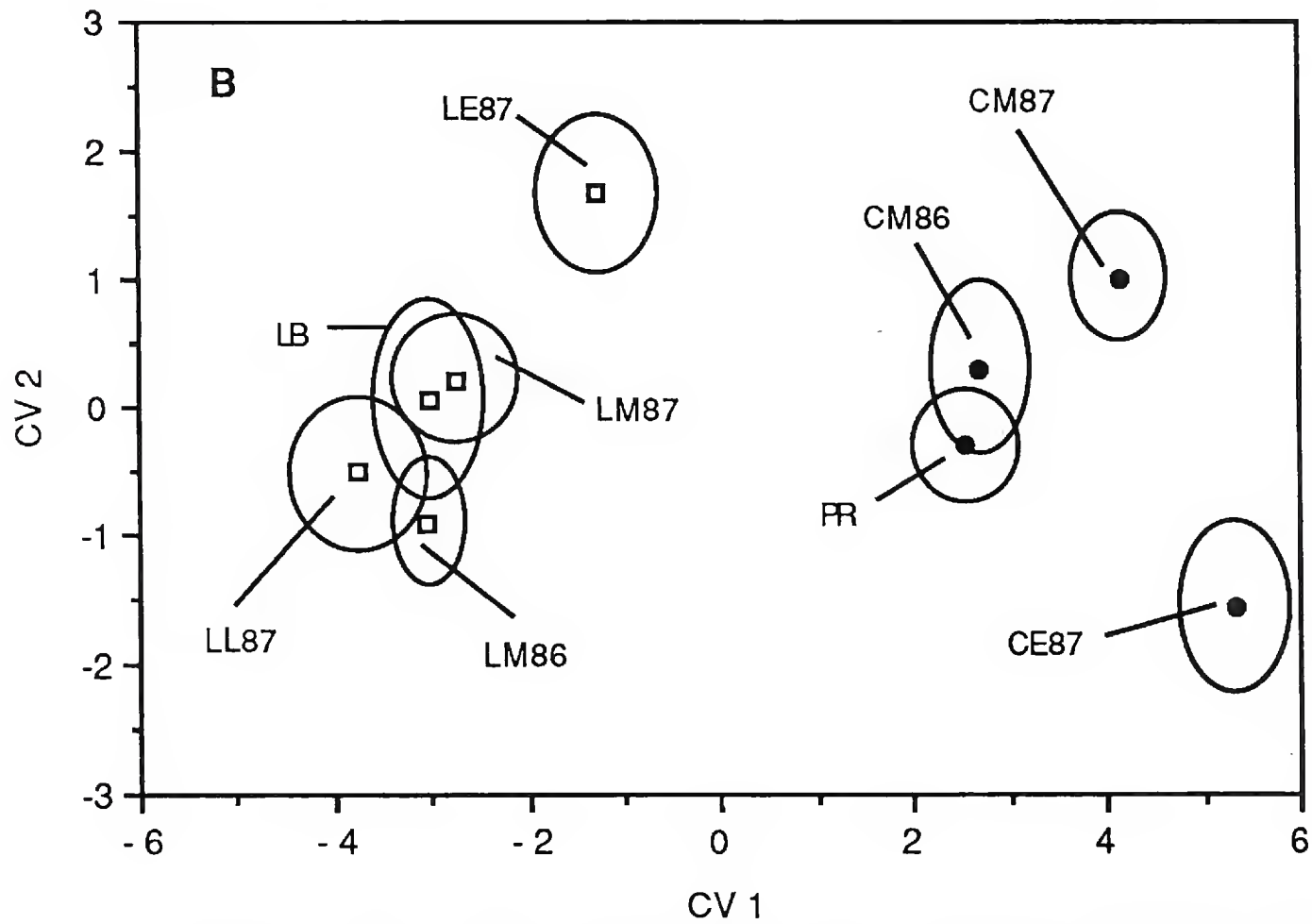


Figure 4. Sample centroids and 95% confidence ellipses from the t distribution of canonical variate scores of CV1 and CV2. A. Females. B. Males. Sample abbreviations as in Table 1.

ticollis Los Banos populations suggests that the Coyote Point and Livermore populations are not atypical *I. gemina* and *I. denticollis* populations. Since both the Point Reyes and Los Banos samples overlap considerably with the Coyote Point and Livermore samples, respectively, on the first and second canonical variates (Figs. 4A, 4B), it is likely that the variation within the Coyote Point and Livermore populations is fairly representative of *I. gemina* and *I. denticollis.* It is difficult, however, to assess the full amount of interpopulational variation among the *I. gemina* Coyote Point and Point Reyes and *I. denticollis* Livermore and Los Banos populations because the Point Reyes and Los Banos populations were sampled only once.

Discussion

Canonical analysis of discriminance and classification of individuals reveal that *I. denticollis* and *I. gemina* are phenetically distinct despite the presence of strong seasonal variation within populations of both species. By sampling the *I. gemina* Coyote Point and *I. denticollis* Livermore populations repeatedly throughout the flight season, we have been able to thoroughly characterize, by morphometric means, the variation inherent in each population. This evidence indicates that the morphometric characters used in this study can be used to potentially diagnose individuals from the hybrid zone (Leong 1989). Therefore, for females, thorax length and head width may be more useful species discriminators than the structure of the prothorax, which is difficult to assess in the hybrid zone. Similarly, for males, head width and number of wing crossveins may be more useful species discriminators than the structure of the abdominal appendages. In addition, these morphometric characters have the advantage over traditional genitalic characters of being easily quantifiable, whereas differences in prothoracic or abdominal appendage structure are not.

The large amount of seasonal variation within the *I. gemina* Coyote Point and *I. denticollis* Livermore populations suggests that most of the morphometric variation in these populations is environmentally induced. The range of morphometric responses to environmental conditions seems to be limited, however, because both species are phenetically distinct. Variation in proportional head width is the predominant seasonal difference in both species and because it is correlated with overall body size, *I. gemina* and *I. denticollis* individuals also show a decrease in body size with later emergence. Similar patterns of seasonal size decrease commonly occur in natural populations of odonates (Dumont & Dumont 1969, Banks & Thompson 1985, Harvey & Corbet 1985, Van Buskirk 1987a, Baker 1989), including *I. gemina* (A. Balmy, unpublished data).

In addition to changes in body size, our data show that more subtle patterns of seasonal variation occur in *I. gemina* and *I. denticollis* as indicated by differences on the second axis (Figs. 4A, 4B). Each species and each sex within each species display separate patterns of seasonal variation. This implies that phenotypic responses to environmental variation differ between the sexes as well as between the two species. However, because random outliers are particularly prone to confound the interpretation of patterns that account for a small portion of the total variance, it is possible that variation on the second axis may reflect some random noise.

The seasonal decrease in body size of later emerging adult *I. gemina* and *I.*

denticollis most likely reflects the differing environmental conditions experienced by individuals during larval development. The body size of adults does not change after emergence and mortality has been found to be random with respect to size (Van Buskirk 1987a; A. Balmy, unpublished data; J. E. Hafernik, Jr., unpublished data). It is, therefore, unlikely that the seasonal size differences found in adults are an artifact of some type of size-related selection on adults. Consequently, the seasonal differences in adult size must actually represent seasonal differences in larval size in the *I. gemina* Coyote Point and *I. denticollis* Livermore populations.

Several factors may account for seasonal differences in larval size. Experimental studies of larval odonates have demonstrated the separate effects that temperature, photoperiod and food availability have on the rate of larval development and larval size (Lutz 1968, 1974a, b; Thompson 1978; Lawton et al. 1980; Harvey & Corbet 1985). Other studies have concluded that larval density affects larval size through interference competition which reduces larval feeding rates (Johnson et al. 1984, Pierce et al. 1985, Van Buskirk 1987b). Baker (1989), however, found no evidence to support this conclusion. Unfortunately, little is known about how the synergistic effect of all these factors affect larval, and thus adult size in natural populations. Harvey & Corbet (1985) suggest that overwintering in the final instar somehow causes an increase in larval size because this cohort subsequently gives rise to the larger early emerging adults. Perhaps environmental conditions experienced by the final instar most heavily influence adult size.

Acknowledgment

We thank S. C. Williams, V. T. Parker, R. W. Garrison and P. S. Ward for their helpful comments. Valuable discussions were provided by A. Balmy and D. Herlocker. This research was supported in part by a Sigma Xi Grant-in-Aid of Research.

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Received 10 October 1991; accepted 15 January 1992.

PAN-PACIFIC ENTOMOLOGIST
68(4): 279–280, (1992)

Scientific Note

"BAJA CALIFORNIA NORTE": A CASE FOR "GEOGRAPHICAL INEXACTITUDE"

We address herein Snelling's (Snelling, R. R. 1987. Pan-Pacific Entomol., 63: 339–340) concern for certain nomenclature of the Mexican peninsula, Baja California—"geographical inexactitude," as he called it. His main complaint was that the widespread use of "Baja California Norte" (BCN) for the northern state, Baja California (BC), is "geopolitically incorrect." It may thus be, but it certainly is "geo-logically" correct and readily serves to distinguish the state from the peninsula. Snelling proposed the anglicized, anachronistic "Lower California" to designate the peninsula, and his argument for its "historical precedent" in the entomological literature is specious.

The confusion stems from the old peninsular territories attaining statehood, the history and terminology of which was inaccurately discussed by Snelling. According to W. Michael Mathes (in litt.), in 1930 the peninsula was divided into Baja California, Territorio Norte and Baja California, Territorio Sur (no "del" included). The northern unit became a state (BC) in 1953 (not 1952), the southern unit a state (BCS) in 1975 (not 1974).

We looked at approximately 50 references dating from 1950, mostly biological, and all but one used BC as the name for the peninsula. However, many were not exempt from the problems which Snelling addressed, namely that locality data have been presented in a number of confusing ways. Some of this stems from an author's failure to properly, if at all, distinguish the peninsula from a state thereof. To confuse BCS would be inexcusable. The northern state (BC) is not so easy. Much past confusion probably cannot be clarified and it seems naive to think that all will be reconciled in the future. The use of BCN provides complete clarification; however, purists will persist. According to W. Michael Mathes (in litt.), many Mexican deputies and senators have attempted the necessary constitutional amendment to no avail.

Despite the foregoing we feel that Snelling clouds the main issue, which is to effect accurate labeling of specimens. Often the primary difficulty is not identifying the state, but locating a specific place therein. We agree with Snelling that a standardized format should be implemented and suggest the following parameters for scientific writing and specimen labels: 1) Baja California Norte to be unofficially adopted to avoid confusion—Mexican and U.S. colleagues to whom we have talked or written agree. 2) The peninsula must retain its proper Mexican name, Baja California, but this should not be used alone or on labels; therefore, those that persist in using BC can be interpreted as having collected in the northern state. 3) "Baja" and "Baja Sur," terms incorrectly attributed by Snelling as commonly used by Mexicans, should never be used. 4) **Most importantly,** for most localities latitude and longitude should be placed on specimen labels. High quality topographic maps are available which simplify this task. Besides clarification, the addition of these coordinates obviates the need to interpret "BC"!

Acknowledgment.—For valuable information and discussion, we thank P. E.

Blom, University of Idaho, Moscow; R. D. Bratz, Albertson College of Idaho, Caldwell; W. M. Mathes, Sutro Library, San Francisco, California; and B. Villa R., Universidad Nacional Autónoma de México, Mexico City.

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Received 5 April 1991; accepted 12 July 1991.

PAN-PACIFIC ENTOMOLOGIST
68(4): 280–281, (1992)

Scientific Note

NEW RECORD OF THE BLOWFLY, *CHRYSOMYA MEGACEPHALA* (FABR.), FROM ECUADOR (DIPTERA: CALLIPHORIDAE)

The Oriental Latrine Fly, *Chrysomya megacephala* (Fabr.) is an Old World blowfly that has been introduced into the Western Hemisphere within the past two decades. It has been reported from Argentina, Brazil, Paraguay, Peru and Venezuela in the Neotropical Region. It is established in Mexico and southern California in the Nearctic. We recently found evidence that *C. megacephala* is also present in Ecuador, a new Neotropical record for this species.

Our examination of frozen fillets of mahi mahi (dophinfish) imported from Ecuador found an adult female *C. megacephala* embedded in a fillet, beneath an exterior coating of ice glace. The mahi mahi fillets had been prepared, glaced and frozen in Guayaquil, Ecuador, prior to shipment to Los Angeles, California, where the fillets were examined. The entire shipment of fillets is documented as having been continuously held in frozen storage at 0° C from the time it left Ecuador until we examined it. The fillet that we examined was prepared in Ecuador in 1989 or earlier. Because the specimen of *C. megacephala* was found underneath the original ice glace, we conclude that it came from Ecuador along with the fillet. We also conclude that *C. megacephala* has been present in Ecuador for over a year, based on the packing date of the fillet that we examined. This is the first time that we have observed *C. megacephala* on mahi mahi, although it has been recorded from other varieties of seafood. It is also the first indication that this species has extended its Neotropical range into Ecuador. Wherever this filth fly occurs, public health officials are concerned over the role that this species may play in the transmission of foodborne pathogens and other diseases.

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Received 25 June 1991; accepted 12 July 1991.

PAN-PACIFIC ENTOMOLOGIST
68(4): 281–282, (1992)

Scientific Note

PASSALUS (*PERTINAX*) *PUNCTATOSTRIATUS* PERCHERON (COLEOPTERA: PASSALIDAE) IN THE SIERRA DE MANANTLAN, JALISCO, MEXICO

As a contribution to the knowledge of the Sierra de Manantlán passalid fauna (Castillo, C. et al. 1988. Acta Zool. Mex. (ns), 30: 1–20) an additional record of *Passalus* (*Pertinax*) *punctatostriatus* Percheron is reported. This Passalini species has a wide distribution and is found from México, south to Venezuela, Colombia and Brazil. In eastern México, its range follows the gulf coast plain north to the Sierra Madre Oriental (Reyes-Castillo, P. 1970. Folia Entomol. Mex., 20–22: 1–240), while in the west it is limited to the tropics from Guerrero, south to Chiapas; it occurs from sea level to 1400 m. This species has a large environmental tolerance and is found in evergreen tropical forests, humid pine oak forests, cloud forests, secondary forests and coffee cultures.

We found it in decaying logs, under bark and in heartwood, where decomposition varied widely, from incipient to high. There is no apparent preference for tree species selected for nest building; individuals can be found even in decomposed fruits, which underscores the species' great plasticity.

In the Biosphere Reserve of Manantlán in southwestern Jalisco, 12 adults were found in the localities of El Puerto de Los Mazos (cloud forest), El Tigre and La Calera (subdeciduous tropical forest). Two separate reproducing couples collected in October 1989 and February 1990, and kept under ideal laboratory conditions, produced broods in April and May. The brood sizes were three and 14. Additional observations in other parts of the country yielded an average brood size value for the species of 6.11 ± 4.6 ($n = 76$). Groups of larvae and adults have been collected together showing the characteristic subsocial behavior attributed to the family.

In Sierra de Manantlán the reproduction period is prolonged. Under laboratory conditions couples copulated from the end of March to the middle of April, and at the beginning of October individuals were collected from all the development stages. This agrees with the general pattern found in many species of passalids, where reproductive periods extend throughout the year without pronounced seasonality. Likewise, the copulation behavior observed is similar to the generalized

copulation behavior pattern of other passalid species (Castillo, M. L. & P. Reyes-Castillo. 1989. Coleopts. Bull., 43: 162–164).

The localities El Tigre (19°39′47″ N, 104°25′51″ W), La Calera (19°39′26″ N, 104°25′45″ W) and El Puerto de Los Mazos (19°41′56″ N, 104°23′29″ W) are found in the northwest portion of the Sierra de Manantlán Biosphere Reserve between 700 and 1350 m and present a high species diversity of animals and plants because of the homogeneous temperature, relative humidity and rainfall throughout the year.

In Los Tuxtlas, Veracruz, *P.* (*P.*) *punctatostriatus* had the highest frequency of occurrence (32.2%) of the 14 passalid species observed (Castillo, M. L. 1987. Tesis de Licenciatura. Facultad de Ciencias, Universidad Nacional Autónoma de México). The abundance and diversity of the passalid fauna from the Sierra de Manantlán is unknown, but the number of species documented is lower than in Los Tuxtlas; this record brings the total to five species.

Material Examined.—MEXICO. *JALISCO:* Biosphere Reserve of Manantlán, El Puerto de Los Mazos, 15 km (SW) of Autlán, 1350 m, 16 Oct 1989, L. E. Rivera Cervantes, 1 male, 2 females; same reserve, El Tigre, 12 km (SW) of Autlán, 700 m, 5 Feb 1990, M. L. Castillo and L. E. Rivera Cervantes, 1 male, 2 females; same reserve, La Calera, 10 km (SW) of Autlán, 760 m, 4 Feb 1990, M. L. Castillo and L. E. Rivera Cervantes, 3 males, 3 females.

Acknowledgment.—We thank Pedro Reyes-Castillo for comments on an earlier draft of this note. This work was supported by CONACYT, México, contribution 05 to the program "Diagnóstico y Conservación de la Biodiversidad en México. Subproyecto Biodiversidad de Cinco Grupos de Insectos," and "Estudios Ecológicos de los Coleópteros Degradadores de la Sierra de Manantlán" supported by Universidad de Guadalajara and the WWF, U.S.A.

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Received 26 August 1991; accepted 1 December 1991.

PAN-PACIFIC ENTOMOLOGIST
68(4): 283, (1992)

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