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The Pan-Pacific Entomologist

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Pacific Coast Entomological Society

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PACIFIC COAST ENTOMOLOGICAL SOCIETY

Organized 15 August 1901

ARTICLES OF INCORPORATION

Know all men by these presents:

That we, the undersigned, do hereby voluntarily associate ourselves together for the purpose of forming a nonprofit corporation under the laws of the State of California, and we hereby certify that:

First: The name of this corporation shall be the Pacific Coast Entomological Society.

Second: The purposes for which this corporation is formed are to promote, sponsor, foster, and stimulate research in the field of entomology; to provide facilities and opportunities for research and analysis of any and all phases of entomology by lectures, forums, discussions, symposia, and analyses; to publish books, pamphlets, monographs, and in general to disseminate information about entomology and the results of entomological research; to accumulate and record historical facts and materials relating to entomology in general; to give, grant, and sponsor the granting of fellowships and awards for study or research in the field of entomology; and research in entomology between the members of this corporation and scientists and entomologists throughout the world. To do any and all things necessary, suitable, convenient, or proper for or in connection with or incidental to the accomplishment of any of the purposes, or the attainment of any one or more of the objects herein enumerated or designed, directly or indirectly to promote the interests of this corporation, and to do any and all things and to exercise any and all powers which may now or hereafter be lawful for this corporation to do or to exercise under the laws of the State of California; *provided, however* that this corporation is and shall be a corporation which does not contemplate pecuniary gain or profits to the members thereof. No part of the net earnings of this corporation shall inure to the benefit of any member whatsoever, and no part of the activities of this corporation shall be or constitute carrying on propaganda or otherwise attempting to influence legislation.

Third: The county in the State of California where the principal office for the transaction of the business of this corporation is to be located is the City and County of San Francisco.

Fourth: The number of this corporation's directors who shall be known as the members of the Executive Board of this corporation is eleven (11), and the names and addresses of the persons who are to act in the capacity of members of the Executive Board until election of their successors are:

E. Gorton Linsley, University of California, Berkeley
H. M. Armitage, State Dept. of Agriculture, San Francisco
Peter C. Ting, State Dept. of Agriculture, San Francisco
E. R. Leach, 217 Hillside Avenue, Piedmont, California
R. L. Usinger, University of California, Berkeley
E. O. Essig, University of California, Berkeley
Gordon F. Ferris, Stanford University, California
Edward S. Ross, California Acad. of Sciences, San Francisco
Carl S. Duncan, San Jose State College, California

The number of members of the Executive Board may be changed from time to time by the bylaws duly adopted; *provided, however*, that the number of the members of the Executive Board shall not be less than three (3).

Fifth: The authorized number and qualifications of the members of this corporation, the different classes of membership, if any, the property, voting, and other rights and privileges of each class of membership, and the liability of each and all classes of members to dues and assessments, and the method of collection thereof, shall be as set forth in the bylaws of this corporation.

Sixth: The name of the existing unincorporated association which is hereby being incorporated is Pacific Coast Entomological Society.

Seventh: The property of this corporation is irrevocably dedicated to educational and scientific purposes and no part of net income or assets of this organization shall ever enure to the benefit of any director, officer, or member thereof or to the benefit of any private persons. Upon dissolution or winding up of the corporation, its assets, remaining after payment of, or provisions for payment of,

all debts and liabilities of this corporation, shall be distributed to the California Academy of Sciences, located in San Francisco, California, a nonprofit corporation which has established its tax-exempt status under Section 501(c)(3) of the Internal Revenue Code of 1954. In the event the Academy or any successor organization is not in existence or is not tax-exempt under Section 501(c)(3), distribution shall be made to a nonprofit fund, foundation, or corporation which has established its tax-exempt status under Section 501(c)(3) of the Internal Revenue Code of 1954.

If this corporation holds any assets in trust, or the corporation is formed for charitable purposes, such assets shall be disposed of in such a manner as may be directed by decree of the superior court of the city in which the corporation has its principal office, upon petition therefore by the Attorney General or by a person concerned in the liquidation, in a proceeding to which the Attorney General is a party.

In Witness Whereof, the president and secretary of the Pacific Coast Entomological Society, an existing unincorporated association, have hereunto set their hands this 28th day of August, 1940.

E. Gorton Linsley
President of Pacific Coast Entomological
Society, an Existing Unincorporated
Association

Peter C. Ting
Secretary of Pacific Coast Entomological
Society, an Existing Unincorporated
Association

Endorsed and filed in the
office of the Secretary of
State of the State of California,
11 September 1940.

Paul Peek, *Secretary of State*
By Chas. J. Hagerty, *Deputy*

BYLAWS

Incorporating Amendments dated 16 February 1951; 28 November 1953; 29 October 1955; 15 February 1963; 12 November 1965; 15 October 1971; 19 December 1975; 19 January 1979; 16 November 1979; 14 December 1990.

ARTICLE I

Offices

Section 1. The principal office for the transaction of the purposes of the corporation is hereby fixed at the California Academy of Sciences, Golden Gate Park, in the City and County of San Francisco, State of California. The Executive Board is hereby granted full power and authority to change said principal office from one location to another in said county.

ARTICLE II

Executive Board

Section 1. Subject to the limitations of the Articles of Incorporation, the Bylaws, and the laws of the State of California, all corporate powers shall be exercised under the authority of the board of directors who shall be known as and who are herein designated as the members of the Executive Board of the corporation. Without prejudice to such general powers, but subject to the same limitations, it is hereby expressly declared that the Executive Board shall have the following powers:

First: to select or remove all other officers, agents, and employees of the corporation, prescribe such powers and duties for them as may not be inconsistent with law, with the Articles of Incorporation, or Bylaws, fix their compensation and require from them security for faithful service.

Second: To make such rules and regulations in respect to the management of the affairs of the corporation not inconsistent with law, with the Articles of Incorporation, or Bylaws, as they deem best.

The action of the members of the Executive Board shall be subject to the holders of the membership of the Society and none of its acts shall conflict with action authorized by such membership.

Sec. 2. The authorized number of members of the Executive Board shall be eleven (11) until changed by an amendment of the Articles of Incorporation or by an amendment of this section as provided by law.

Sec. 3. The Executive Board members shall consist of the chairpersons of standing committees, the officers of the Society, and the editors of The Pan-Pacific Entomologist. In the event that one person holds two or more of the above positions, additional members-at-large shall be elected in the same manner as the regular elective officers, to fill the Executive Board of eleven (11) members. The members of the Executive Board who shall be officers of the Society shall serve until the next annual meeting of the members of the Society, and until their successors are duly elected and qualified. The members of the Executive Board who serve as such because of their positions as chairpersons of the standing committees shall serve until their successors have been appointed by the president and confirmed by the Executive Board, and have qualified.

Sec. 4. Meetings of the members of the Executive Board for any purpose or purposes shall be called at any time by the president, or if he is absent, unable or refuses to act, by any three (3) members of the Executive Board. Notice of the time and place of any such meetings shall be given so that it will be delivered to the Board members or to their addresses at least twenty-four (24) hours prior to the time fixed for such meetings but preferably seven (7) days or more in advance.

Sec. 5. The Executive Board shall fill, by appointments, any vacancies occurring in any elective office between annual elections.

Sec. 6. At least six (6) members of the Executive Board shall be necessary to constitute a quorum for the transaction of business. Every act or decision done or made by a majority of the members of the Executive Board shall be the act of the Executive Board unless a greater number be required by law or by the Articles of Incorporation.

ARTICLE III

Officers

Section 1. The officers of the Society shall be a president, president-elect, managing secretary, recording secretary, and treasurer.

Sec. 2. At the last regular meeting prior to the annual meeting, a nominating committee of at least three members shall be appointed by the president from among those members who are not holding any elective office at the time and who did not serve on the nominating committee of the previous year. It shall be the duty of this committee to nominate candidates for the offices to be filled at the annual meeting. Nominations may likewise be made from the floor.

Sec. 3. The president, president-elect, managing secretary, recording secretary, and treasurer shall be elected by a majority of the members present at the annual meeting to serve for one (1) year, their term in office beginning with the close of the annual meeting at which they were elected, and until their successors are elected and qualified.

Sec. 4. The president and president-elect shall hold office for no longer than two consecutive years but are eligible for re-election after the lapse of one year from the time of leaving office. The managing secretary and treasurer shall be selected with a view to continuity of tenure of their offices, and hence, other things being equal, may be re-elected each year, subject to their own desires in the matter.

Sec. 5. No member shall hold more than one elective office at one time.

Sec. 6. Vacancies occurring in any elective office between annual elections shall be filled by action of the Executive Board.

ARTICLE IV

Duties of Officers

Section 1. The president shall preside at all meetings of the Executive Board and regular meetings of the membership. He/she shall appoint temporary committees including a nominating committee, appoint members to fill vacancies in standing committees, act as *ex officio* member of all standing committees, appoint a new Program Committee and its chairperson soon after taking office and during

his/her term of office may replace any members as necessary, arrange details of meetings in cooperation with the Program Committee, and call any special meetings. The president shall, at the regular meeting prior to the annual meeting, appoint an Auditing Committee, no member of which is an officer of the Society, to review the financial records of the Society and to report to the members of the Society at the annual meeting. At the annual meeting he/she shall appoint two (2) members to the Publication Committee to replace retiring members, and name the Chairperson, report on the state of the Society, and deliver an annual address.

Sec. 2. The president-elect shall assume all responsibilities of the president in the event of the temporary absence of the latter. The president and president-elect being absent, a chairperson may be selected *pro tempore* from among the members present. The temporary chairperson shall conduct such business as is absolutely necessary, postponing consideration of other matters until such time as the regular officers may be in attendance.

Sec. 3. The managing secretary shall send out notices of all meetings at the order of the president, handle all correspondence of the Society, and keep a record of past and current members. He/she shall maintain a supply of copies of the Articles of Incorporation and the Bylaws, including new amendments, and shall furnish a copy to each new member of the Executive Board, and to other members of the Executive Board at their request. The recording secretary shall keep a list of members and visitors present at each meeting, and of the proceedings of said meetings, and submit an edited manuscript of the proceedings for each year to be published preferably in the October number of the following year's Pan-Pacific Entomologist.

Sec. 4. The treasurer shall handle all financial matters of the Society and shall maintain bank accounts in the Society's name. Current receipts, unless otherwise specified, become a part of the general funds of the Society, administered by the Executive Board through the treasurer who is hereby granted authority to expend the money necessary to send out notices of meetings and to defray expenses, send out bills, etc., in connection with publications of the Society and such other necessary expenses of the Society as are approved by the Executive Board.

ARTICLE V

Committees

Section 1. Standing committees shall include the following: Publication Committee, Program Committee, Historical Committee, and Membership Committee. The president shall be invited to each meeting of a standing committee as an *ex officio* member. The chairperson shall call the meetings and preside. The membership of these committees may be reviewed at any meeting of the Executive Board, which may make such changes as may be deemed necessary. Committee vacancies occurring between Executive Board meetings may be filled by presidential appointment, subject to confirmation by the Executive Board at its next meeting.

Sec. 2. The Publication Committee shall be responsible for the publications of the Society. It shall consist of six members appointed by the president for three-year terms, groups of two expiring in successive years. The Publication Committee shall meet at least once a year before the annual meeting to formulate an annual report for the Society. Four members shall constitute a quorum.

Sec. 3. The Historical Committee of five members shall cooperate with the California Academy of Sciences in accumulating historical entomological material to be deposited with the Academy.

Sec. 4. The Membership Committee of three members shall consult with applicants or prospective members, acquaint them with the purposes of the Society and with the obligations incurred with membership, and consider such persons and propose their names, if satisfactory, to the Society for election to membership. It shall further be the duty of the committee to consider members' applications for student status and to review the membership from time to time for persons to be nominated as Honored Members. The Committee shall meet at least once, early in the year, to establish a new list of nonmembers, including organizations, to whom Society meeting announcements shall be sent, in an effort to increase membership and meeting attendance. The chairperson shall provide the managing secretary with a copy of the list and retain a copy for the committee records.

Sec. 5. The Program Committee shall plan the various meetings, including the field days, arrange for speakers, encourage members to bring exhibits, and contribute short notes and observations, and improve the meetings of the Society in other ways. The chairperson shall call all meetings of the committee after consultation with the president. The committee shall inform the managing secretary of the Society as to the programs of the meetings in sufficient time to permit the issuing of the specific notices of the meetings.

Sec. 6. Prior to the annual meeting of the Society, the chairperson of each standing committee shall contact the members of his/her committee and determine whether or not each wishes to continue his/her committee service for another year. Each chairperson shall then immediately notify the president, in writing, whether or not members have resigned for the following year. Committee vacancies known at this time shall be filled by appointment by the president not later than the next regular meeting of the membership.

ARTICLE VI

Members

Section 1. Membership shall be open to persons interested in insects or other Arthropoda.

Sec. 2. An applicant for membership will communicate with a member of the Membership Committee and pay his or her dues in advance. The Membership Committee shall then nominate the applicant for membership at the next regular meeting of the Society. An affirmative vote of two-thirds of the members present at any meeting is required, whereupon the applicant becomes a member. The chairperson shall furnish the managing secretary and treasurer with the names and mailing addresses of the newly-elected members.

Sec. 3. The Executive Board shall fix the annual dues for regular members and student members, the annual subscription rate for *The Pan-Pacific Entomologist*, and the prices for back issues of *The Pan-Pacific Entomologist* and other Society publications. Changes in dues, rates, and prices shall be announced at the next regular meeting of the Society and published in the proceedings. The dues are payable in advance. Each additional member (called a family member) in the immediate family of a regular member may pay dues of only \$1.00 per year, but this shall entitle said family to only one subscription to *The Pan-Pacific Entomologist*.

Sec. 4. Members at retirement with at least ten (10) years of active membership may, on request, be continued as active members without payment of dues. Moreover, such members, if they desire, may receive *The Pan-Pacific Entomologist* upon payment of one-half regular membership dues per year.

Sec. 5. Students registered at any school or recognized institution of higher learning are eligible for student membership. Student members shall have all the privileges of regular members.

Sec. 6. Any member who, through long and distinguished service to the Society, is deemed worthy of special recognition may be elected an Honored Member. Candidates for honored membership shall be nominated by the Membership Committee at the Society meeting prior to their election by the membership, or they may be elected directly by the Executive Board, with announcement of the election made at the next Society meeting and recorded in the Society's proceedings. Such members shall be free from the payment of dues or other financial obligations but shall retain all privileges of regular members.

Sec. 7. All members, except retired members or as herein otherwise provided, shall receive *The Pan-Pacific Entomologist* with no additional charge.

ARTICLE VII

Meetings

Section 1. At least four regular meetings shall be held each year, preferably with two in the fall and two in the spring, with an annual Field Day or equivalent. Regular notice of such meetings shall be given to each member at his or her request either personally or by mail, or other means of communication, charges prepaid, addressed to such member at his or her address, if any, appearing upon the books of the Society, or given by him or her to the Society for the purpose of notice. All such notices shall be sent to the members not less than ten (10) days before such meeting.

Sec. 2. Special meetings may be called at any time at the discretion of the president, or shall be called at the request of five members, provided that written notice is sent to all members at least two weeks in advance of the meeting.

Sec. 3. The December meeting of each year shall be known as the Annual Meeting. At this time, in addition to the election of officers and the transacting of other regular and special business, annual reports of all committees shall be submitted as well as an annual report of the treasurer.

Sec. 4. The presence in person of ten (10) members of the Society at any regular or special meeting shall constitute a quorum for the transaction of business, but less than a quorum may adjourn any meeting from time to time and the meeting may be held as adjournment without further notice.

ARTICLE VIII

Delegates

The Society may accredit delegates, appointed by the president, to national and international meetings such as the American Association for the Advancement of Science and the International Entomological Congresses. Members may be accredited by a two-thirds vote of the members present at any meeting.

ARTICLE IX

Amendments

These Bylaws may be amended or repealed by the Executive Board, subject always to the power of the members to change or repeal such Bylaws; or by the vote or written assent of a majority of the members; or by a majority of a quorum at a meeting of the members duly called for the purpose of amending the Bylaws.

**OMANONABIS: A NEW GENUS OF NABIDAE
(HETEROPTERA) FROM WESTERN NORTH AMERICA,
WITH A REVIEW OF *NABIS EDAX* BLATCHLEY**

ADAM ASQUITH AND JOHN D. LATTIN

Systematic Entomology Laboratory, Department of Entomology,
Oregon State University, Corvallis, Oregon 97331

Abstract.—*Omanonabis* NEW GENUS is proposed for the species *Nabis lovetti* Harris. Distinguishing features including illustrations of genitalia and scanning electron micrographs are provided. *Nabis edax* Blatchley is reviewed and distinguishing features, including illustrations of genitalia, are provided. Its morphology is compared with that of other species of *Nabis* and its taxonomic position is reevaluated.

Key Words.—Insecta, Heteroptera Nabidae, *Omanonabis*, *Nabis lovetti*, *Nabis edax*

Two species of Nabidae found along the Pacific coast of North America have puzzled heteropterists for some time, *Nabis lovetti* Harris and *Nabis edax* Blatchley. Harris recognized the distinctiveness of *lovetti* when he described it from California and Oregon in 1925, noting especially the dorsal pubescence, the spine-like tubercles on the genital capsule and the lance-like parameres. Even though Harris recognized subgenera of *Nabis* in his monograph of North American Nabidae (1928), he left *lovetti* in the nominal subgenus *Nabis* despite its unique characters. Although Mitri (1960) suggested that *lovetti* might deserve separate subgeneric placement based on its distinctive seminal depository, Henry & Lattin (1988) left it in the subgenus *Nabis* pending clarification of its proper position.

Nabis edax was described by Blatchley from Los Angeles, California in 1929, just after the appearance of Harris' monograph (1928). No other references to the species were published until Henry & Lattin (1988) retained it in the subgenus *Nabis* based on information received from Dr. Kerzhner of Leningrad. However, Mitri (1960) illustrated the female genitalia of a specimen from Alameda County, California, that could not be placed in any recognized species of North American *Nabis*; we now believe that this specimen represents *N. edax*. In this paper, we compare the morphology of these two species with other members of the genus *Nabis* and discuss their probable relationships, creating a new genus for *N. lovetti*.

**OMANONABIS ASQUITH & LATTIN, NEW GENUS
(Figs. 1-7)**

Type-Species.—*Nabis lovetti* Harris 1925:205 (California).

Description.—*Macropterous male:* Large, broadly linear, widest across middle of clavus; length (apex of tylus to apices of hemelytra) 7.9-9.1 mm. *Head:* Short, eyes large; ocelli raised above surface of vertex, but not prominent; head testaceous with broad median longitudinal black stripe. Ventral surface of head yellow, with two broad, longitudinal, pale fuscous stripes either side of midline. Antennal segment I slightly curved laterally, distal half slightly enlarged, yellow with ventral surface infuscated, with long, inclined, yellow setae. Antennal segment II linear, distinctly thinner than segment one, yellow with apex fuscous to black, with semierect, yellow setae. Segment III linear, testaceous; segment IV slightly but evenly enlarged distally, testaceous to black; both segments III and IV with semierect yellow setae. *Pronotum:* Campanulate, broader than long, widest across posterior margin; lateral

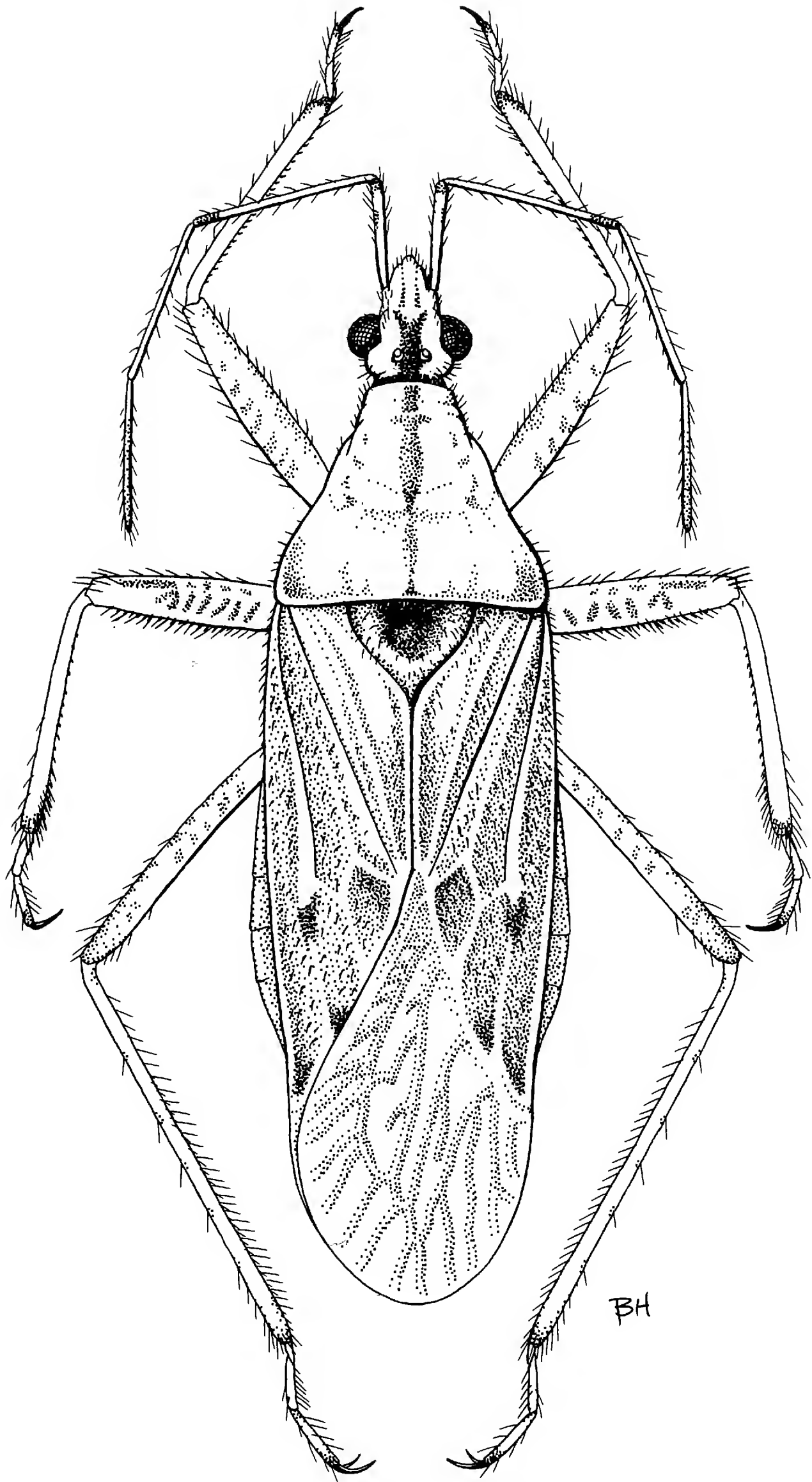


Figure 1. *Omanonabis lovetti* (Harris). Dorsal habitus.

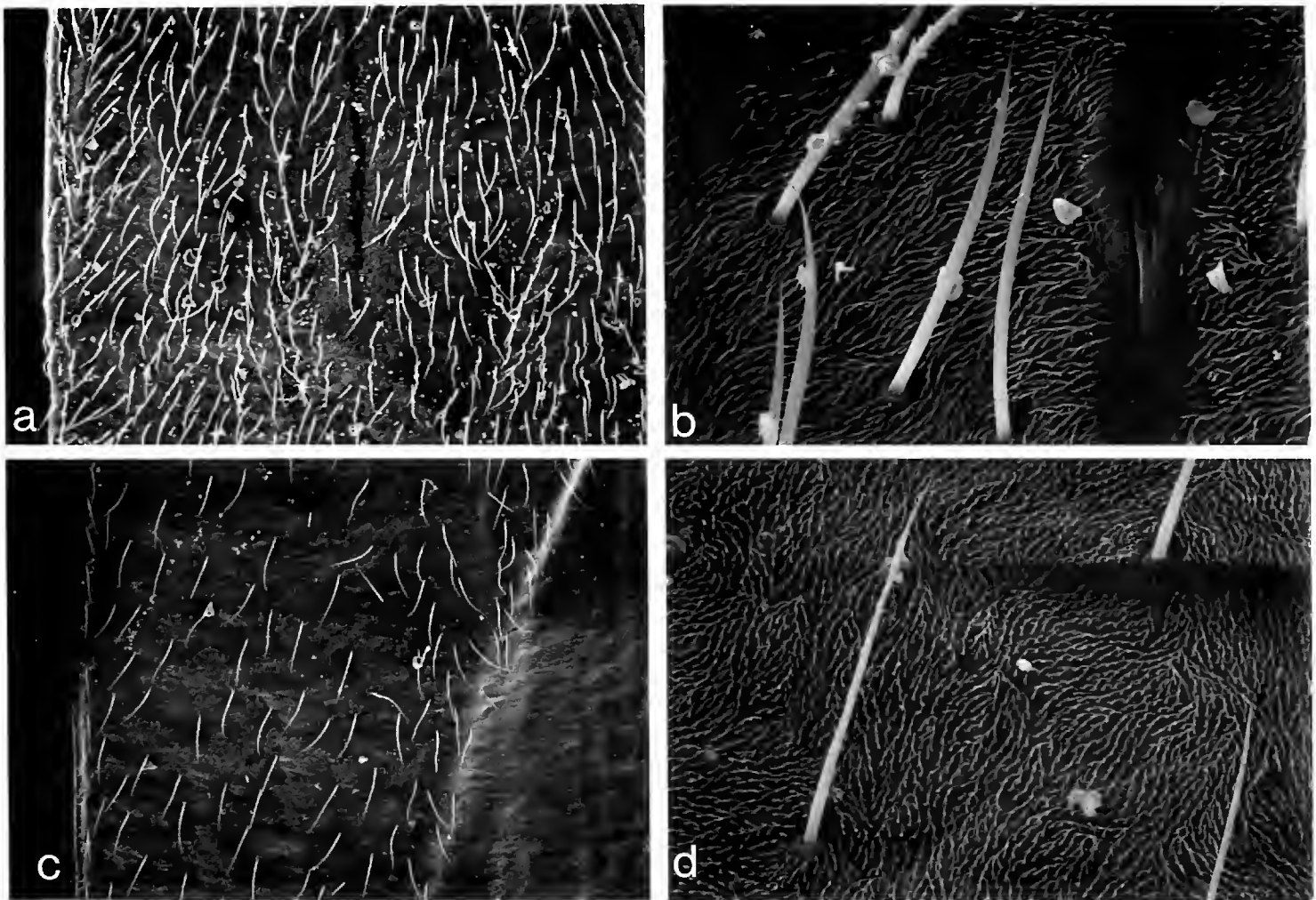


Figure 2. Hemelytral setae. a–b. *Omanonabis lovetti*. c–d. *Nabis roseipennis* Reuter.

margins slightly sinuous; posterior margin straight or slightly convex; posterior angles bluntly rounded; lateral and posterior margins weakly carinate. Collar distinct, length equal to width of eye, weakly punctate. Dorsal surface of anterior lobe with paired transverse rectangular areas either side of midline, surface slightly depressed, granulose. Posterior lobe with minute shallow punctures, dull yellow or testaceous, with fuscous median stripe; surface with short, reclined, golden setae and elongate, erect hairs. Scutellum broad, wider than long, two distinct fovea present either side of midline; fuscous, with anterior corners yellow; surface with short reclined golden setae and elongate erect hairs. *Hemelytra*: Elongate, tapering to apices; sides slightly arcuate, extending beyond end of abdomen; all veins distinctly elevated; anterior surface minutely, shallowly punctate; membrane with three closed cells, middle cell very narrow, gray-yellow, veins pale, bordered with fuscous; dorsal surface densely covered with short, reclined, golden setae (Fig. 2). *Venter*: Connexivum very broad, dorsolateral and midventral fuscous stripes running length of ventral surface. Lateral and ventral surface of abdomen with long, silver, silky pubescence. Channel of ostiolar peritreme very broad, surface smooth, dorsal half of posterior margin elevated and convex (Fig. 3). Tibiae relatively short. Apical pads on pro- and mesotibiae large, reaching to base of second tarsal segment. Profemora swollen, tapering distally. Mesofemora slightly enlarged, tapering distally; ventral surface with numerous long black teeth. Metafemora thick but not swollen, short, just reaching end of abdomen, slightly curved posteriorly. All appendages dotted with fuscous. Base of claws slightly swollen, occasionally with blunt tooth at base. *Genitalia*: Genital capsule extremely large, length equal to all anterior segments combined; anterolateral surface with small tooth on either side, oriented anteriorly (Fig. 4a). Posterior surface of genital capsule concave, with posterior corners rounded and slightly enlarged. Parameres very narrow and elongate with apex strongly recurved dorsally (Fig. 4b); lateral margin with strong keel; base of lateral surface with broad band of erect pale setae. Aedeagus long and narrow, twisted at middle, with four large sclerites (Fig. 5).

Brachypterous Male.—As macropterous male, except: more oval in outline, total length 7.2–8.3 mm. Pronotum more evenly triangular, less campanulate; posterior lobe narrower. Hemelytra narrow, connexivum visible in dorsal view, reaching to anterior margin of genital capsule; apex narrowed to blunt point; membrane with only two closed cells. Hind wings reaching to 4th or 5th abdominal tergite.



Figure 3. Left metathoracic scent gland of *Omanonabis lovetti*.

Female.—Similar to male, slightly smaller (Table 1), total length 7.2–8.6 mm. All antennal segments shorter than male. Hemelytra of macropterous form reaching to last abdominal tergite. *Genitalia*: Seminal depository oblong oval, basally constricted (Fig. 6); oviducts arise separately from dorsal surface, separated by a raised sclerotized structure; spermatheca prominent, arising baso-medially and directed basally to cover base of ovipositor. Two paired, elongate-oval sclerotized rings present on ventro-lateral surface.

Diagnosis.—This genus is readily distinguished by the short, dense, golden pubescence on the hemelytra (Fig. 2a); the broad, flat, anterior surface of the ostiolar peritreme (Fig. 3); the extremely large male genital capsule with spines present on the anterolateral margins (Fig. 4a), and the elongate, lanceolate parameres (Fig. 4b).

Etymology.—This genus is named in honor of our esteemed colleague, Dr. Paul Oman, Professor Emeritus of Entomology at Oregon State University. He has shared with us his vast knowledge of entomology and his friendship.

OMANONABIS LOVETTII (HARRIS) 1925:205, NEW COMBINATION

Type.—Holotype male, *Nabis lovetti* Harris. CALIFORNIA. SAN FRANCISCO Co.: Ingleside, 20 Dec 1920, H. Dietrich; deposited U.S. National Museum of Natural History, Washington, D.C.

Redescription.—*Male*.—Most characters as in generic description. *Genitalia*: Aedeagus with four large sclerites (Fig. 5); basalmost sclerite smallest, linear, gradually tapering distally with apex oriented towards apex of aedeagus; second sclerite just basad of twist in aedeagus, linear, slightly curved, widest at base, tapering to a sharp apex, oriented towards apex of aedeagus; third sclerite largest, linear, blade-shaped, distal half incompletely bifid into two blades, oriented towards apex of aedeagus; distalmost sclerite just basad of sclerotized “cap,” comb-shaped, with three large teeth of unequal shape and size. Aedeagus with two patches of minute denticles, one area just basad of middle twist, the other basad and underneath sclerotized “cap.”

Distribution.—This species occurs along the Pacific coast from southwestern

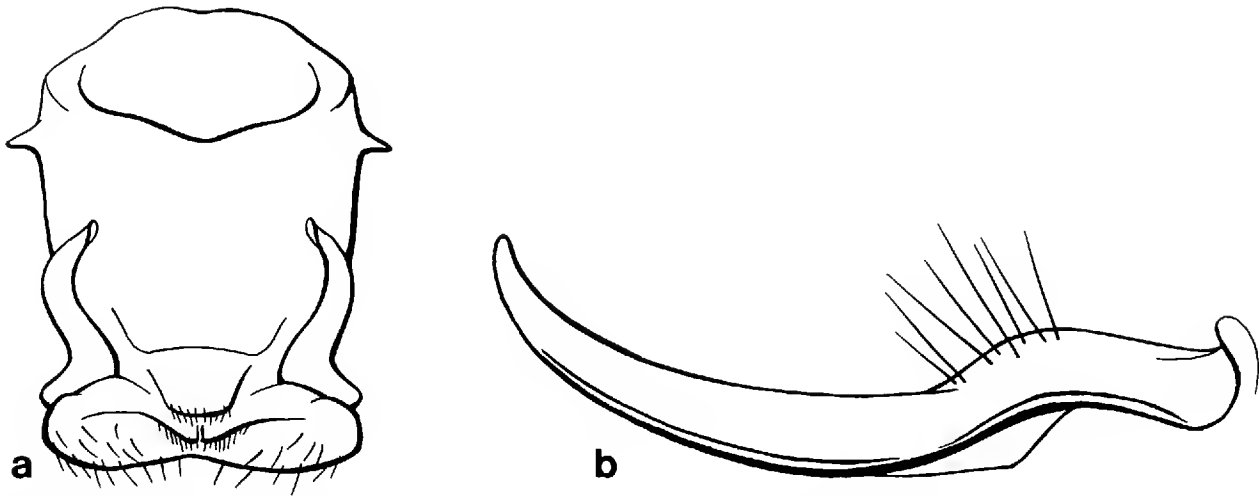


Figure 4. Genitalia of *Omanonabis lovetti*. a. Male genital capsule, dorsal view. b. Paramere, lateral view.

British Columbia (Scudder 1985) south to Monterey, California (Harris 1925, 1928) (Fig. 7). It is most common in the coastal salt marshes, and in the Willamette-Puget Lowlands, but is also found in a few marshy habitats east of the Cascade Mountains in southern Oregon. This species has also been reported from Lake Provo, Utah (Torre-Bueno 1934). This locality is greatly disjunct from the known range of *lovetti* and needs to be confirmed.

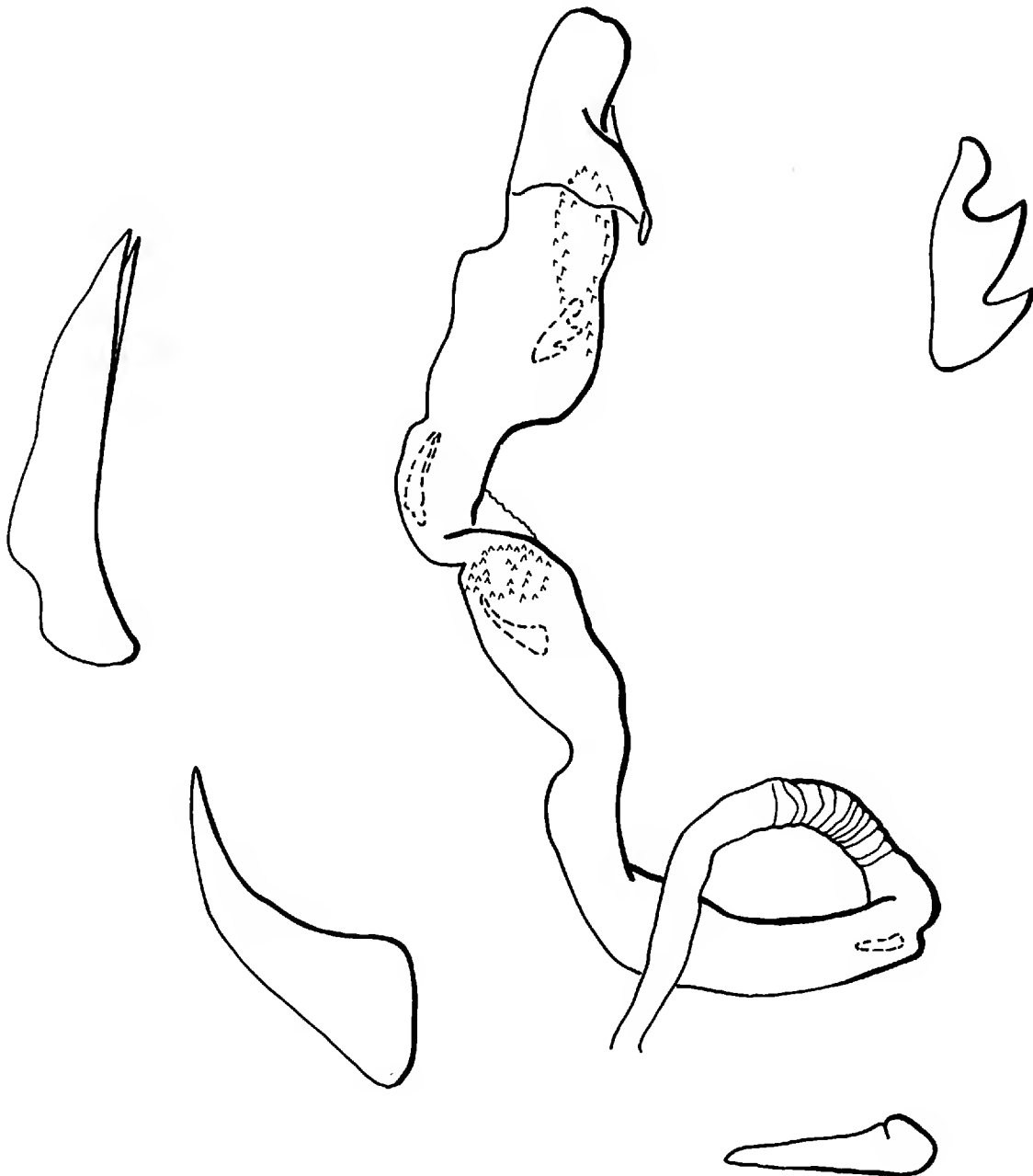


Figure 5. Genitalia of *Omanonabis lovetti*, Aedeagus.

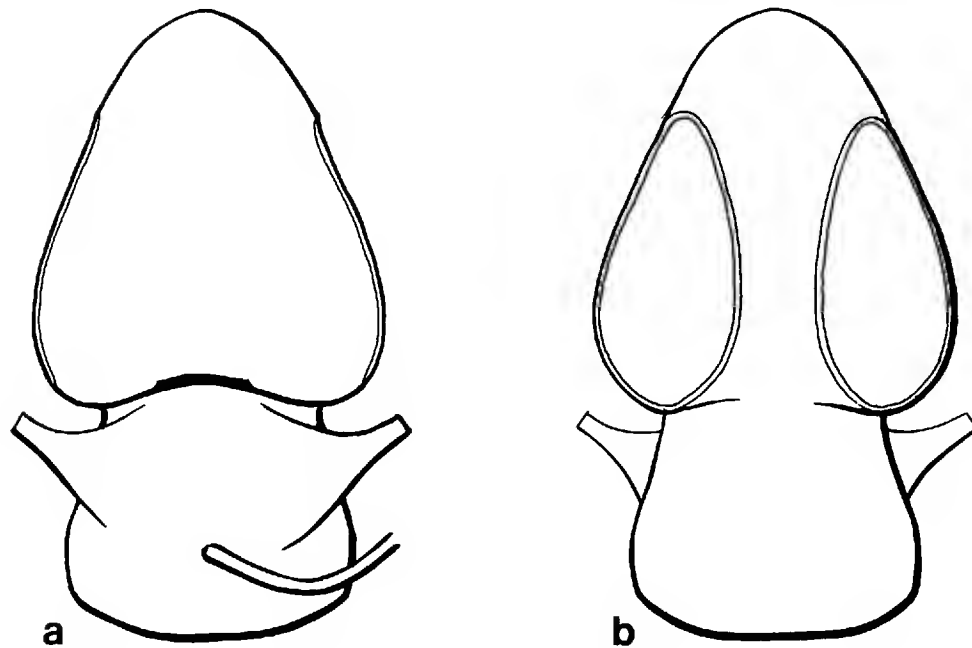


Figure 6. Genitalia of *Omanonabis lovetti*, Seminal depository. a. Ventral view. b. Dorsal view.

Material Examined.—USA. CALIFORNIA. *DEL NORTE Co.*: Lake Earl, 24 Nov 1959, J. Schuh (AMNH). *MARIN Co.*: 1.7 km (1 mi) S of Inverness, 11 Dec 1953, P. D. Ashlock, salt marsh; Point Reyes, 21 Aug 1952, P. D. Ashlock; (5 mi) SW of Point Reyes Sta., 14 Nov 1952, J. D. Lattin. *MONTEREY Co.*: Carmel, 27 May 1922. *SAN FRANCISCO Co.*: Ingleside, 20 Dec 1920, H. Dietrich. *SAN MATEO Co.*: San Bruno Mts, 16 Aug 1969, R. P. Rapp. *SONOMA Co.*: Sonoma. OREGON. *BENTON Co.*: Corvallis, 1918, A. L. Lovett (Harris 1925); Corvallis, 10 Oct 1957; MacDonal Forest, 1 Oct 1975; McFadden Pond, 16.7 km (10 mi) S of Corvallis, 17 Oct 1967, P. Oman; Peavy Arboretum, 21 Oct 1980, G. Cassis, sweeping; 5.8 km (3.5 mi) NE of Summit, 5 Oct 1961, J. D. Lattin; Willamette Riv, 12 Oct 1977, J. D. Lattin, ex willow; Winkle Lake, 16.7 km (10 mi) S of Corvallis, 8 Oct 1959, J. D. Lattin. *COLUMBIA Co.*: Scappoose, 16 Apr 1958, K. Gray; Vernonia, 21 Apr 1936, K. Gray. *CURRY Co.*: South Slough Sanctuary, S of Charleston, 24 Sep 1988, A. Asquith. *DESCHUTES Co.*: Indian Ford, 6 Jun 1957, B. Malkin. *JACKSON Co.*: Buckhorn Mineral Springs, 18.3 km (11 mi) ESE of Ashland, 853 mm (2800 ft), 19 May 1960, J. D. Lattin. *KLAMATH Co.*: Klamath Falls, Algoma, 10 May 1955, J. Schuh; Lost River, 13.3 km (8 mi) SE of Dairy, 4 Aug 1966, W. Gagne & J. Haddock. *LANE Co.*: 6.7 km (4 mi) N of Noti, 19 Mar 1963, J. D. Lattin; Siltcoos Park, 2 Nov 1968, M. Stock; Winchester Bay, 13 Jun 1947, B. Malkin & I. M. Newell. *LINCOLN Co.*: 5.8 km (3.5 mi) NE of Harlan, 7 Apr 1960, J. D. Lattin; South Beach St. Park, 1.6 km (2 mi) S of Newport, 7 Nov 1988, A. Asquith, in deflation plain; Yachats, flood plain of Yachats Riv, 14 Apr 1970, P. Oman. *POLK Co.*: 4H Education Center, 7 Jul 1973, L. Russell. *TILLAMOOK Co.*: Cape Lookout St. Park, 11 Sep 1988, A. Asquith; 1.6 km (2 mi) SE of Pacific City, 1 May 1973, J. D. Lattin; Sandlake, peat bog, 20 Sep 1962, K. Goeden; 1.6 km (2 mi) S of Sand Lake, 13 Jun 1972, W.N. Mathis; hwy 101, N of Siletz Riv, 11 Sep 1988, A. Asquith. *WASHINGTON Co.*: Hillsboro, Apr 1919, L.P. Rockwood, ex skunk cabbage. WASHINGTON. *KING Co.*: Bothell, 28 Apr 1964; Lake Sammamish St Park, 6 May 1969, R. Levenson.

THE RELATIONSHIPS OF *OMANONABIS*

We have seen neither the dense pubescence nor the teeth on the genital capsule in any other genus of nabids, and these characters may be unique to *Omanonabis*. The setae are not unusual in their structure and are only slightly larger in diameter than those of *Nabis roseipennis* (Fig. 2). Also distinctive is the broad, flat anterior surface of the peritreme channel. In species of *Nabis* and *Halonabis* the channel is clearly much narrower (Fig. 11).

Omanonabis does not appear to be related to any other North American genus of Nabini. Although it shares several characters in common with Palearctic genera, we suspect that these characters are plesiomorphic. For example, several to many small sclerites in the aedeagus are found in the Palearctic genera *Himacerus*, *Aptus*, *Stalia*, *Halonabis*, *Aspilaspis* and in *Omanonabis*. In almost all

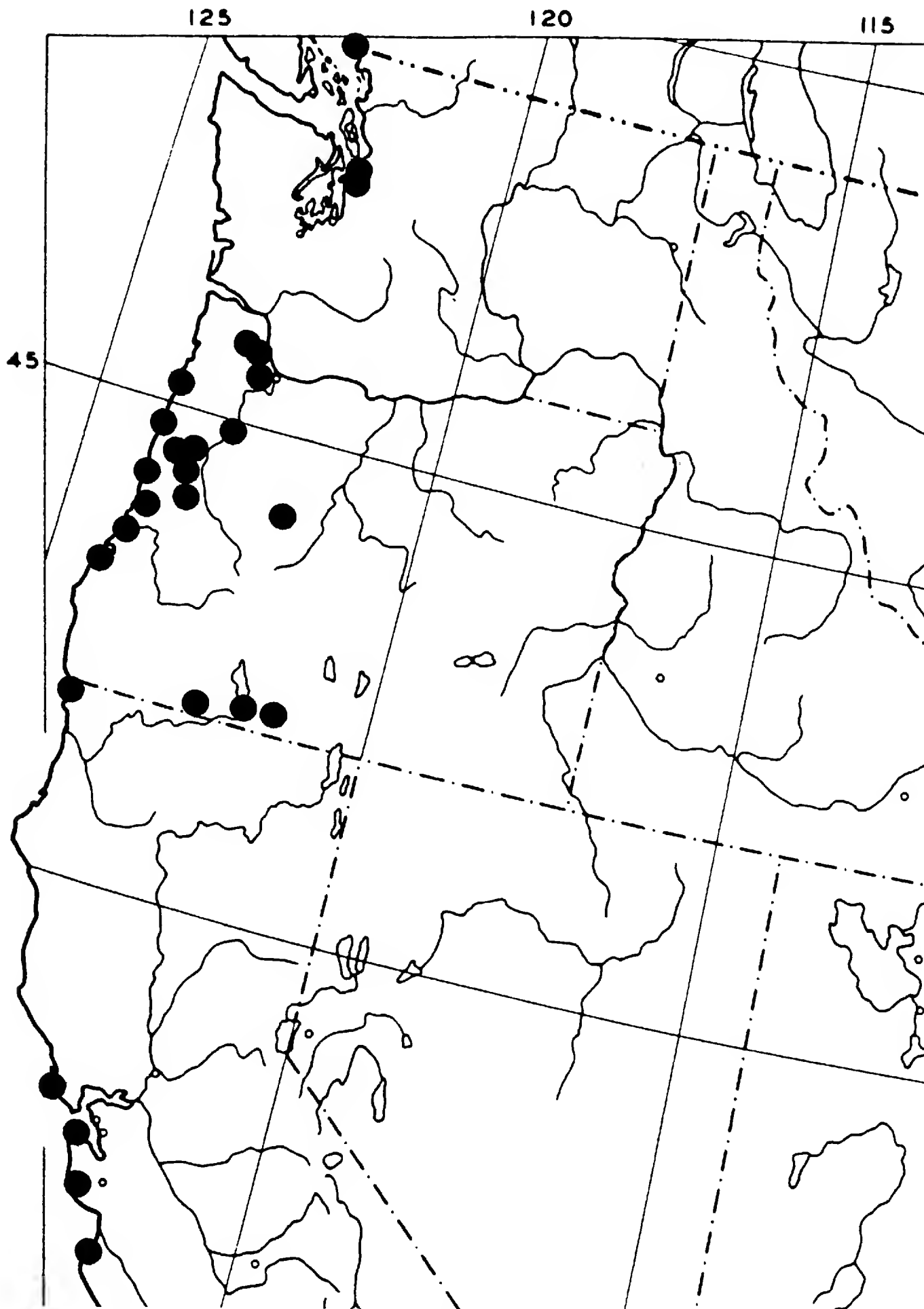


Figure 7. Distribution of *Omanonabis lovetti*.

species of *Nabicula* and *Nabis*, the small distal sclerites have been lost, and one or two large basal sclerites are retained (Fig. 8). In some species (*N. (Reduviolus) alternatus*) even the two basal sclerites have been lost (Fig. 9). We believe that the coalescence and loss of the distal sclerites in *Nabicula* and *Nabis* is more parsimonious than several independent origins of multiple, small sclerites. There-

Table 1. Comparison of macropterous and brachypterous male and female *Omanonabis lovetti*. Measurements are given in millimeters as mean plus range.

Measurement \bar{x} (range)	Male		Female	
	Macropterous	Brachypterous	Macropterous	Brachypterous
Total length	8.7 (7.9–9.1)	7.8 (7.2–8.3)	8.2 (8.0–8.6)	7.4 (7.2–7.6)
Pronotum length	1.78 (1.60–1.88)	1.68 (1.55–1.79)	1.74 (1.69–1.81)	1.61 (1.55–1.67)
Pronotum width	2.26 (2.04–2.36)	2.02 (1.91–2.14)	2.22 (2.13–2.28)	1.93 (1.85–1.99)
Head width	1.03 (0.95–1.01)	1.04 (0.99–1.09)	0.97 (0.92–1.01)	0.99 (0.95–1.02)
Antennal segment I	0.90 (0.83–0.95)	0.92 (0.87–0.96)	0.78 (0.53–0.87)	0.86 (0.77–0.89)
Antennal segment II	1.46 (1.37–1.51)	1.56 (1.06–1.41)	1.32 (1.17–1.27)	1.22 (1.15–1.29)
Antennal segment III	1.30 (1.26–1.40)	1.31 (1.06–1.41)	1.21 (1.17–1.27)	1.22 (1.15–1.29)
Antennal segment IV	1.04 (0.92–1.10)	1.07 (1.03–1.22)	1.03 (1.01–1.03)	1.06 (0.96–1.18)

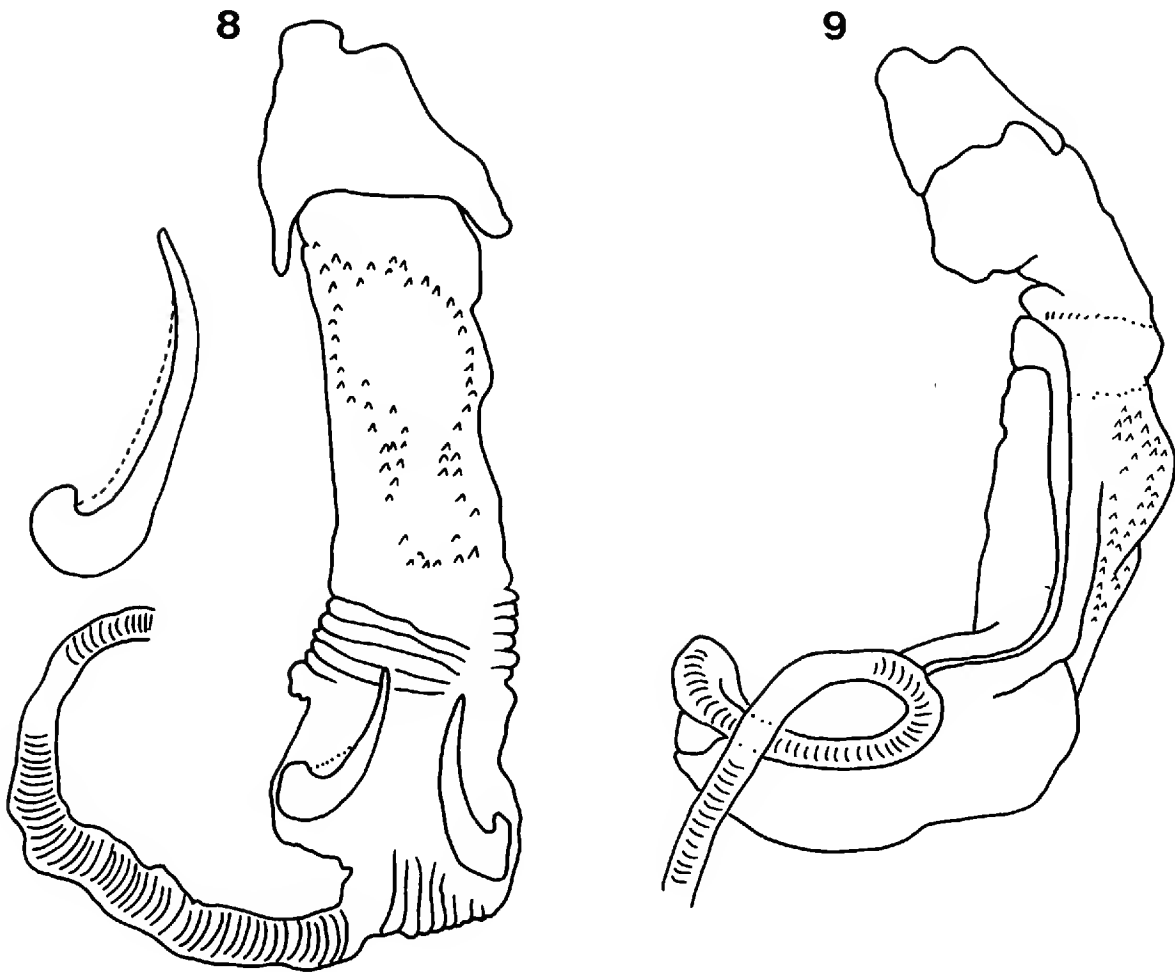
fore, although *Omanonabis* retains several distal sclerites, it cannot be grouped with the other genera that display this morphology, but it can be removed from the genus *Nabis*, which has lost this condition.

Superficially, the parameres of *Omanonabis* closely resemble those of *Halonabis*. In the latter genus, however, a wide, longitudinal groove is present which begins basally on the ventral margin of the paramere, but turns dorsal to run along the lateral margin distally. In *Omanonabis*, this groove is present, but it is much narrower and is restricted to the ventral margin of the paramere. Besides lacking the other diagnostic features of *Omanonabis*, *Halonabis* also differs by lacking spinules on the ventral surface of the fore femora, having proportionately much larger eyes and having the apical third of the head weakly curved ventrally. Species of *Aspilaspis* also have a rather elongate, linear paramere. If the lanceolate paramere is homologous, then *Omanonabis* may be related to *Halonabis* and *Aspilaspis*. The two Palearctic genera are Mediterranean in distribution and are also ground inhabiting, preferring moist habitats (Pericart 1987).

THE RELATIONSHIPS OF *NABIS EDAX*

Nabis edax Blatchley was described from a single male specimen from Los Angeles, California (Blatchley 1929). This species has not been reported since, and was apparently known only from the specimen used in the original description. Based on an examination of this specimen, Kerzhner (reported in Henry & Lattin 1988) placed this species in the subgenus *Nabis*, with *N. roseipennis* Reuter and *rufusculus* Reuter. Here, we provide a description of the female of *N. edax*, detail the male and female genitalia, and reassess its taxonomic position.

In an unpublished Master's thesis dealing with the female genitalia of the Nabidae, Mitri (1960) figured the seminal depository of a specimen from Milpitas, Alameda Co., California. He noted that the structure of the seminal depository was unlike that of any other North American species for which females were known. Recently, additional single females were discovered in the collections of the California Academy of Sciences and the University of California, Berkeley that also possess this unique seminal depository structure. Mitri (1960) stated that he could not discern sclerotized rings in this species, but presumed they were present and merely lightly sclerotized. We have reexamined the specimen he dissected and one additional specimen. We also could not identify sclerotized



Figures 8–9. Aedeagus. 8. *Nabis (Nabis) roseipennis*. 9. Aedeagus of *Nabis (Reduviolus) alternatus*.

rings, although a thin structure at the ventral surface of the base may represent the vestiges of the rings. In addition, male specimens of *N. edax* were also discovered. All specimens were collected from central and southern California, from San Francisco to Los Angeles.

There are two possible explanations for this scenario. First, that there are two species in southern California, *N. edax*, known only from male specimens, and an undescribed species, known only from female specimens. We consider this very unlikely, because most North American Nabidae have relatively large ranges, and two closely related species confined to the same restricted area would be most unusual. Second, that the female specimens are *N. edax*. We believe this to be the case, because both male and female specimens share combinations of characters not possessed by any other North American species.

Taxonomic Position.—Kerzhner assigned *edax* to the subgenus *Nabis* (Henry and Lattin 1988) with the other two North American members, *N. roseipennis* Reuter and *N. rufusculus* Reuter. However, *N. roseipennis* has two sclerites in the aedeagus both with large hooks at the base (Fig. 8), and *N. rufusculus* has two large sclerites at the base and one small sclerite at the distal end of the aedeagus. The seminal depositories of *roseipennis* and *rufusculus* are broadly spindle shaped, and both have a single, large, bilobed sclerotized ring covering the anterior and antero-ventral surface of the depositories. *N. edax* shares no characters in common with these species and therefore clearly is not a member of the subgenus *Nabis*.

Remane (1964) designated several species groups in the genus *Nabis*, two of which contain species with a single sclerite in the aedeagus similar to *N. edax*. In the *rugosus* group, *N. brevis* Schultz has only a single sclerite, but it bears a tooth

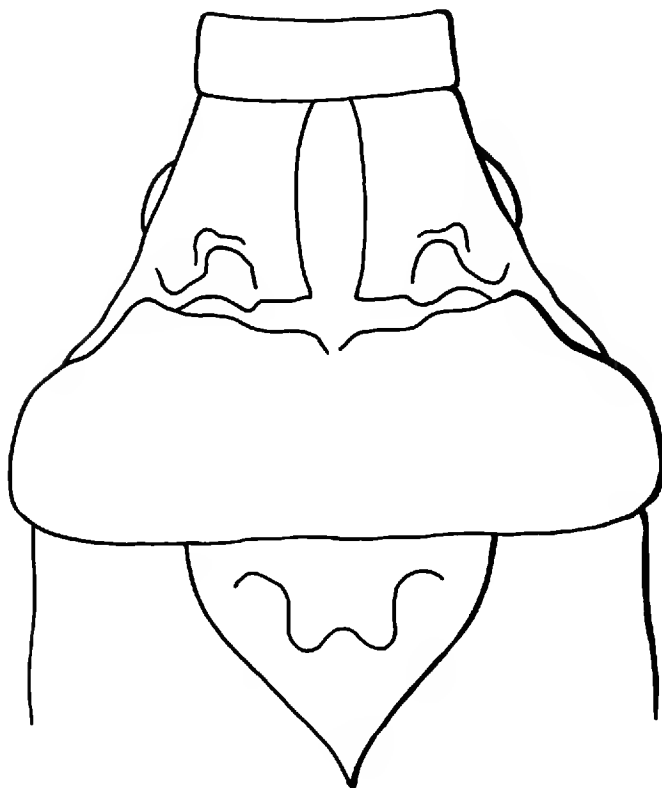


Figure 10. Dorsal view of the pronotum of *Nabis edax* Blatchley. Female.

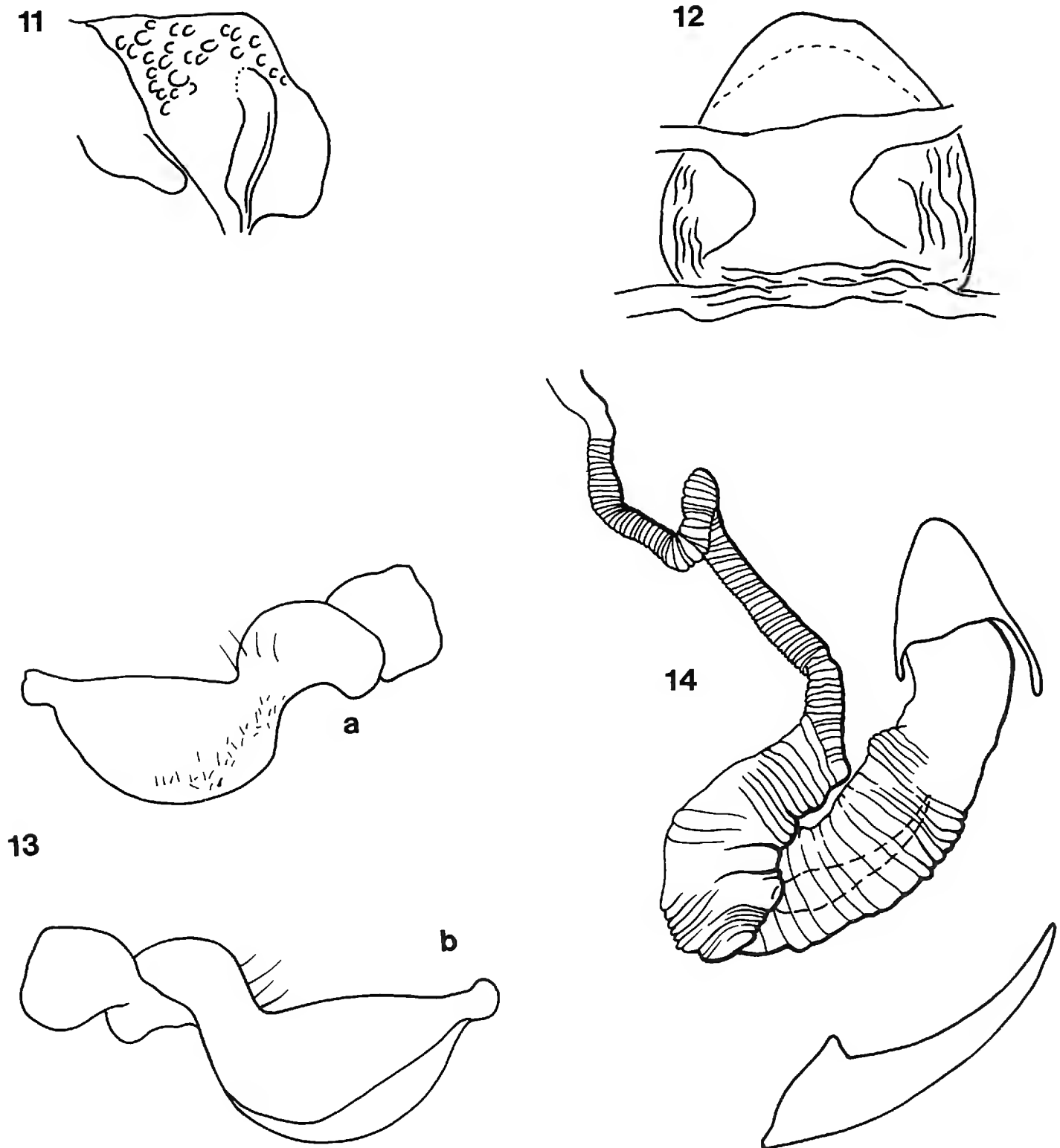
near its base and it is situated near the base of the aedeagus. In addition, this group contains predominately short-winged forms, and *N. edax* is known only from macropterous specimens. In the *ferus* group, both *N. ferus* (L.) and *N. palifer* Seid. have but a single sclerite. In *ferus*, however, the sclerite has a large, well developed hook at the base, and in *palifer*, the sclerite is very small, only half the length of that in *edax*. In addition, the seminal depository of the *ferus* group is large, membranous, with a large sclerotized ring that occupies most of the antero-ventral surface of the seminal depository.

The subgenus *Reduviolus* Kirby which includes *N. alternatus* Parshley and *N. americanoferus* Carayon, is predominately a North American group, with the exception of *N. inscriptus* (Kirby) which is Holarctic in distribution. The female depository in this group is short and symmetric with a small thin sclerotized ring on the postero-ventral surface, very similar to *N. edax*. However, all members of the *inscriptus* group lack any sclerites in the aedeagus.

It appears that *N. edax* Blatchley cannot be placed in any of the taxonomic subdivisions presently recognized in the genus *Nabis*. It is most similar to members of the subgenus *Reduviolus*, but is not closely related to any of these North American species. Examinations of a few Mexican and South American species of *Nabis* also failed to find any which appear to be related to *N. edax*. Rather than create a new subgeneric taxon for *N. edax*, we believe it more prudent simply to recognized its uniqueness and label this species *incertae sedis* within the genus *Nabis* pending a more detailed and broader geographic study of the genus.

NABIS EDAX BLATCHLEY
(Figs. 10–14)

Type. — Holotype male. Data: "Cal[ifornia]: Los Angeles, W.S.R., 12-6-27/ Purdue Blatchley Collection/ TYPE/ LECTOTYPE *Nabis edax* Blatchley, Des. W.S. Blatchley, 1930." In the Purdue University Insect Collection.



Figures 11–14. *Nabis edax* 11. Left metathoracic scent gland. 12. Female seminal depository, dorsal view. 13. Left paramere in lateral (a) and medial (b) views. 14. Aedeagus.

The Lectotype designation by Blatchley was never validated in a publication. Although Blatchley did not designate a holotype in the original description, the specimen should now be considered the holotype by monotypy (ICZN Recommendation 73F, ICZN 1985).

Redescription.—*Female.*—Medium sized species, total length (7.1–7.8 mm), broadly linear in outline, widest just posterior of clavus. *Head:* Porrect, longer than wide; eyes large, dorsal edges reaching just above vertex, ocelli prominent; pale yellow, area posterior of eye fuscous, ventral surface of head immaculate; antennae linear, I (0.87–1.02 mm), II (1.51–1.69 mm), yellow, segment I with longitudinal fuscous stripe on medial surface, fuscous stripe on dorsal surface of segment II. *Pronotum:* Broad, length (1.43–1.64 mm), posterior width (1.77–2.04 mm), posterior width–collar width ratio >2.5, strongly campanulate, abruptly expanded posteriorly with corners angular (Fig. 10), posterior lobe

elevated, with numerous shallow punctures, posterior margin distinctly carinate, pale yellow. Collar distinct, longer than distance from posterior margin of eyes to posterior margin of head, anterior portion shallowly punctate. Scutellum very broad, wider than long, middle depressed and margins slightly elevated, pale yellow. *Hemelytra*: Shiny, smooth or minutely granulose, anterior one third of clavus and corium with small shallow punctures; clavus short and broad, straw yellow, small fuscous spot at apex of claval suture; veins of membrane indistinct, membrane with indistinct, broad fuscous stripe, more defined apically. Dorsum covered with long, inclined yellow setae. *Venter*: Ventral surface pale yellow. Metathoracic scent gland distinct, elongate oval, apex evenly rounded (Fig. 11). Legs immaculate or with light brown spots at base of setae. Fore and hind femora without black teeth or denticles on ventral surface, middle femora occasionally with a single short row near apex. Hind legs more robust than other *Nabis* spp.; hind tibia pilose, with erect hairs, the longest of which are almost 2× the width of the tibia. Seminal depository short, thick and symmetric (Fig. 12), strongly wrinkled along the sides and base; oviducts wide, arising from a meso-dorsal position on the seminal depository.

Male.—Similar in size and shape to females but much darker, with color patterns more distinct. Length (7.18 mm). *Head*: Grey on dorsum, ventral surface testaceous. *Pronotum*: Less wide or campanulate than female, length (1.54 mm) posterior width (1.86 mm), with a dark fuscous middorsal stripe. Scutellum also with wide dark fuscous median stripe. *Hemelytra*: Midline of membrane with an irregular, broad fuscous or smoky stripe. Propleuron fuscous; abdomen with testaceous to fuscous lateral stripe. Meso- and metafemora and tibiae with fuscous spots. *Genitalia*: Paramere most similar to that of *N. rufusculus* (Fig. 13). Apex produced, with a short, squared tip. Ventrolateral surface with a wide row of erect setae, following curve of ventral margin of paramere. Aedeagus with a single large sclerite without a tooth at its base (Fig. 14), situated in distal half of aedeagus.

Diagnosis.—To serve as a diagnosis, we have revised a portion of Harris' key to North American Nabidae (1928) to include *N. edax*:

19. Head beneath in greater part fuscous to black; posterior tibiae dotted with fuscous; brachypterous form with closed cells in the membrane; male paramere with long sinuate stem *roseipennis* Reuter
 Head beneath in greater part yellow to testaceous; posterior spotted or immaculate; male paramere with short rectangular stem 20
20. Maximum width of posterior femora > distance between eye and ocellus; ventral surface of mesofemora lacking black denticles or with only a short row near apex; posterior tibiae of male spotted with fuscous; aedeagus with a single sclerite; posterior tibiae of female pilose, longest setae nearly at right angles with axis of tibia and 2× its width; seminal depository without sclerotized ring; coastal California *edax* Blatchley
 Maximum width of posterior femora ≤ distance between eye and ocellus; ventral surface of mesofemora with black denticles; posterior tibia of male usually immaculate; aedeagus with two sclerites; posterior tibiae of female not pilose, all setae short; seminal depository with sclerotized ring present, wide spread 20a
- 20a. First antennal segment thickened distally, somewhat sinuate above; brachypterous form common, usually with no closed cells in membrane; diameter of blade of male paramere greater than that of an eye viewed from above *rufusculus* Reuter
 First antennal segment scarcely thickened distally, from above almost straight; brachypterous form unknown; diameter of blade of male equal to that of an eye *kalmii* Reuter

Material Examined.—USA. CALIFORNIA. *CONTRA COSTA Co.*: Pittsburg, 18 Nov 1923, J.D. Martin. *FRESNO Co.*: Tranquillity, Fresno Slough, 8 Jul 1962, P. F. Torchio. *LOS ANGELES Co.*: Los Angeles, Hancock Park, 6 Dec 1927, W. S. Blatchley; Milpitas, 23 Jun 1955, (Acc. No. 121), P. F. Torchio. *SANTA CLARA Co.*: San Jose, 30 Sep 1954, D. R. Bale. *COUNTY UNCERTAIN*: South Eastern California, 8 Jun 1962, light trap, USDA.

ACKNOWLEDGMENT

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LARVAL DEVELOPMENT OF *DARGIDA PROCINCTA* (GROTE) (LEPIDOPTERA: NOCTUIDAE) IN THE PACIFIC NORTHWEST

J. A. KAMM

National Forage Seed Production Research Center,
U.S. Department of Agriculture, Agricultural Research Service,
Corvallis, Oregon 97331-7102

Abstract.—Larval growth of *D. procincta* (Grote) was regulated by temperature and larvae required 20.5 days at 27° C to complete larval development vs 51.2 days at 15° C. Duration of the pupal stage was 11.7 days at 27° C vs 36.7 days at 15° C. Photoperiod had no observable effect on larval development. The six instars were readily distinguished by the width of head capsule. Third instars, observed in the field in early April, are believed to emerge as adults in June and lay eggs for a second generation. Dense infestations of larvae were observed to develop on the lush spring growth of grasses but not on the fall regrowth of established or seedling stands of ryegrass.

Key Words.—Insecta, cutworm, grass pest, larval growth

Dargida procincta (Grote) is one of two representatives of the genus in the continental United States (Holland 1903, Hodges 1983). In the Pacific Northwest, the larvae are known to defoliate ryegrasses (Kamm 1985). Legumes are also host plants (Tietz 1972). The seasonal flight of adults is unknown because they are rarely captured in blacklight traps, even in fields with dense populations of larvae (Kamm 1985). Dyar (1898) and Godfrey (1972) briefly described the larvae and Spencer (1946) observed the oviposition behavior of females. Thompson (1943) considered the species an important pest of grasses in the Pacific Northwest. *Dargida procincta* was the most abundant cutworm species in commercial ryegrass grown for seed, but nothing is known about its larval development or the number of generations each year (Kamm 1985).

This paper reports the results of laboratory tests that document the number of instars and the influence of photoperiod and temperature on the rate of larval growth. Field observations were made and are discussed in relation to the seasonal cycle of *D. procincta* in ryegrass grown for seed in the Willamette Valley of Oregon.

MATERIALS AND METHODS

A laboratory culture of *D. procincta* was initiated from larvae collected in a field of ryegrass near Corvallis, Oregon. All larvae were reared individually in stender dishes (5.0 × 2.5 cm), the bottoms of which were lined with damp blotting paper. Larvae were supplied with freshly cut leaves of ryegrass, *Lolium multiflorum* Lamarck, every 1–3 days. Controlled environment chambers were used to rear the stock cultures and to provide experimental treatments of light and temperature. A short day was a regime of 10 h light and 14 h dark (10:14 LD) and a long day was a regime of 16 h light and 8 h dark (16:8 LD). Adults obtained from larvae reared in the laboratory were confined in cages (20 × 20 × 50 cm) on ryegrass grown in the greenhouse to mate and to obtain eggs. Eggs laid on the

foliage were removed and kept in stender dishes until they hatched. Experimental treatments were initiated the day of egg hatch.

Head capsule size was the criterion used to determine larval instars. Measurements were made across the widest part of the head capsule in dorsal view by using an ocular micrometer in a stereoscopic microscope. Head capsules were measured every other day during the test. Adults were dissected at different ages to determine the stage of ovarial development by methods described elsewhere (Kamm & Ritcher 1972). Specimens of reared adults have been deposited in the insect museum at Oregon State University. A sweep net was used to sample fields for larvae.

RESULTS AND DISCUSSION

Description of Eggs and Larvae.—Females glue milky white eggs to the undersides of grass leaves and within leaf sheaths. The eggs are pumpkin shaped. Several days before hatch they develop a brown ring that encircles the egg, with a brown dot in the center of the ring. Each ovary has four ovarioles about twice the length of the abdomen. No mature eggs are visible in the ovaries when females emerge, but after females were fed a solution of 10% honey and water for a week, eggs of various sizes were present in the ovaries and females initiated oviposition. The ovaries removed from females collected in the field during July and August contained mature eggs.

Dargida procincta is described as being green with pale stripes or black with the pale stripes distinct (Crumb 1956, Godfrey 1972). When a large lot of larvae was reared in the laboratory to fourth instars, the basic body color was numerous shades of green (110), black (59), or brown (14). The color of the pale stripes was usually tan or brown, which may or may not have interrupted black markings that parallel the stripes. Because *D. procincta* is a leaf feeder, the different color morphs probably conceal some larvae from predators during seasonal changes in color of the grass.

Larval Growth.—Figure 1 shows the cumulative rates of growth of larvae exposed to a long-day regime at 21° C. Each instar was easily discerned by measurement of the head capsule. Progression through the instars was remarkably uniform, both in time between molt and the size of head capsule, except for the sixth instar. Unlike many Lepidoptera larvae (Beck 1980), photoperiod had no significant effect on the rate of larval growth at either 15 or 21° C (Table 1). No evidence was found that exposure of small larvae to short days and/or low temperatures induced diapause in either larvae or pupae. In temperature treatments with the same photoperiod, the rate of larval and pupal development nearly doubled ($P < 0.05$) when larvae were exposed to 15° C compared with those larvae exposed to 21° C.

Another experiment confirmed that larval growth was regulated by temperature when larvae were exposed to an expanded range of temperatures (Table 2). The duration of development for larvae, from egg to pupal stage, ranged from 20.5 days to 51.2 days. The duration of the pupal stage was 11.7 days at 27° C vs 36.7 days at 15° C. The ability of *D. procincta* to develop in cool temperatures and short daylengths without diapause or apparent pathological effect gives the species the advantage of using the early spring and autumn growth of cool-season grasses in the Pacific Northwest. During winter, larvae have been observed to feed during

Table 1. Effect of photoperiod at 15° and 21° C on the development of *D. procincta* larvae from time of egg hatch to adult.

Photoperiod	Temperature (°C)	No. of insects	\bar{x} Time to develop (days)		
			Larvae	Pupae	Total (\pm SD)
16:8 LD	21	65	29.5	16.9	46.4 \pm 1.9 ^a
10:14 LD	21	61	28.8	18.5	47.3 \pm 2.2
16:8 LD	15	31	54.4	34.4	88.8 \pm 2.8
10:14 LD	15	34	52.0	39.7	91.7 \pm 2.9

^a Rate of development of larvae exposed to the same temperature and different photoperiods were not significantly different, but that of larvae exposed to the same photoperiod and different temperatures was significantly different (Mann-Whitney *U*-test, $P < 0.05$). Each treatment was initiated using 80 larvae.

warm periods in January. Second and third instars were easily collected on ryegrass foliage where they feed by sweeping fields during early April and are believed to be first-generation larvae that mature and pupate in ryegrass fields windrowed for harvest in mid-June (Kamm 1985). The presence of gravid females from May through August suggests a second generation of larvae in late summer. A few mature larvae that developed during the typical arid summer have been collected from September to December and are believed to be the wintering stage. In no case have dense larval infestations been observed in established or seedling fields of ryegrass during October and November suggesting that the species primarily exploits the lush spring growth of grass.

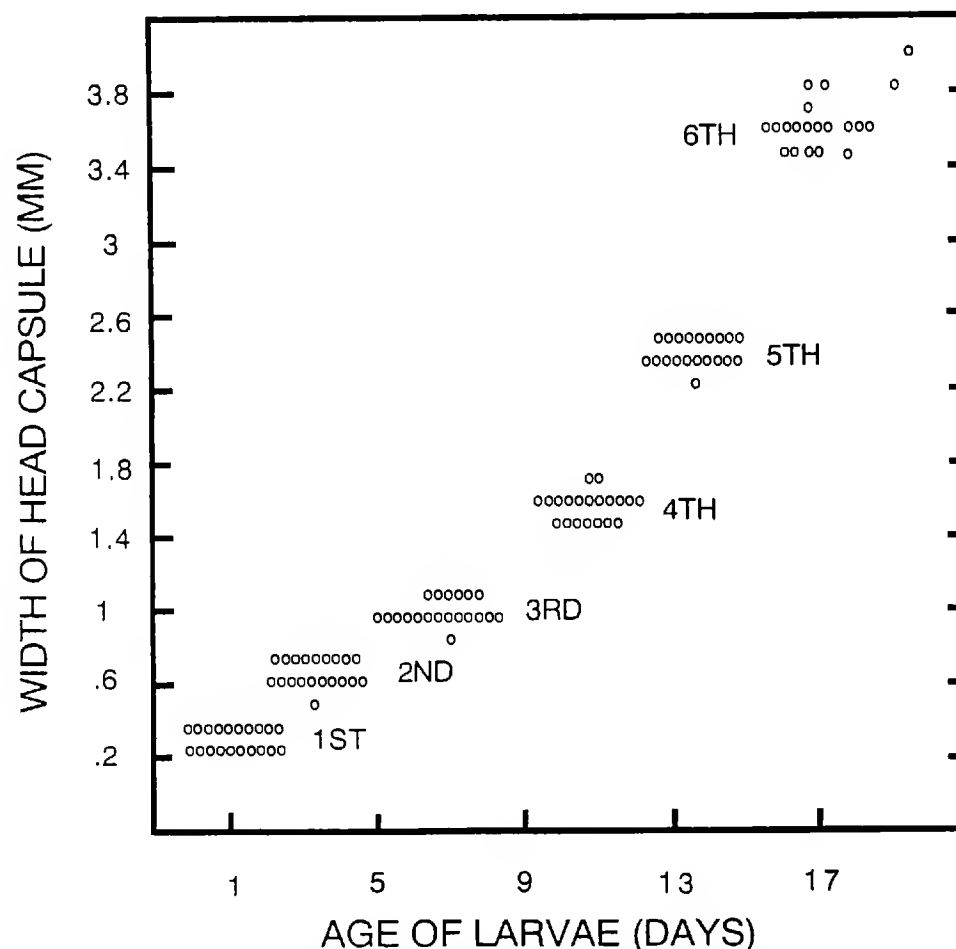


Figure 1. Progressive increase in the size of head capsule of larvae of *D. procincta* exposed to long daylengths at 21° C.

Table 2. Effect of temperature on rate of development when *D. procincta* larvae were exposed to different temperatures and long days (16:8 LD) from time of egg hatch to adult.

Temperature (°C)	No. of insects ^a	\bar{x} Time to develop (days)		
		Larvae	Pupae	Total (\pm SD)
27	22	20.5	11.7	32.2 \pm 2.1
24	30	24.6	14.9	39.5 \pm 1.2
21	44	25.0	16.4	41.4 \pm 0.8
18	32	35.9	24.4	60.3 \pm 3.3
15	29	51.2	36.7	87.9 \pm 2.7

^a Each treatment was initiated using 60 larvae.

ACKNOWLEDGMENT

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**A NEW *DROSOPHILA* SPECIES IN THE *MONTIUM*
MEIJERE SUBGROUP OF THE *MELANOGASTER* MEIGEN
SPECIES-GROUP IN THE SUBGENUS *SOPHOPHORA*
STURTEVANT FROM TAIWAN
(DIPTERA: DROSOPHILIDAE)**

SHUN-CHERN TSAUR AND FEI-JANN LIN¹

Institute of Zoology, Academia Sinica, Nankang, Taipei, Taiwan 11529,
Republic of China

Abstract.—A new *Drosophila* from Taiwan, *D. austroheptica* NEW SPECIES is described and illustrated. It belongs to the *melanogaster* species-group, and is closely allied to *D. quadraria* Bock & Wheeler.

Key Words.—Insecta, Diptera, *Sophophora*, *Drosophila austroheptica*

The *Drosophila montium* Meijere subgroup was first established by Hsu (1949: 121) with the following characters: “A large tooth-bearing secondary clasper present, seemingly originated by separation from anal plate; marginal bristles of primary clasper greatly enlarged.” This diagnosis was subsequently defined more completely by Bock & Wheeler (1972).

The subgroup is by far the largest in the *melanogaster* species-group and presently accomodates 79 taxa (Lemeunier et al. 1986), occurring from the Oriental to Afrotropical regions. Seven species in the subgroup have hitherto been recorded from Taiwan: *D. ashahinai* Okada, *D. auraria* Peng, *D. bocki* Baimai, *D. jumbulina* Parshad & Paika, *D. kikkawai* Burla, *D. lini* Bock & Wheeler, and *D. quadraria* Bock & Wheeler (Chen and Lin, unpublished data). This paper describes an additional species, *D. austroheptica*.

MATERIALS AND METHODS

All the isofemale laboratory culture stocks available for this study were obtained by field collections in Nanjenshan (Kenting National Park) by either sweeping on grasses or using beer-banana traps beside streams. Stocks were reared on standard corn meal medium at 22° C and 75% RH. During the study, fresh specimens were dissected directly in a weak solution of phenol, but pinned flies were first boiled in 1N potassium hydroxide for several minutes until clear and then washed in tap water. All drawings were made with a Nikon Optiphot® drawing tube at the same magnification (ca. 200×). All dissected parts were slide-mounted.

The terminology employed in the descriptions is largely patterned after that proposed by Sturtevant (1942), although more standardized terminology for the Diptera is noted within parentheses.

DROSOPHILA (SOPHOPHORA) AUSTROHEPTICA
TSAUR & LIN, NEW SPECIES
(Fig. 1)

Types.—Holotype: male; data: REPUBLIC OF CHINA. TAIWAN. Taipei: Nankang, 25 May 1990, taken from isofemale line stock culture 0211.24 in the

¹ To whom reprint request should be sent.

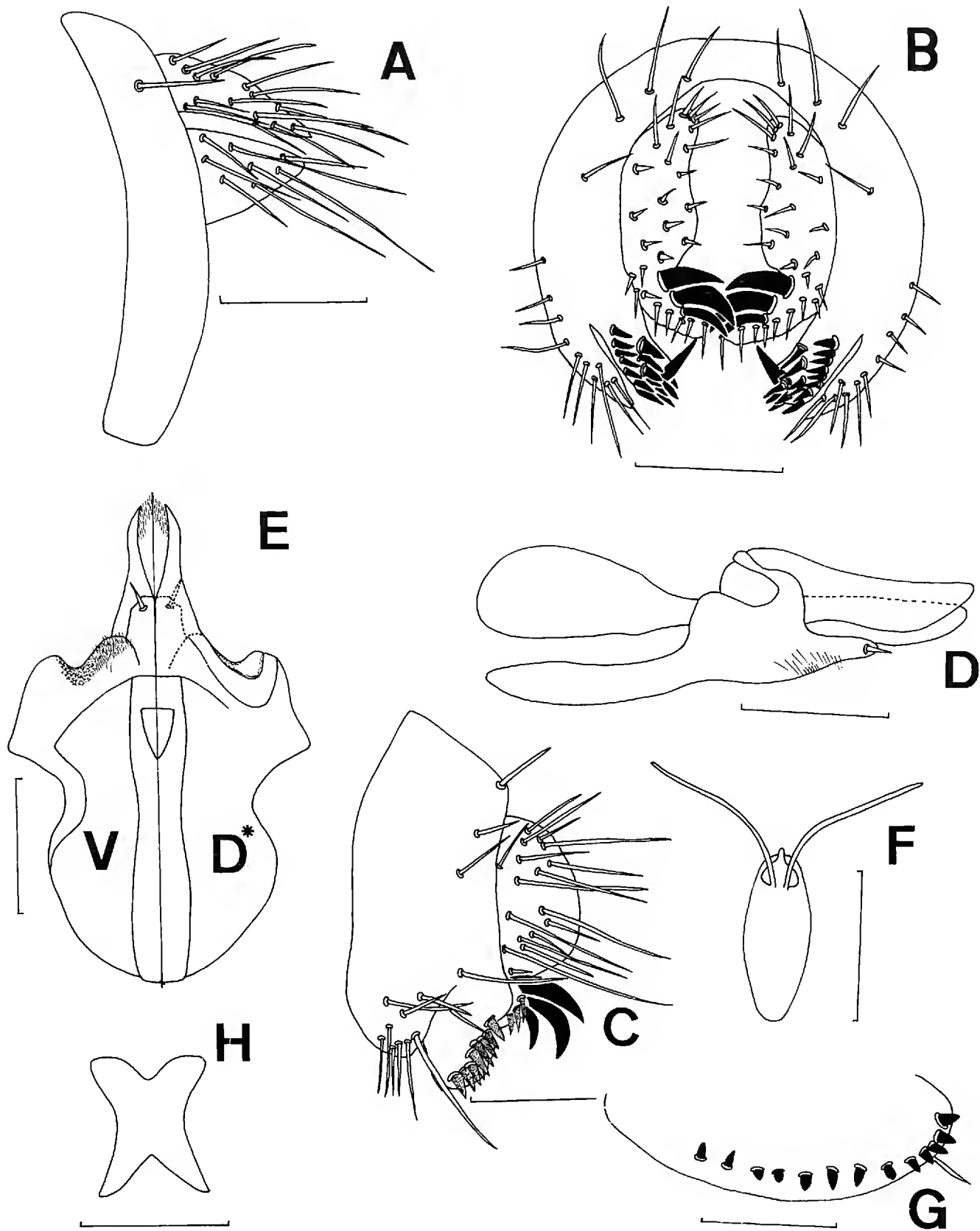


Figure 1. Genitalia and egg of *Drosophila (Sophophora) austroheptica* NEW SPECIES. A. genital arch (female), lateral view. B. caudal view (male). C. lateral view (male). Phallic organs: D. lateral view of phallic organ (male). E. ventral (V) and dorsal (D*) views of phallic organs (male). F. egg. G. egg guide (female). H. decasternum (male). (Scale lines = 1 mm.)

Institute of Zoology, Academia Sinica (originally provisioned with field material from Nanjenshan, Pingtung Hsien, 13 Nov 1989, S. C. Tsauro and C. T. Ting). Paratypes: 10 males, 10 females; same data as holotype. Holotype and paratypes deposited in the Institute of Zoology, Academia Sinica, Taipei, Taiwan, Republic of China.

Male.—Body length: 2.3 mm (live specimens); wing length: 1.9 mm. Head: Antennae, second segment black-yellow, with two large setae, several medium to small setae, third segment darker.

Arista with four branches above, three below plus a terminal fork. Front pale brown, with a transverse, yellow band between antennae *orb-3* (proclinate orbital). Periorbitals moderately small, four to six. Orbitals: *orb-1* (posterior reclinate orbital) obviously nearer to *orb-3* than to inner vertical bristles; *orb-2* (anterior reclinate orbital) situated between *orb-1* and *orb-3*, closer to *orb-1* than to *orb-3* about 1:2.5, more than one-third length of *orb-1*, less than one-third length of *orb-3*. Three oral vibrissae, second almost same length of first, third about two-thirds length of others. Carina yellow-white, moderately elevated. Face dark brown. Palpi dark brown, with single apical and subapical bristles pointed downward. Proboscis entirely yellow-brown. Ocellar triangle dark brown. Ocellars normal, yellow. Ocelli orange. Eyes red, piled, slightly oblique to body axis. Maximum width of cheek about one-seventh maximal diameter of eye. Mesonotum and scutellum: Shining brown, lacking markings. Acrostichal hairs in six rows. Dorsocentral bristles with anterior four-fifths the length of the posteriors, both sets parallel; cross distance between anterior dorsocentrals about $2 \times$ distance from anteriors to posteriors. Prescutellar bristles absent. Pleurae brown, lacking stripes. Humeral two, lower longer than upper, about 1.5:1. Sternopleural bristles three. Sterno-index about 0.6. Anterior scutellar bristle parallel to convergent, slightly shorter than posteriors. Posterior scutellar bristles crossed at mid-length. Halteres tan. Legs yellow-brown, inner side of fore femur with three long bristles from mid-length to subapex, divided in equal length. Preapical bristles on all tibiae, apical bristles on first and second tibiae. Sex-comb longitudinal along entire length of first and second tarsal segments; first tarsal comb consisting of about 24 uniform teeth; comb on second tarsal segment with a similar row of about 14 teeth, all nearly same length. Abdominal tergites: Brown-yellow, segments II–IV black, segment V with or without inconspicuous yellow-brown band, all bands occupied varying from apical one-fifth to one-half, except segment V that is only slightly pigmented posteriorly. Some stout bristles on posterior margin of tergites in regular rows. Wings: Slightly grey diffused, veins brown-black. Second vein (R_{2+3}) straight. Third (R_{4+5}) and 4th veins (M_{1+2}) parallel. Two C-1 bristles. C-3 fringe on its basal half. Approximate indices: C index 2.1; 4c index 1.4; 4V index 2.3; $5 \times$ index 2.2. Periphallic organs: Genital arch (epandrium) broad laterally, ventral lobe with one long, four to five moderately long bristles, without triangular process covering base of primary clasper. Primary (surstylus) and secondary (ventral margin of cercus) claspers present. Primary clasper with a lateral row of five to six small pointed teeth and medial cluster of about 11 larger teeth, one stout and elongated. Secondary clasper with three large, curved black medial teeth and several fine setae ventrally and dorsally. Anal plate dark brown, with long bristles. Median lobe of decasternum bicornuted. Phallic organs: Brown. Aedeagus broadly rounded and finely hirsute at apex, slightly constricted subapically, lacking pointed lateral expansions. Anterior parameres large, well separated, broadly subtriangular, without minute apical sensilla. Posterior parameres spoon-shaped, long, surpassing tip of aedeagus. Ventral phragma narrowed medially, shovel-shaped. Caudal margin of novasternum (hyandrium) with hexagonal median truncated process, apically bearing two short spines.

Female. — Body length: 2.4 mm (live specimens); wing length 2.1 mm. As in male except for sexual dimorphic characters, and abdominal tergites of segments II–V with dark brown bands. Egg guide (oviscapt): Yellow-brown, with about 13 teeth and a subterminal hair. Egg filaments: Two long slender filaments.

Pupae. — Anterior spiracles with 10 branches. Horn index: 0.08.

Diagnosis. — *Drosophila austroheptica* can be separated from the other *Drosophila* of the *montium* subgroup in Taiwan by its unique combination of the following characters: secondary clasper with only two teeth and both the caudal margin of the novasternum with a hexagonal medium truncated process plus the posterior paramere extending slightly past the tip of the aedeagus.

Life Cycle. — One generation takes about 14 days at 22°C, 75% RH.

Distribution. — Only known from the type locality in Taiwan.

Etymology. — The specific name indicates that it has been collected from Southern Taiwan.

Material Examined. — (*Maintained Cultures*) Stock cultures in Academia Sinica: 0211.24 to 0211.25 (2 stocks, isofemale lines, collected from Nanjenshan, Pingtung Hsien, 13 Nov 1989 by S. C. Tsaur and C. T. Ting).

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**PHYLOGENETIC CHARACTER RESPONSES FOR SHAPE
COMPONENT VARIANCE DURING THE MULTIVARIATE
EVOLUTION OF EULACHNINE APHIDS:
REDESCRIPTION OF *PSEUDESSIGELLA* HILLE RIS
LAMBERS (HOMOPTERA: APHIDIDAE: LACHNINAE)**

JOHN T. SORENSEN

Insect Taxonomy Laboratory, California Department of Food & Agriculture,
Sacramento, California 95814

Abstract.—Although suitable for conventional taxonomic purposes, previous descriptions of the monotypic aphid genus *Pseudessigella* Hille Ris Lambers and its species *Pseudessigella brachychaeta* Hille Ris Lambers are inadequate to characterize important phylogenetic trends in character evolution in the Eulachnina; therefore, these taxa are redescribed. The evolutionary responses of morphometric traits for *Pseudessigella*, *Essigella* (as a whole) and two primitive *Essigella* species are deduced and interpreted with reference to Lande's models of multivariate phenotypic evolution. Twenty-six traits among these taxa were analyzed for their shape component variance using principal components analysis; ranks for the relative contribution of each trait upon the dominant two shape vectors were assigned on the basis of character loading coefficients. Between the genera, 42% of the traits were considered to be stable in their partitioned shape variance over the implied evolutionary episode; 39% of the traits showed moderate stability, while 19% were judged to be unstable. The average similarity of evolutionary response for the traits on the dominant shape vectors between these genera was 0.56; the primitive *Essigella* species showed higher similarities (0.71, 0.62) with *Pseudessigella* than did *Essigella* overall. When discriminant function analysis was used as a measure of Landean minimum selective mortality to determine the multivariately optimal traits that separate *Essigella* species, both traits with predominantly general-size variance and traits with predominantly shape variance appeared to be important in species separation. The most influential traits with the highest shape variance on the discriminant vectors, however, appeared to largely separate clades of species (i.e., species-groups or above) within the genus, rather than chiefly separating species within such groups.

Key Words.—Insecta, multivariate evolution, phylogenetic characters, natural selection, principal components analysis, discriminant function analysis

The monotypic aphid genus *Pseudessigella* Hille Ris Lambers and its type-species, *P. brachychaeta* Hille Ris Lambers, were described from a single collection in central Asia. This interesting species represents a phylogenetic intermediate between *Eulachnus* del Guercio and *Essigella* del Guercio within the subtribe Eulachnina (Sorensen 1990), and was used as an out-group to root the phylogenetic network devised for *Essigella* (Sorensen 1987a). Because of *Pseudessigella*'s phylogenetic position, it has assumed a new importance for the study of character transformations within the Eulachnina, and for *Essigella* in particular. As a result, Hille Ris Lambers' (1966) descriptions for *Pseudessigella* and *P. brachychaeta*, although sufficient for previous taxonomic and diagnostic purposes, now fail to adequately characterize the variation, within that genus, for several traits that have been found to be important in evolution at the species and species-group levels in *Essigella* (Sorensen 1983, 1988).

This article, and Sorensen (1990), deal with the phylogenetic aspects of the Eulachnina. The latter provided an analysis of discrete, coded phylogenetic traits

and determined the phylogenetic sequence among the genera of the subtribe. This study provides analyses that indicate the multivariate evolutionary interaction of traits in both *Pseudessigella* and *Essigella*, and it serves as a base for future studies of character evolution and transformations within *Essigella* (unpublished data). The paper also redescribes *Pseudessigella* and *P. brachychaeta* in the form previously used for descriptions of *Essigella* species (Sorensen 1988), and that will also be used in a pending generic revision of *Essigella* (unpublished data).

TAXONOMY

Pseudessigella Hille Ris Lambers, 1966

Pseudessigella Hille Ris Lambers 1966, Tijdschrift voor Entomologie, 109: 219.

Type Species.—*Pseudessigella brachychaeta* Hille Ris Lambers 1966, Tijdschrift voor Entomologie, 109: 219–220; by monotypy.

Redescription.—*Viviparous Apteræ*. Body elongate, linear, with few hairs. Antennae five segmented, processus terminalis short. Head very slightly wider than long, unfused with pronotum. Eyes without distinct triommatidia. Rostrum retractile; last rostral segment not subdivided but short, blunt. Mesothoracic notum lightly but entirely sclerotic. Metathoracic notum mostly membranous laterally and posteriorly but with a lightly sclerotized subhemispherical shaped patch anteromesally. Abdominal dorsum with terga I–VII membranous with dorsal and marginal setae on defined sclerotic bases; tergum VIII lightly but entirely sclerotic. Siphunculi as rimmed pores on short truncated sclerotic cones, hairless, base well defined from membranous field of abdominal terga. Basitarsus with five ventral setae, lacking dorsal setae in apterae; metabasitarsus ventrally $1.5\times$ as long as dorsally. Cauda rounded, lacking median protuberance. Profemora dorsoproximad base moderately swollen. Tarsal claws simple, not incised or bifid; tip sharp, relatively drawn out.

Other Morphs.—Unknown.

Diagnosis.—*Pseudessigella* is separated from *Eulachnus* by its five segmented antennae, and from *Essigella* by its simple unincised tarsal claws.

Pseudessigella brachychaeta Hille Ris Lambers, 1966

(Figs. 1–3)

Pseudessigella brachychaeta Hille Ris Lambers 1966. Tijdschrift voor Entomologie, 109: 219–220.

Types.—*Holotype*—viviparous aptera; data: (“WEST”) PAKISTAN. Murree, 4 Jul 1964, R. van den Bosch (P-VII-4d), *Pinus griffithii* McClelland. *Paratypes*—viviparous apterae and nymphs. Holotype and paratypes slides deposited British Museum (Natural History), London, ex Hille Ris Lambers aphid collection.

Redescription.—*Viviparous Apteræ*. *Morphology* ($n = 14$, measurements and counts as: range [$\bar{x} \pm$ SD]): Body length 1.950–2.505 (2.225 ± 0.206) mm. HEAD—Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim slightly greater than $0.5 \times$ diameter of rhinarium, rhinarial membrane not conspicuously protuberant. Length of: antennal segment V 98–118 (106 ± 6) μm , processus terminalis 25–40 (34 ± 5) μm , IV 75–95 (87 ± 5) μm , III 180–220 (204 ± 11) μm , II 73–85 (79 ± 4) μm . Longest frontal setae 5–15 (12 ± 5) μm long, tips incrassate. Head width 226–390 (300 ± 46) μm . Length of: stylets 475–542 (509 ± 24) μm , ultimate rostral segment 70–93 (74 ± 6) μm ; rostral tip reaching slightly past mesocoxae. Head and pronotum not fused, their combined length 390–447 (422 ± 21) μm . THORAX—Length of: mesothorax 304–371 (331 ± 17) μm , metathorax 63–93 (76 ± 10) μm . Meso-, metathorax and abdominal segment I not fused. ABDOMEN—Maximum distal width of flange on

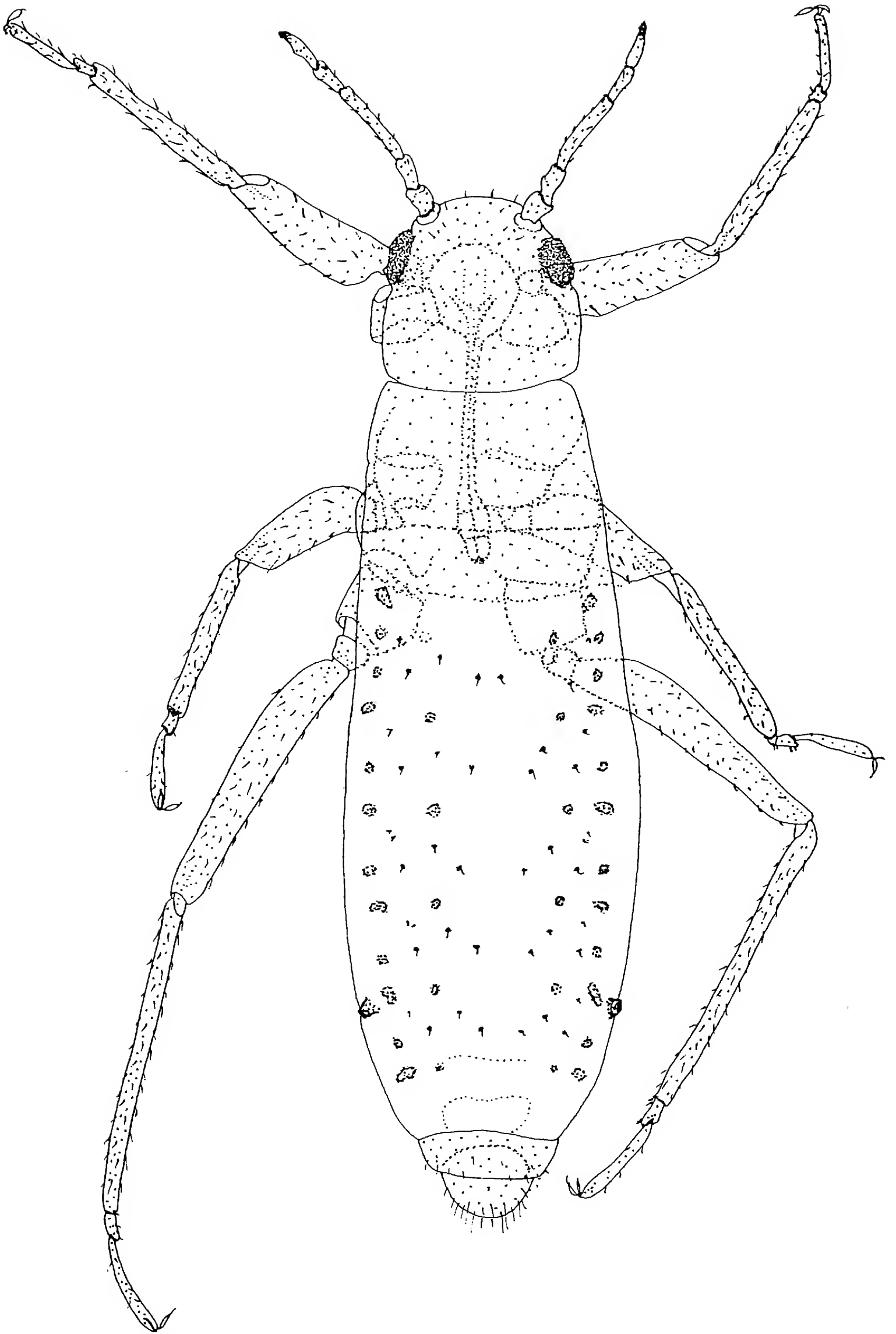


Figure 1. *Pseudessigella brachychaeta* Hille Ris Lambers. Body setae omitted except frontals and setal positions on dorsum of abdomen. Sclerotic areas stippled.

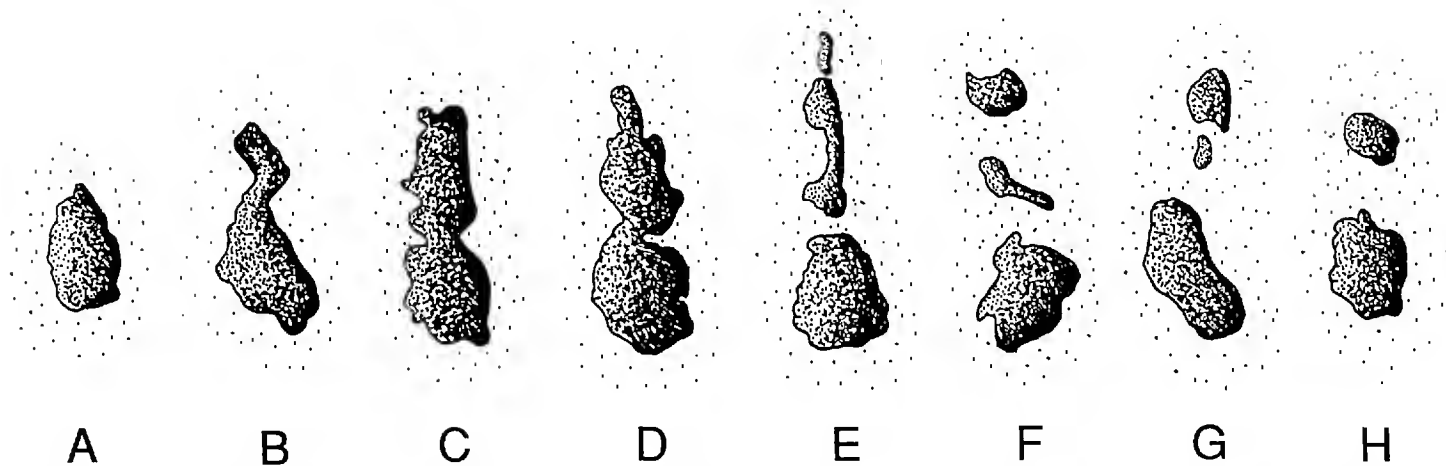


Figure 2. Expression of ventral abdominal sclerites on abdominal segments II-IV in *Pseudessigella*. The sclerites, which serve as muscle attachment points, vary from a single, subelliptical to linear sclerite (A-D), often with constrictions (B-D), to a bipartite (H) or tripartite (E-G) series of sclerites, in which the anterior (E) or usually the central (F, G) sclerite is diminished. (Shading indicates sclerotization; no transformation is implied.)

siphunculi 23-28 (24 ± 2) μm ; siphunculi truncated sclerotic cones, protruding to $0.5 \times$ maximal distal width. Ventral abdominal sclerite shape on segments II-IV (Fig. 2) variable, often linear with posterior enlarged but anterior narrow, sometimes broken into two to several minor plates: the posterior then subquadrate, subcircular to subelliptical and the anterior plate(s) smaller, more irregular, size $0.2-0.5 \times$ posterior plate and more variable in shape from subquadrate, subcircular or subelliptical to asterisk-like, mere specks or absent; entire linear sclerite (or series of broken platelets) 35-95 (63 ± 19) μm long, $1.0-2.0 \times$ metatibial diameter. Dorsal setae on abdominal terga II-IV (Fig. 3) dividable into major and minor series; six major dorsal setae across medial portion of tergum of each abdominal segment, arranged in roughly transverse irregular, meandering or staggered row, positions (if numbered left to right) of setae number 1, 3, 4 and 6 nearly in straight row, but setae number 2 and 5 slightly to moderately anterior of that row, on relatively larger ($12-15 \mu\text{m}$ diameter) scleroites (sclerotized platelets at setal bases), with incrassate tips; minor dorsal setae on relatively smaller scleroites ($8-10 \mu\text{m}$ diameter), like marginal setae but present mesally between lateral most dorsal abdominal muscle

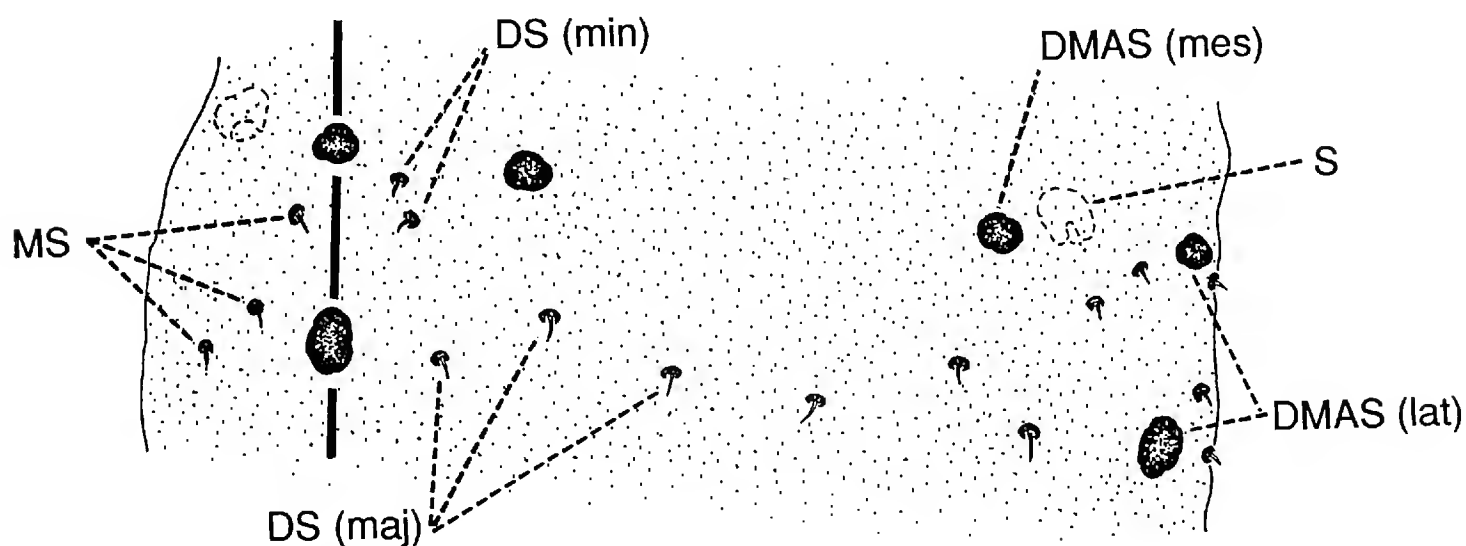


Figure 3. Setal positions on dorsum of abdominal terga II-IV in *Pseudessigella*. The abdominal segment shown is slightly skewed to the right showing more of its left lateral face; items are indicated on one side only. Dorsal muscle attachment sclerites occur as three sclerites on each side of the segment and are represented by a single mesad sclerite, DMAS (mes), and a pair of laterad sclerites, DMAS (lat); the dark bar oriented through the laterad sclerites on the left indicates the "territorial" line that is used here to separate (define) the minor dorsal versus marginal setae. Dorsal setae occur in two series, a transversely oriented and staggered set of six major setae, DS (maj), which cross the center of the segment, and a cluster of no to four minor setae, DS (min), on each side of the segment just mesad to the lateral dorsal muscle attachment sclerites. Marginal setae, MS, occur as a set of two to six setae laterad of all dorsal muscle attachment sclerites. Spiracles, S, that occur ventrally may be confused with other sclerites in slide preparations.

attachment plates and slightly mesad to them, all tips incrassate, arranged in loose cluster(s) anterolaterally and also sometimes posterolateral of major dorsals, each side with 0–4 (1.7 ± 0.8) component setae. Marginal setae (lateral to lateral most dorsal abdominal muscle attachment plates) with incrassate tips, on small scleroites (8–10 μm diameter), 4–12 per segment, each side with 2–6 (4.6 ± 0.6), apparently arranged in two to four subgroupings. Abdominal tergum VIII with 10–16 (14.3 ± 1.8) hairs, 10–15 (11 ± 2) μm long, tips incrassate, subregularly placed. Cauda rounded, caudal protuberance absent, longest caudal setae 40–80 (67 ± 10) μm long, tips sharp. LEGS—Length of: metafemora 561–646 (624 ± 30) μm , metatibiae 637–741 (700 ± 30) μm ; longest dorsal setae on central one-third of metatibiae 8–18 (12 ± 3) μm long, 0.1–0.5 \times metatibial diameter, tips incrassate, approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae 23–30 (27 ± 3) μm long, tips sharp. Length of: metabasitarsus 50–88 (69 ± 9) μm , metadistitarsus: 225–255 (243 ± 8) μm . Ratio of metabasitarsus to metadistitarsus averaging 1.0:3.6, ranging from 1.0:2.8 to nearly 1:5. *Pigmentation.* Color in life pale green (Hille Ris Lambers 1966). Prepared specimens: background of sclerotic body dorsum pale (to approximately 40% pigment density [as solid black in a 54 line/cm screen]), unicolorous. Frontal setal bases concolorous with surrounding terga, undifferentiated. Thoracic muscle attachment plates dusky, inconspicuous to conspicuous. Dorsal and marginal setal bases on abdomen dark, conspicuous, arising from distinct scleroites that contrast the membranous abdominal field. Dorsal muscle attachment plates of abdomen, spiracular plates, siphuncular cones and ventral abdominal sclerites pale, usually dusky light brown (to 60% pigment density), conspicuous. Cauda, anal and subgenital plates concolorous, slightly less dark than head and mesothorax. Antennal segments V and IV slightly to moderately dusky over entire segment, to moderately brown distally, III pale to moderately dusky distally, II concolorous with proximad section of III and I concolorous with frons. Pro-, meso- and metatibiae dusky, concolorous, slightly more dusky than remaining sclerotic body dorsum.

Ultimate Stadium Nymphs of Viviparous Apteræ.—Nonmorphometrics and pigmentation of prepared specimens as described for viviparous apteræ.

Viviparous Alatae, Males, Oviparae, Fundatrices.—Unknown.

Diagnosis.—*Pseudessigella brachychaeta* is the only species in the genus, and the only known linear-bodied aphid feeding on the needles of Pinaceae which has both a five segmented antennae in adults and simple, unincised tarsal claws.

Host.—*Pinus griffithii* McClelland, stated to be "*Pinus excelsa*" on the type series slides and "*Pinus wallichiana (excelsa)*" in the original description (Hille Ris Lambers 1966). *Pinus wallichiana* A. B. Jacks and *Pinus excelsa* Wallich ex Lambert are synonyms of *P. griffithii* (Critchfield & Little 1966, Mirov 1967, Little & Critchfield 1969).

Range.—Known from one collection in ("West") Pakistan at Murree. Potential native range (see discussion), assumed to be the distribution of *P. griffithii* (Fig. 4), is throughout Himalaya Mountains to eastern Afghanistan, northeastern Burma and Yunnan Province, China (Troup 1921, Vavilov 1959, Critchfield & Little 1966, Mirov 1967); in mid- and high elevation forests, especially in drier inner valleys (Critchfield & Little 1966). Neither the collection sample nor description quote an elevation, but Hille Ris Lambers (1966) described several other new aphid species, also taken by van den Bosch in a sequence of field collections at Murree between 30 Jun–5 Jul 1966, and cited elevations of 2132–2284 m (7000–7500 ft) for those collections. These elevations agree with Mirov's (1967) notation that in the "Murree Hills, Rawalpindi," *P. griffithii* grows from 1200 m (in cool, moist conditions) to above 2000 m, where it occurs in pure stands or mixed with broad-leaf trees.

Etymology.—The species was named for its short setae.

Discussion.—*Pseudessigella* is phylogenetically intermediate between *Eulachnus* and *Essigella*, the more ancestral and derived genera respectively, of the subtribe Eulachnina (Sorensen 1990). *Pseudessigella*, like *Eulachnus*, appears to be

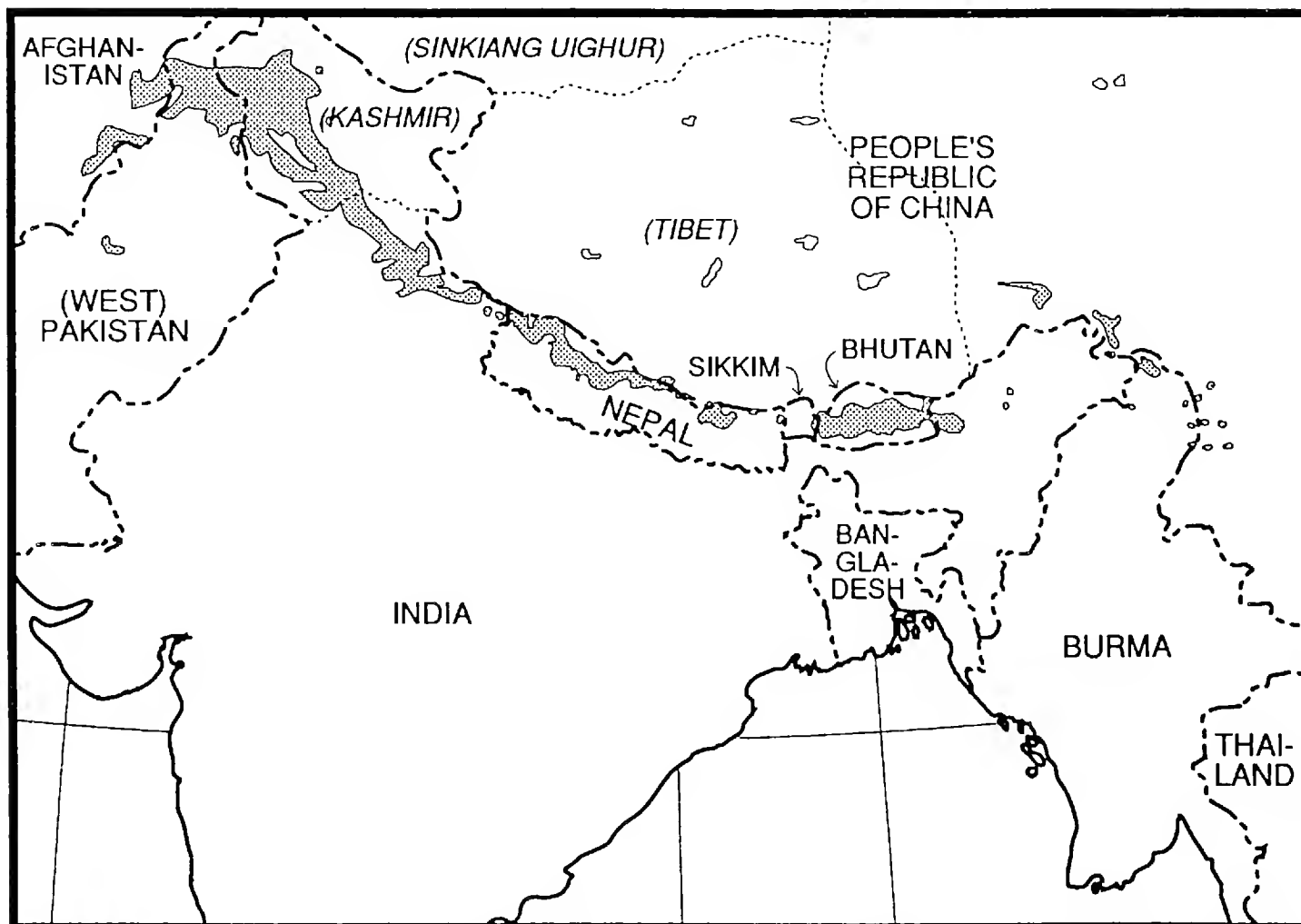


Figure 4. Potential range of *Pseudessigella brachychaeta* (= distribution of *Pinus griffithii* [Critchfield & Little 1966]).

paraphyletically defined; although monotypic, *Pseudessigella* lacks a unique defining autapomorphy. *Pseudessigella* shares with *Essigella* the following apomorphic character states: differentiation in size, shape, tip condition or projection angle of dorsal versus ventral setae on antennal segments and tibiae (partially shared with *Eulachnus*); absence of secondary rhinaria on ultimate and penultimate antennal segments (a homoplasy with *Schizolachnus*); a reduction of antennal segments to five in adults; and representation of abdominal tergum VIII as a single, entire sclerotized field not apparently formed from fused lateral sclerites associated with dorsal setal bases (see Sorensen 1990). *Pseudessigella* resembles *Eulachnus* in having the following symplesiomorphies: unincised tarsal claws, a membranous abdominal dorsum, and a head separated from the pronotum in adult viviparous apterae.

Slide mounted adult viviparous apterae of *Pseudessigella* are somewhat superficially similar to late stadium nymphs of the apterae of *Essigella*, especially the most plesiomorphic species (e.g., "group I" of Sorensen [1987a]: *E. kathleenae* Sorensen and *E. kirki* Sorensen, although usually darker than both) or slightly more derived species (e.g., "group II" of Sorensen [1987a]: *E. fusca* Gillette & Palmer and its relatives). Adult *Pseudessigella* differ most noticeably from the nymphs of any *Essigella* species (other than in adult genitalic traits) by their elongated metabasitarsus to distitarsus ratio; averaging 1.0:3.6 for *Pseudessigella* versus slightly over 1.0:2.05 for *E. kathleenae*, the longest among *Essigella*. This "long distitarsus" ratio probably represents a relative plesiomorphy for *Pseudessigella* (see discussion of analyses below) within the Eulachnina, despite impli-

cations of Mamontova (1972) to the contrary for the Cinarini, and is more similar to conditions in *Cinara* and *Schizolachnus*.

The tarsal trait is homoplasious among the Cinarini, including the Eulachnina (Sorensen 1990). In contrast to *Pseudessigella*, *Eulachnus* and *Essigella* appear to have homoplasiously evolved an apomorphically shorted metatarsal ratio among species-groups occupying differing niches in varying pine groups (unpublished data). In at least the case of *Essigella* this may possibly represent a "resource-tracking" attribute (sensu Brooks 1981, see Moran 1986). A more detailed discussion of the relationship of *Pseudessigella* within the Eulachnina is dealt with in Sorensen (1990), which comments more fully upon character states thought to be of phylogenetic significance for the genus and discusses Mamontova's (1972) contrasting phylogenetic concepts and character transformations, considered erroneous in part, for the eulachnine aphids.

The phylogenetic relationships among (Sorensen 1990), and biological associations within (Sorensen 1987a), the eulachnine genera make ecological predictions possible for *Pseudessigella* allowing future corroboration. Among the Eulachnina, *Pseudessigella* and *Eulachnus* are Palaeartic, although the latter has been introduced into the Nearctic where it apparently feeds chiefly on cultivated old world pines; I have taken *Eulachnus* only on Palaeartic species of cultivated *Pinus* in the western Nearctic (unpublished data), despite intensive collecting for *Essigella* on natural and planted stands of native Nearctic pines (Sorensen 1983). *Essigella* is Nearctic and shows phylogenetic associations among *Pinus*, but dissident derived species (in "group III," Sorensen [1987a]) also feed upon *Pseudotsuga* and *Picea*. Because nothing is known of the biology of *P. brachychaeta*, except that the single collection of it in the Himalayas was on *Pinus griffithii*, biological predictions for *Pseudessigella* must be based on *Eulachnus* and especially *Essigella*, particularly "groups I and II" (Sorensen 1987a).

Based upon biological knowledge of "group I" *Essigella* (Sorensen 1983, 1987a, 1988, unpublished data), I suspect that *P. brachychaeta* shares the rather monophagous feeding habits of *E. kathleenae* and *E. kirki*. It, therefore, seems reasonable that the range of *Pinus griffithii* itself (Fig. 4) should be a probable indicator of the potential native distribution of *P. brachychaeta*, as has been found in these group I *Essigella*. The host of *P. brachychaeta*, *Pinus griffithii*, is a haploxylon pine in the section *Strobis*, subsection *Strobi* of *Pinus* (*Strobis*) (Little & Critchfield 1969). Subsection *Strobi* also contains the hosts of these two most primitive *Essigella*: *Pinus lambertiana* Douglas for *E. kathleenae*, and *Pinus flexilis* James and *P. strobiformis* Engelm (a slightly overlapping allopatric species previously considered a variation [*reflexa* Engelm] of *flexilis* [Critchfield & Little 1966: 7, map 8]) for *E. kirki* (Sorensen 1987a, 1988).

Species of *Essigella* and *Eulachnus* are fast moving when disturbed, and relatively solitary; these behavioral traits are assumed to be typical of *Pseudessigella* also. I suspect the (now unknown) alatae of *Pseudessigella* are (will be found to be) relatively uncommon, because alatae of *E. kathleenae* and *E. kirki* remain unknown despite extensive sampling (Sorensen 1983), although alatae of more derived *Essigella* groups, particularly some group III representatives (e.g., *E. californica* (Essig) and *E. hoerneri* Gillette & Palmer) can be quite common.

In previous phylogenetic studies on *Essigella*, I have referred to *P. brachychaeta* using the acronym "PLES" (Sorensen 1983) and "Sp. X" (Sorensen 1987a). In

the latter study, which used a maximum-likelihood algorithm (Felsenstein 1984) to construct a phylogenetic network based upon centroid values on discriminant functions, *E. kirki* (Sorensen 1987a: sp. K) was considered to be the most plesiomorphic *Essigella* species because it showed the shortest distance on the phylogenetic pathway to *Pseudessigella*; *E. kathleenae* (Sorensen 1987a: sp. J) was slightly more "advanced" on that network. This study, however, provides evidence that *E. kathleenae*, rather than *E. kirki*, displays several attributes that may be more plesiomorphic in their similarity to those of *Pseudessigella*: (a) *P. griffithii*, the host of *Pseudessigella*, is genetically close enough to be one of the few pines that hybridizes with the *Pinus lambertiana* (Sorensen 1987a; W. B. Critchfield, personal communication), the host of *Essigella kathleenae*: (b) *E. kathleenae* displays the relatively highest (more plesiomorphic) ratio of the metadistitarsus to metabasitarsus within *Essigella* (Sorensen 1988); and (c), perhaps most convincing, *E. kathleenae*, rather than *E. kirki*, shows a higher similarity value for shape component variance with *Pseudessigella* (see multivariate evolution section).

Material Examined.—The type-series viviparous apterae and nymphs have been examined, and represent the only known specimens.

MULTIVARIATE EVOLUTIONARY RESPONSES FOR CHARACTERS

In any organism, continuous phenotypic variation is caused by genetically correlated characters that are linked by many covarying genes (Lande 1980). The evolutionary aspects of such correlated traits are assumed to be predominantly under the genetic influence (Falconer 1981). Each gene has a relatively minor influence in the evolutionary change of either the overall phenotype or any particular phenotypic attribute, because these changes are due to an integrated, additive genetic effect, plus minor additive environmental influences (Lande 1985, 1988). The evolution of species and character interactions under such quantitative genetic systems is based upon an (admittedly simplistic) phenotypic model for the multivariate evolution of correlated morphological character suites developed by Lande (1979). This model has been employed previously to determine the phylogenetic relationships among aphids (Sorensen 1983, 1987a) and birds (Schluter 1984), as well as phenological shifts in phenotype between sibling species of leafhoppers (Sorensen 1987b, Sorensen & Sawyer 1989).

Lande's model allows reconstruction of the net gradients of genetic selection (taken as phenotypic responses where the environmental component is effectively null) within and between groups with approximately equal genetic covariance matrices. The model permits an estimation of the degree to which net selective pressures have acted upon characters within suites of correlated phenotypic traits during evolution. Under this multivariate model of evolution the traits respond to given historical net selection gradients, to drive the mean group phenotype for a species or population through the dimensional multivariate evolutionary space defined by all such gradients.

For a given individual's phenotype, a single trait, z_i , contributes to the evolution of that phenotype and thus itself evolves in relation to other traits, z_j , as (Lande 1979: equation 7b):

$$\Delta \bar{z}_i = \sum_{j=1}^m G_{ij} \partial \ln \bar{W} / \partial \bar{z}_j$$

where minor selective change on trait z_i is the sole cause of differences in Malthusian mean fitness ($\partial \ln \bar{W} / \partial z_i$); and z_i shows no correlated effects, whereas other traits, z_j , are constant with $j \neq i$ (Lande 1979). Therefore, over each generation, changes in the trait z_i include genetic gains from selection that act upon both it and z_j , as other genetically correlated characters. The measurement of selection on correlated traits is discussed in more detail by Lande & Arnold (1983).

Principal components analysis (PCA) is particularly suited as a practical, analytical probe to determine the multivariate evolutionary responses of characters in covariant suites as they react in unison to historically imposed selection regimes (Sorensen 1987a, b; Sorensen & Sawyer 1989). In a usual (Q-type) PCA, each eigenvector represents a historical net natural selection gradient (as: $\nabla \ln \bar{W}$, sensu Lande 1979) in multivariate evolution; the mean group phenotype of a species evolves along these gradients (eigenvectors) due to the concert action between its genetic covariance matrix and the vector as a selection regime. The relative input weight of each character on any given eigenvector shows the relative amount of its partitioned and sequestered variance that can be attributed to the covariant character suite that is defined by that vector (Sorensen 1987b, Sorensen & Sawyer 1989).

During multivariate evolution, the characters in any such covariant suite of traits respond to the net evolutionary selective pressures of their eigenvector in an integrated fashion, according to the relative degree and sign of their vector loading coefficients. All traits belong in varying degrees to all covariant character suites, with each suite responding to a particular vector's selection gradient; this is because the traits each have a contributing (weighted) input on each eigenvector which varies among the vectors.

During evolutionary response to selection pressures, each covariant suite of traits is driven chiefly by dominating traits ("drivers") which are those characters with the highest absolute loading coefficients (and correlations) on the given vector. In contrast, traits with near zero loading coefficients on any vector are more subordinate for that suite and accordingly more neutral in response to the net selection pressures defined by that eigenvector as an evolutionary selection gradient. Therefore, when selection is imposed upon any suite, it acts largely upon the dominating "driver" traits but causes modification of all traits in proportion to their loading input and correlation for the given vector.

Although stabilizing selection maintains linkages, and thus integrated reaction to selection, among the traits in each character suite, if enough disruptive selection force is applied to a given trait in a suite it may cause the "shearing" of that trait from the suite. The remaining traits in the suite would be initially modified also by the disruptive selection, along with the trait to which it was applied, but they would eventually "break-away" as an integrated unit and return to their former expression values leaving the disrupted trait to evolve separately from the suite. Zeng (1988) discusses the complicating effects of stabilizing and disruptive selection upon characters in multivariate evolution.

Character interaction during multivariate evolution can be examined using an R-type analysis in PCA. In an R-type analysis, each of the individuals, rather than the attributes (as in Q-type PCA), provides the input coefficient along the orthogonal eigenvectors, and the positions of the original characters are plotted along these vectors in the I-space defined by the values derived from individuals

(Williams & Dale 1965, Sneath & Sokal 1973). An R-type analysis thus depicts spatially the relative degree of association and interaction between each trait along orthogonal eigenvectors as character, rather than populational, responsive models of Landean gradients of net natural selection.

R-type PCA also allows a perspective dependant portrayal of the relative integrated response of functional (virtual) groups of characters to several independent selection gradients (as orthogonal eigenvectors). Such functional groups of characters may show an orchestrated response to simultaneously imposed multiple selection regimes during multivariate evolution. These virtual groups of characters are recognizable by their relative spatial affiliations when more than one R-type eigenvector is plotted; the apparent groups of characters may react relatively similarly to the equally induced selection pressures on the vectors. Such virtual character groups defined by multiple vector plots may exist over any partial subsets of the summarized $n-1$ eigenvectors.

Because of its usefulness as an analytical probe, R-type PCA was used here to determine the historical interaction of characters among the taxa during the multivariate evolution of the eulachnine aphids.

Methods

Determination of "Shape" as a Character Component.—To determine the relative influence and stability of shape component variance among traits during the multivariate evolutionary episode between *Pseudessigella* and *Essigella*, and within group I (Sorensen 1987a) of *Essigella*, data were analyzed for all taxa and compared. Although many controversial criteria and experimental methods have been advanced to completely partition multivariate "shape" from "size" in data matrices (e.g., Burnaby 1966; Bookstein 1986, 1989; Bookstein et al. 1985; Humphries et al. 1981; Rohlf & Bookstein 1987; Somers 1986, 1989; Sundberg 1989) none have been completely successful, and all adulterate the generated evolutionary space by various methods, such as shearing. To avoid the philosophical problems inherent in such methods, especially with reference to existing models of multivariate evolution, it was decided to represent "shape" here as simply principal component vectors 2- n , with vector 1 taken as (chiefly) a size factor if there appeared to be high loadings and correlations for traits such as segmental body lengths, which normally are overtly general-size dependant.

Material and Data Examined.—Analysis of *Pseudessigella brachychaeta* employed the paratype adult viviparous apterae ($n = 14$), which represent the only known collection (see taxonomy: material examined). Analyses of *Essigella* used exemplars of adult viviparous apterae that represented the nonclonal, intraspecific variance shown within *E. kathleenae* ($n = 13$, morphometric data in Sorensen [1983: appendix E1, "KATH"]), *E. kirki* ($n = 12$, morphometric data in Sorensen [1983: appendix E1, "HOTT"]), and all *Essigella* species ($n = 255$, morphometric data in Sorensen [1983: appendix E1, all acronyms excluding "PLES"]); hereafter, the use of "*Essigella*" refers to the collective concept of its pan-generic variance, including that shown by *E. kathleenae* and *E. kirki*. Locality data for examined material of *E. kathleenae* and *E. kirki* is listed in Sorensen (1988); it is available for all examined material of *Essigella* in Sorensen (1983) by cross-checking the collection numbers in appendix E1 with locations in appendix A1.

All specimens were measured from the slide mounted material, employing the

Table 1. Morphometric characters.

Number	Acronym ^a	Character descriptions
1	LBODY	length of body, vertex to posterior of abdominal segment VIII excluding cauda.
2	LANT5	length of total antennal segment V.
3	LANT5PT	length of processus terminalis, proximal rim of accessory rhinaria to tip.
4	LANT4	length of antennal segment IV.
5	LANT3	length of antennal segment III.
6	LANT2	length of antennal segment II.
7	LHFRON	length of longest seta on the frons.
8	WOANT	(body) width taken at lateral most (outer) portion of the rim of the antennal sockets.
9	LSTY	length of the stylets.
10	LUROST	length of the ultimate rostral segment.
11	LHEAD	combined length of the unfused head plus pronotum, along the median dorsal body axis.
12	L2THOR	length of the mesothoracic notum, along the median dorsal body axis.
13	L3THOR	length of the metathoracic notum, represented as a sclerotic plate in the otherwise membranous metathoracic field, along the median dorsal body axis.
14	WSIPH	maximal distal width of the siphuncular flange.
15	LVABSC	maximum length of the longest ventral abdominal muscle attachment sclerite(s) on abdominal segments II-IV (combined length in the case of bi- or multi-partite subsclerites in quasilinear array).
16	NHAB2DT	maximum total number of combined major and minor dorsal setae (between dorsal muscle attachment sites) on abdominal terga II-IV.
17	NHAB2M	maximum number of marginal setae (lateral to dorsal muscle attachment sites) on abdominal terga II-IV.
18	NHAB8	number of setae on abdominal tergum VIII.
19	LHAB8	length of longest seta on abdominal tergum VIII.
20	LHCAUD	length of longest seta on cauda.
21	L3FEM	length of metafemur.
22	L3TIB	length of metatibia.
23	LH3TIBD	length of longest seta along the central one-third of the dorsal surface of the metatibia.
24	LH3TIBV	length of longest seta along the central one-third of the ventral surface of the metatibia.
25	L3TAR1	length of the metabasitarsus.
26	L3TAR2	length of the metadistitarsus.

^a Acronym for trait used in Sorensen (1983).

26 traits (Table 1) used previously for *Essigella* (Sorensen 1983, 1987a, 1988). Measurements were done with a Zeiss compound microscope using an ocular scale at up to 400 \times , and are assumed accurate to 2 μ m for the smallest structures observed. The data for *Pseudessigella*, *E. kathleenae* and *E. kirki* were log-transformed to minimize the influence of scaling. The data for *Essigella*, however, were not log-transformed; analyses of log-transformed versus nonlog-transformed data for sequestered parts of that matrix suggested that the obtained vector loading coefficients did not appear to differ significantly.

Algorithms and Analyses.—All data were subjected to an R-type principal component analysis. Analyses for *Pseudessigella*, *E. kathleenae* and *E. kirki* were conducted on a Macintosh® computer and used Statview512+® (BrainPower, Inc., Calabasas, California). Analyses for *Essigella* were conducted on a CDC6400 computer using the algorithm “PNCOMP” (Duncan & Phillips 1980); analytical checks of smaller subsections of the *Essigella* data indicated that the output for PNCOMP was equivalent to that of Statview512+, as used for the other data. All PCA solutions yielded unrotated, orthogonal vectors, and the derived loading coefficients for the characters were used to portray each trait’s influence on the vectors. To determine the multivariate diagnostic value of characters for separating all species within *Essigella*, that matrix underwent discriminant function analysis (SPSS version 7 subprogram “DISCRIMINANT,” direct selection, Wilks- λ criterion; Klecka [1975]).

Results of the analysis on *Pseudessigella* are presented using histogram illustrations of the loading coefficients were created with Excel® (Microsoft Corporation, Redmond, Washington). For *Pseudessigella*, the virtual groupings of characters that occur in the evolutionary space defined by multiple vectors, were assessed by transferring the vector loading coefficients derived from the unrotated factor matrix to MacSpin® (D² Software, Austin, Texas), a three-dimensional X-Y-Z coordinate rotation program on the Macintosh; scattergrams composed of orthogonal combinations of multiple vectors were then rotated to assess the potential groupings of characters in the differing rotational perspectives.

To determine the relative importance of each trait upon any generated eigenvector, the vector loading coefficients of the traits were grouped and ranked into three classes. This was done by dividing the scale between the highest and lowest absolute (sign-less) vector loading coefficients for a given vector into equal sized class partitions, and then assigning each trait to its appropriate class, based upon its loading coefficient for the vector. The values of shape influence for traits were determined for all taxa by assigning to each trait its greatest ranking on either vectors 2 or 3 of the PCA (as the dominant shape vectors) for the taxa. The ranking of traits as multivariate separators within *Essigella* was similar, except that discriminant vectors 1–3 were ranked.

Shape Stability between Taxa.—The evolutionary stability of shape components between pairs of taxa was calculated as intertaxon similarities. These were determined by assigning a distance value of 0.5 to any one-rank-step change for a character between two taxa; a value of 1.0 was assigned for any two-rank-step change. The summed total distance between any given taxon-pair was then divided by 26, which represented the total potential distance for changes among all characters. The derived distance fraction was converted to a similarity fraction by subtracting it from 1.0, which represented absolute similarity.

Results and Discussion

Histograms in Figs. 5 and 6 depict the relative contributions of the traits for *Pseudessigella*, among the character suites defined by vectors 1–6. In those figures, the trait contributions for each suite are represented as the absolute values for loading coefficients of the traits on vectors 1–3 (Figs. 5A–C) and 4–6 (Figs. 6A–C). Despite the log-transformation conducted on the data, vector 1 (Fig. 5A) seems to retain a quite high affiliation as a general-size component. The relative influence

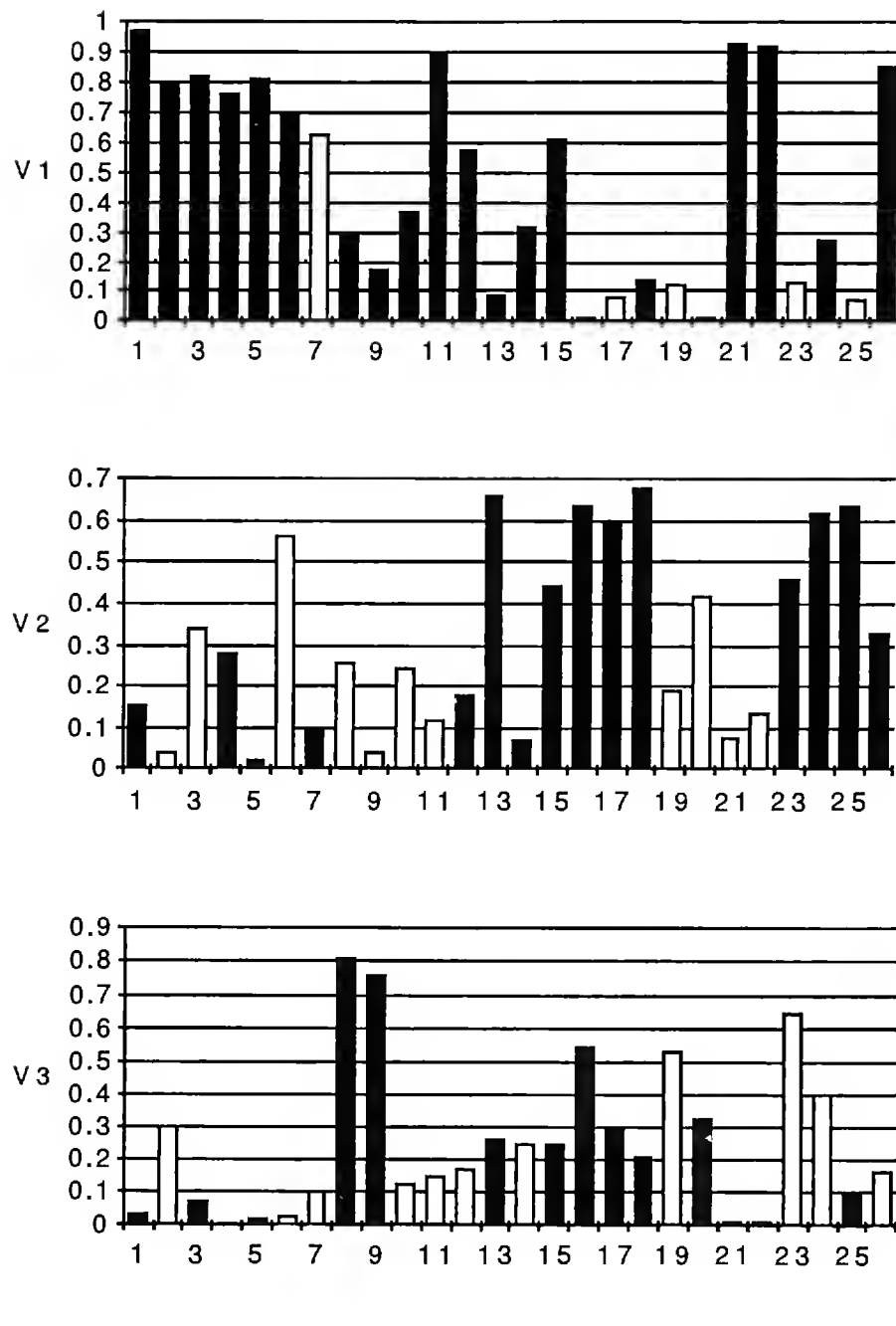


Figure 5. Histograms indicating each trait's relative influence in covariant character suites. Each suite is represented as an orthogonal PCA vector upon which the trait responds in proportion to its vector loading coefficient value; a black bar indicates positively loading traits, a white bar indicates negatively loading traits. (A) vector 1, (B) vector 2, (C) vector 3.

of allometric size versus shape, as separable components of total variance, is illustrated in Fig. 7A, which compares the percentage of summed absolute vector loading coefficients for the traits on vector 1 (Fig. 7A: white), as a size component, versus vectors 2–6 (Fig. 7A: black), as shape components. The relative contribution of each trait to size or shape variance is also shown in Fig. 7B, where all influences have been scaled to 100% rather than represented as the summation of vector loading coefficients, as in Fig. 7A. In Fig. 7B the contribution of general size to each trait is shown in white, while its shape contributions are in nonwhite; shape contributions on vectors 2 and 3 (the two most dominant shape vectors) are in gray, and those of vectors 4–6 are in black. An approximation of “uniqueness,” or differentiation, among the traits is depicted in Fig. 7C, as variance not due to common factors in the sense of pleiotropy. A spatial portrayal of character groupings based upon the dominant three shape factors, vectors 2–4, is shown for *Pseudessigella* in Figs. 8A–B. Figure 9 depicts, in tabular form, the rankings of shape variance across all taxa, and the diagnostic value of traits for group

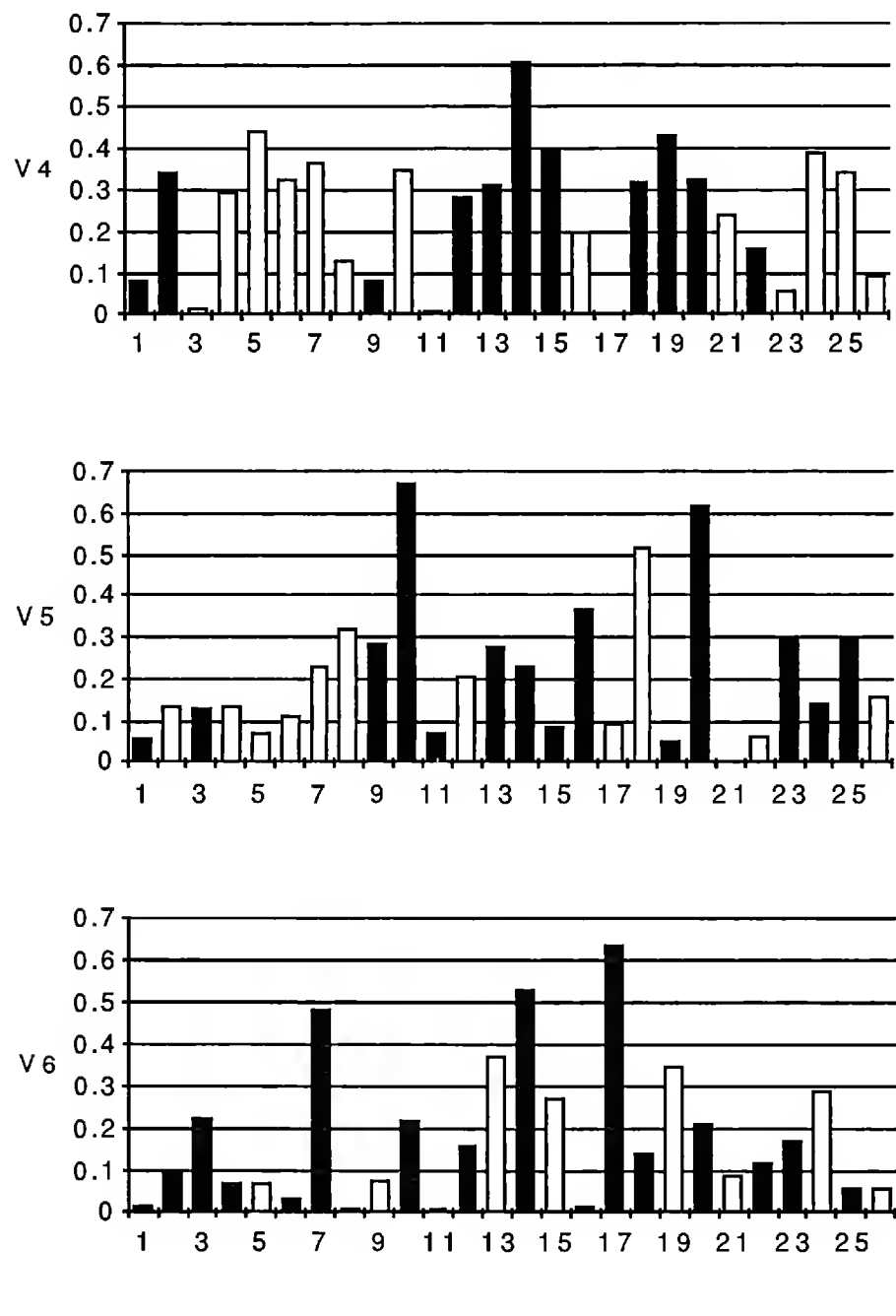


Figure 6. Histograms indicating each trait's relative influence in covariant character suites. Each suite is represented as an orthogonal PCA vector upon which the trait responds in proportion to its vector loading coefficient value; a black bar indicates positively loading traits, a white bar indicates negatively loading traits. (A) vector 4, (B) vector 5, (C) vector 6.

separation within *Essigella*. Figure 10 shows the relative similarity in shape component stability of the taxa analyzed.

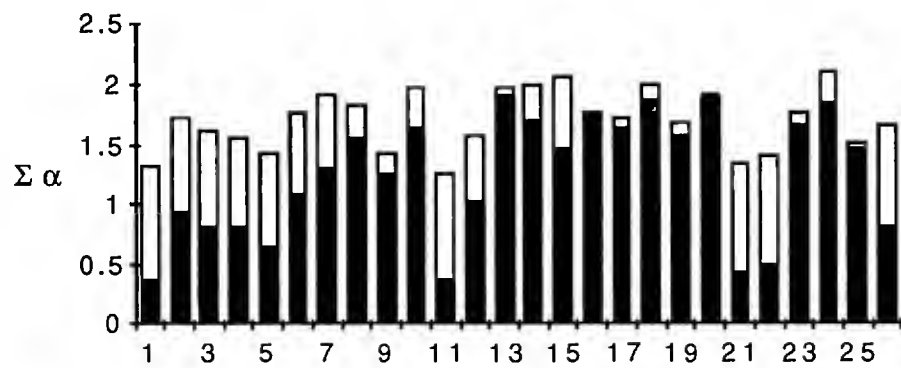
Multivariate Character Suites within Pseudessigella.— The dominant six vectors derived from the *Pseudessigella* matrix accounted for 84.0% of the total variance (34.1, 15.2, 11.8, 8.9, 7.7 and 6.3%, respectively for vectors 1–6), indicating that character variation within *Pseudessigella* is reasonably complex, as found for various species-groups within *Essigella* (Sorensen 1983).

Vector 1 (Fig. 5A) is interpretable as a size factor because most body appendage lengths (characters 1–6, 11, 15, 21, 22 and 26) load and correlate highly and positively upon it. Only those traits poorly related or unrelated to size were not influential on vector 1. Notable exceptions are those traits (13 and 25 as lengths for the metathoracic nota and the metabasitarsus) which might have been expected to load more strongly with general-size; trait 7 (frons setal length) loads highly but negative; traits 8, 9, 13, 14, 16–20, and 23–25 show relatively minor and often negative relations with general-size.

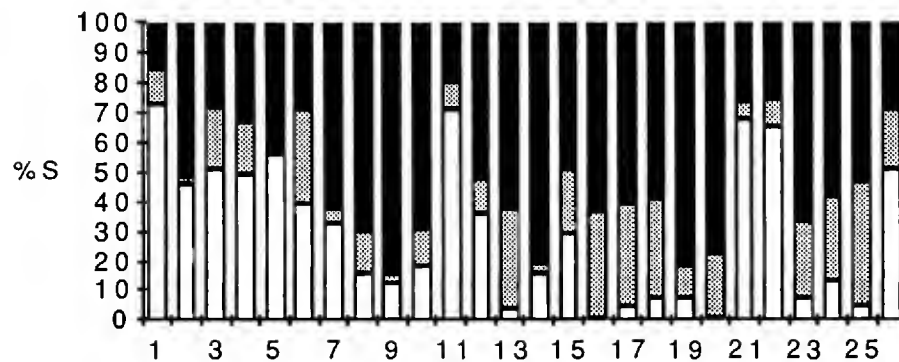
Vector 2 (Fig. 5B) represents a covariant suite driven largely and positively by traits 13, 16–18, 24 and 25, and to a lesser extent by traits 15 and 23; the suite is driven negatively by trait 7 and less so by trait 20. This suite involves the metathoracic nota, the ventral abdominal sclerites, the number of setae on abdominal segments, the metatibial setae and the metabasitarsus, all of which interact negatively with the length of the frons setae. The character suite shown by vector 3 (Fig. 5C) is driven positively by traits 8 and 9, and less so by trait 16; it is driven most negatively by traits 19 and 23. Vector 3 involves body width, stylet length and the number of dorsal setae on the abdomen, all of which interact negatively with the length of setae on abdominal tergum VIII and the length of the dorsal setae on the metatibiae. The suite for vector 4 (Fig. 6A) is more complex, with several traits giving a moderate interactive influence; the suite is driven most strongly, however, by trait 14, a siphuncular width function. The suite for vector 5 (Fig. 6B) is dominated positively by traits 10 and 20, and negatively by trait 18. It involves the lengths of the ultimate rostral segment and the caudal setae, which interact antagonistically with the number of setae on abdominal tergum VIII. The suite for vector 6 (Fig. 6C) is driven positively by traits 7, 14, and 17, with traits 13 and 19 reacting negatively and less strongly. The setae on the frons, the width of the siphunculi and the number of marginal setae on the abdominal segments react positively in this suite, while the metathoracic notum and the length of setae on abdominal tergum VIII react negatively.

For this *Pseudessigella* matrix, the summation of the absolute values for the factor loading coefficients of traits on vectors 2–6 functionally represents the proportion of variance attributable to multivariate “shape” for each trait (Fig. 7A). “Shape” variance, in this sense, is defined as (usually) variance that is subordinate and orthogonal to “size,” or the residual variance after the general-size allometric function is divorced from the matrix. Thus the summed coefficients across vectors other than 1 can be taken to represent shape, in as much as vector 1 actually represents a true approximation of theoretical general-size factor for the matrix. This is quite important from the view point of multivariate evolution, because such models generally assume that genetic covariance matrices are static and involve little or ideally no changes in “shape” over short periods of evolutionary time. Functionally, it is relatively easy for groups that differ only in “size” to evolve “apart” in response to selection; all that is required is a differential, allometric evolutionary response to selection where the differing group means slide away from one another, up or down a multivariate regression line that represents the general-size factor. This kind of evolutionary response does not change “shape” because it does not modify the slope or relative elevation of the allometric multivariate regression line in n -dimensional evolutionary space.

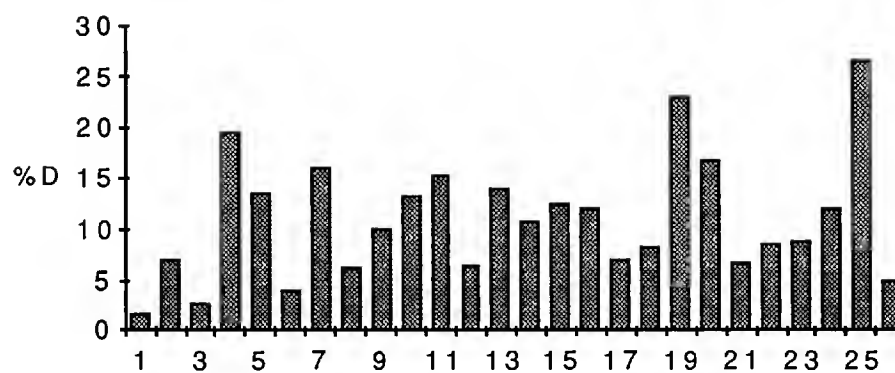
In contrast, evolving a difference in “shape” requires expending considerably more “evolutionary energy.” This is because the elevation and/or slope of the multivariate regression in space must be changed by disruptive and stabilizing selections, which realign the genetic correlations among characters on the shape vectors that are orthogonal to the general-size factor. The amount of difficulty involved in shape evolution depends on the strength of disruptive selection, the amount of pleiotropic linkage for those traits being selected, and the degree of stabilizing selection exerted upon the character suite involved under selective pressure (see Zeng 1988).



A



B



C

Figure 7. Histograms for *Pseudessigella* indicating: (A) the relative contributions of multivariate "shape" (black), as the summed absolute values of the vector loading coefficients [α] for vectors 2–6, and "size" (white) as the absolute values of vector loading coefficients for the traits on vector 1; (B) the scaled contribution of each trait, as a percentage of size/shape [S], to size vector 1 (white), shape vectors 2 and 3 (gray), and shape vectors 4–6 (black); (C) "uniqueness" among the traits, as the percentage of their differentiation [D], derived as the reciprocal of communality (an indication of the degree of genetic linkage) for the traits.

The cost of shape evolution is indicated by Lemen & Freeman (1984), who note that differing bat genera within the Phyllostomidae are quite conservative for intrageneric shape variance. In those genera intrageneric shape averaged only 1.5% of total variance, while size averaged 35%. The conservation of shape change is further demonstrated intraspecifically by the conclusions of Holman & Kindlmann (1987), whose data indicate that shape changes are ontogenetically fixed between instars of the pea aphid, *Acyrtosiphon pisum* (Harris), in the allometry of the developing antennal and leg segments.

In *Pseudessigella*, the summarized "shape" variance among traits varies considerably, as depicted by the "skyline" atop the black bars in Fig. 7A. This figure shows the stacked summation of each trait's absolute loading coefficients for all vectors. The white bar component for each trait shows the character's size con-

tribution, and the overall “skyline” atop the white bars shows the degree of total contribution by each trait to the overall variance represented by vectors 1–6 (80% of the total variance). Traits that load high on vector 1 (Fig. 5A) generally have larger proportions of white to black in Fig. 7A. These traits, which tend to be segmental lengths, form a character group which isolate on vector 1 (Fig. 5A); they are strongly linked pleiotropically and basically respond to selection for allometric size variation. Other traits that load heavily on vectors 2–6 (Figs. 5B–C, 6A–C) show a much higher ratio of shape to size in Fig. 7A; for example, note that trait 25, metabasitarsus length, and trait 20, the length of caudal setae, among others, show predominantly shape variance.

Because Fig. 7A shows that the traits differ in their absolute contributions to the variance sequestered among the vectors, Fig. 7B was created to more easily portray how the relative contributions of each trait are partitioned. The contributions in Fig. 7B are scaled to 100%. Again, the vector 1 general-size contribution is white, but the shape components (Fig. 7B: nonwhite) are partitioned into the contributions of vectors 2 + 3 (Fig. 7B: gray), and those of vectors 4–6 (Fig. 7B: black). Because each subsequent eigenvector decreases in its proportion of total variance in the data matrix, vectors 2 and 3 together represent 27% of the overall variance, after the 34.1% from size vector 1 is accounted for; the three less dominant shape vectors, 4–6, together account for an additional 22.9% of the variance. All other shape vectors that are potentially extractable from the matrix used (19 more beyond vector 6, [as character $n - 1$]) together account for the remaining 20% of variance in the matrix.

Figure 7C shows the proportion of “uniqueness” (differentiation) as a percentage for each character. In this sense, the uniqueness variance is defined as the reciprocal of communality, which is the variance component for a character that is attributable to common factors (Sneath & Sokal 1973). Genetically, communality entails the variance attributable to pleiotropy or other linkage mechanisms between traits; this operationally assumes environmental effects (including measurement errors) are null, as do most quantitative genetic models. Thus, uniqueness is a measure of the independence of the variance of a character, after its linkage correlations are removed. This independence can result from genetic discord, sampling (measurement) error or, of course, environmental variances which are operationally assumed to be zero here. Note that because the vectors here are derived from PCA rather than discriminant function analysis (DFA), the communality referred does not represent plesiomorphy in the sense of Sorensen (1987a, b) and Sorensen & Sawyer (1989), because PCA does not divorce the information common among groups to provide apomorphy, in the sense of group-divergence information, as does DFA when calculating intergroup Mahalanobis’ distance using the Wilks- λ criterion. Because of this important difference, the present figures differ from similar histogram portrayals of variance used elsewhere (Sorensen 1987b: fig. 3, Sorensen & Sawyer 1989: fig. 5) to show the character contributions of apomorphic anagenic distance between groups.

Predictive statements can be made for trait interaction during evolution in eulachnine aphids by comparing the summarized information contained in Figs. 7A–C. Such predictions, however, are based entirely upon the intraspecific variance within *Pseudessigella*, and are dependant upon the stability of the traits that is shown across the genera in the subtribe. This stability is a function, at least in

part, of the genetic independence of the traits (e.g., Fig. 7C), in response to both the disruptive and stabilizing selection pressures that act upon them. Because the information in Figs. 7A–C is multivariately based, however, it should be a better estimator of character interactions during evolution than simple bivariate comparisons of correlations between traits would be; the latter involve a nonmultivariate approach that has been shown to be inferior to multivariately based information in assessing the evolutionary interplay among traits (Willig et al. 1986). Comparing Figs. 7A–C, several observations can be made. For example, of characters 1–7, which show strong general-size affiliation, characters 4, 5 and 7 show relatively elevated levels of uniqueness and are thus assumed to be under less strong genetic linkage; they may, therefore, be more prone to successful disruptive selection. Of characters 2 versus 3 (length of antennal segment V versus the processus terminalis, respectively), 3 shows slightly more total variance of which more is attributable to shape parameters (Figs. 7A, B), although it also shows less genetic independence (Fig. 7C) than trait 2.

Consider the implications for interaction of traits 25 and 26 (metabasitarsal and metadistitarsal length, respectively), during evolution. In comparison to trait 26, trait 25 shows slightly less total contributed variance on vectors 1–6 (Fig. 7A), but its shape influence is larger and thus is more general-size independent; it also shows the greatest level of uniqueness, due to less linkage, of any of the 26 analyzed traits. The metabasitarsal to metadistitarsal ratio shows significant variance throughout the Cinarina and Eulachnina (Mamontova 1972) and within *Essigella* (Sorensen 1983, 1988, unpublished data); previous interpretations of polarity for the interaction of these traits has been questioned (Sorensen 1990). The expression of the variance relationships of the tarsi in *Pseudessigella* is important to potential interpretations for these characters within *Essigella*. By inferring from *Pseudessigella*, if the metatarsal ratio were to evolve differentially among species-groups within *Essigella*, as it has (unpublished data), the metabasitarsus would have necessarily had to undergo shape related evolutionary change via disruptive selection, while the change in the metadistitarsus should be more size related. Although evolution of the metabasitarsus would be more difficult because of its shape variance, it might on the other hand be more easily accomplished because of its lower apparent linkage.

If selective pressure were applied to the metabasitarsus, vector 2 (Fig. 5B), as the suite upon which it loads most heavily, shows that of the linkages that do exist for this trait, it would necessarily have to respond in the most similar fashion to changes in traits 13, 16–18, and 24 (the length of the metanotum [13], the number of dorsal [16] and marginal [17] setae on abdominal terga II–IV and abdominal tergum VIII [18], and the length of ventral setae on the metatibiae). Alternatively, however, if selective pressure were applied to this suite of traits, the metabasitarsus would be the most likely of any of the traits to respond in discord, becoming unstable because of its lower linkage. Disruptive selection would, therefore, most easily act upon this trait.

Character Groups Defined by Multiple Vectors of Shape Selection.—Figures 8A and 8B show the 26 traits in the three-dimensional evolutionary I-space that is generated by the dominant three shape vectors, 2–4. These figures show the same scattergram, but it is rotated 90° in yaw to demonstrate character separation. The original, unrotated, orthogonal vectors were used to define the evolutionary space

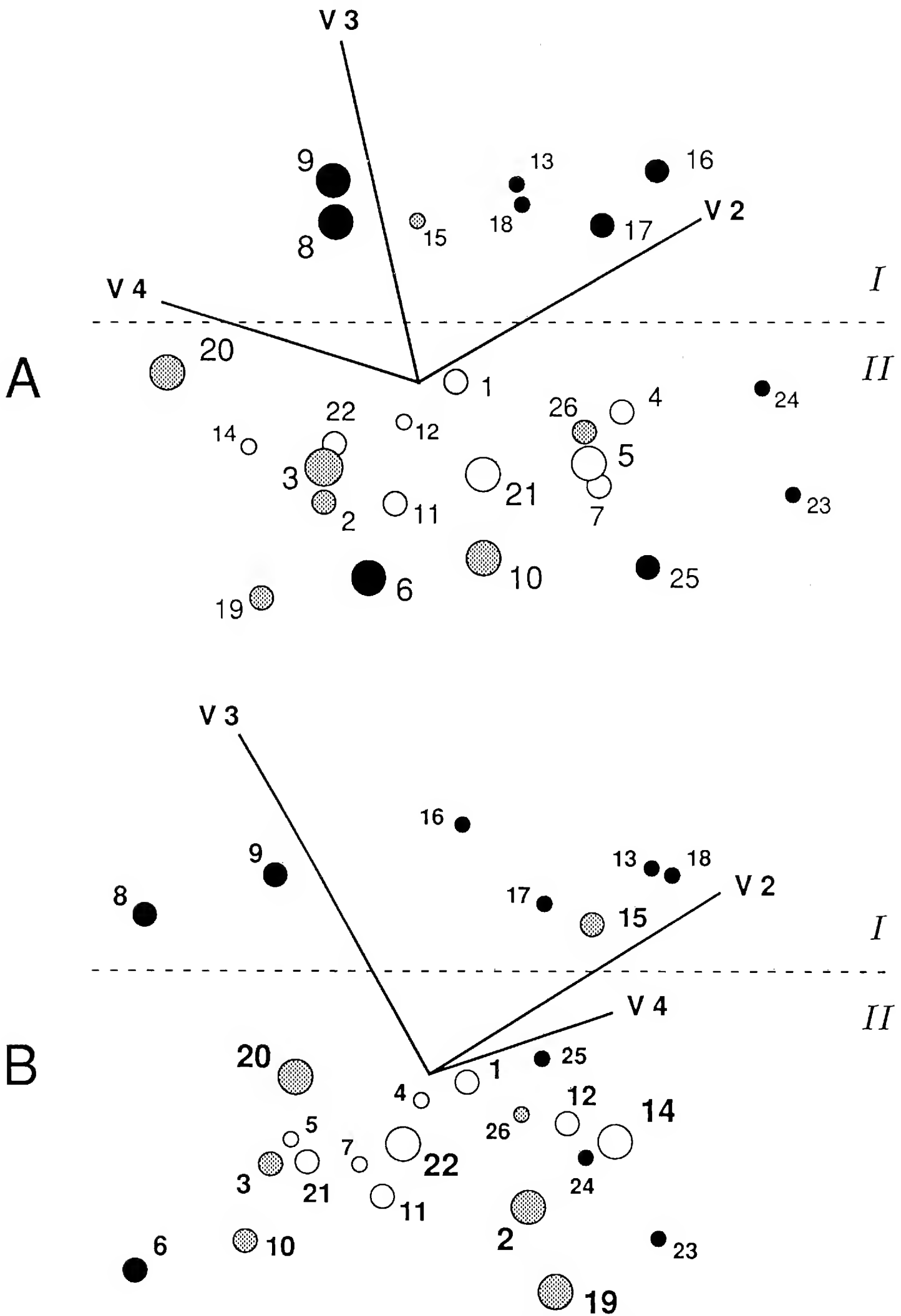


Figure 8. Character groupings for *Pseudessigella* apparent in the evolutionary space defined by a combination of vectors 2-4, as the dominant shape components. Perspectives (A) and (B) represent the same scattergram rotated 90° in yaw. The relative size of each dot and its number shows the relative depth of the point in the third dimension (depth perpendicular to the page). The apparent "groupings" of characters (I and II) are divided with dashed line for emphasis. Traits are assigned to

shown, but the space itself was then rotated to the perspectives depicted. The I-space shown portrays the dominant selective pressure gradients that act upon shape as a component of character variance; it represents 35.9% of the total variance within the *Pseudessigella* matrix, after the elimination of the 34.1% of general-size related variance.

The vectors in Fig. 8 are indicated as intersecting lines, where the distal (labeled) end represents the most positive coefficients on the vectors, and the vector intersection point represents a zero loading coefficient. Note that for this three-dimensional space, as a multivector selection regime for shape, trait 1 occurs the closest to the vector line intersection in both the A and B perspectives. In contrast, traits 12 and 4 also appear close in perspectives A and B, respectively, but are clearly not adjacent to the vector line intersection in the alternative perspectives. Because the location of that intersection represents a zero loading coefficient on all three shape vectors shown, trait 1, overall body size, as the most influential trait in the general-size suite (Fig. 5A) shows almost no residual shape component variance. In contrast, those traits with the highest rank for shape on vectors 2 or 3 occur mostly along the periphery of the distribution field shown.

In Fig. 8, the traits have been ordered into three ranks, showing their relative importance, as drivers, derived from the absolute value of their loading coefficients on the vectors. Although the I-space defined in Fig. 8 represents vectors 2–4, the rank assigned to each trait is the best rank (lowest rank number) that the trait achieved on either vector 2 or 3, as the two most dominant shape vectors. Under this criterion, traits 6, 8, 9, 13, 16–18, and 23–25 have the highest shape influence; traits 2, 3, 15, 19, 20 and 26 are intermediate; and traits 1, 4, 5, 7, 11, 12, 14, 21 and 22, are lowest in shape influence.

The perspectives shown in Fig. 8 depict two character groups are apparent as rough, flattened, somewhat oblong “disks,” each with a horizontal orientation; these groups are labeled I and II in the figures. The disks demonstrate that the 26 traits are not randomly distributed in this three-dimensional I-space, rather the characters apparently separate into two “affiliations” as seen from these perspectives. These trait distributions reflect their responses to selection pressure imposed upon them by the vectors as multiple gradients of net natural selection for shape change in multivariate evolution. The relative rankings of the traits are also nonrandomly distributed in this space. Note that character group I has a preponderance of the Rank I characters (6 of 10); group II contains all (9) rank III traits and nearly all (6 of 7) rank II traits as well. If the traits or their rankings were distributed between these groups randomly, group I would be expected to have 27% of the traits in each rank, or 2.7, 1.9 and 2.4 traits from ranks I–III, respectively. The evolutionary meaning of these perspective-dependant character affiliations, if any, is unclear.

Character Stability During the Evolution of Essigella.—Because *Pseudessigella* is the nearest approximation to a progenitor of *Essigella*, and because (except for mutation) variance must be present for selection to result in evolution (Mayr

←

one of three ranks determined by the relative importance of their contributions to the shape variance sequestered by vectors 2 or 3: rank I (black)—traits with the highest shape variance; rank II (gray)—traits with intermediate shape variance; rank III (white)—traits with the lowest shape variance.

1963), it was postulated that the pattern of variance for traits shown between groups within *Essigella* should also theoretically occur as intraspecific variance among those traits in *Pseudessigella*. This would imply somewhat stable genetic covariance matrices between these genera, as operational mother and daughter groups (sensu Sorensen 1987a). To explore this hypothesis the dominant shape traits occurring on vectors 2 and 3 were analyzed and ranked for *Essigella*, *E. kathleenae* and *E. kirki*, as was done for *Pseudessigella*.

Figure 9 shows these character shape rankings, as color codings, for these taxa as well as *Pseudessigella*. The relative degree of shape instability among the taxa can be deduced from Fig. 9 by comparing the color codings of the traits between the taxa. In that figure, stable traits, regardless of their ranking, maintain their color between taxa; moderately stable traits, which change their ranking by only one rank, are shown by white/gray or gray/black color changes between taxa; unstable traits, which change their ranking by two ranks, are shown by white/black color changes.

In comparison to *Pseudessigella*, less than half of the traits on vectors 2 or 3 remained stable during the evolution to *Essigella*. Traits 16–18, 23 and 24 remained unchanged in rank I (Fig. 9: black) as attributes high in shape variance on vectors 2 or 3. Traits 1, 11, 12, 14, 21, and 22 were unchanged in rank III (Fig. 9: white), but no traits remained unchanged in rank II (Fig. 9: gray). Several traits, however, changed dramatically between the genera: trait 7 changed from rank III (Fig. 9: white) in *Pseudessigella*, from poor in shape variance, to rank I in *Essigella*; traits 6, 9, 13 and 25 behaved the opposite. Many traits (2–5, 8, 10, 15, 19, 20, and 26) changed only one rank, in various directions, between the genera. Thus, between *Pseudessigella* and *Essigella* nearly 42% of traits (11 of 26) are stable with regard to shape variance; 39% (10 of 26) show moderate stability, and 19% (5 of 26) are unstable.

Note that in *Essigella* the metabasitarsus, trait 25, has apparently changed shape from its variance in *Pseudessigella*, becoming unstable and moving from rank I to III. The metabasitarsus, therefore, has decoupled in part from the other dominant traits, 16–18 and 24, in the suite represented by vector 2 (Fig. 6B) in *Pseudessigella*. The same is true for trait 13, although the latter showed considerably less independence in *Pseudessigella* (Fig. 7C). Unfortunately, stability in evolutionary traits remains more easily observable than predictable.

Figure 9 also shows the shape component rankings for *E. kathleenae* and *E. kirki*. For *E. kathleenae*, traits 17, 18 and 23 are rank I; traits 2, 3, 6, 7, 9–11, 15, 19, 20, 22 and 24 are rank II; and traits 1, 4, 5, 8, 12–14, 16, 21, 25 and 26 are rank III. For *E. kirki*, traits 3, 4, 6, 10, 14, 16, and 18 are rank I; traits 2, 5, 8, 20 and 23–25 are rank II; and traits 1, 7, 9, 11–13, 15, 17, 19, 21, 22 and 26 are rank III.

The similarity of shape component variance among all the taxa was calculated for taxon-pairs and represents a measure of shape stability during evolution (Fig. 10). *Pseudessigella* and *Essigella* have a shape similarity of 0.62. *Essigella kathleenae* shows the greatest degree of shape stability in common with *Pseudessigella* (0.71), more so in fact than with *Essigella* (0.67); *E. kirki* has an equal degree of shape stability (0.62) with either genus. Interestingly, however, shape stability between *E. kathleenae* and *E. kirki* (0.60), both group I species, is lower than that between either species versus either genus. These values suggest that *E. kirki* has

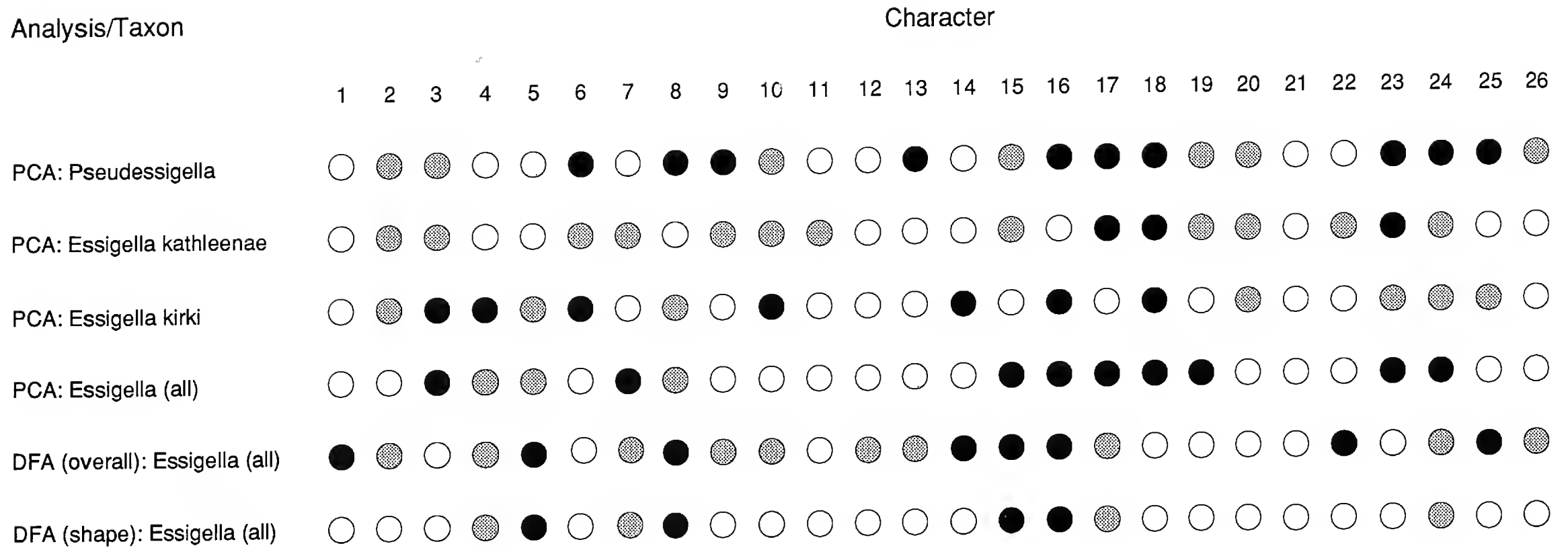


Figure 9. Relative ranking and stability of the shape component variance for each trait on PCA vectors 2 or 3 among taxa, and the DFA diagnostic ranking of traits for *Essigella*. For PCAs (either vector 2 or 3): rank I (black)—traits with the highest shape variance; rank II (gray)—traits with intermediate shape variance; rank III (white)—traits with the lowest shape variance. For DFA (overall) (vectors 1-3): rank I (black)—best multivariate separators; rank II (gray)—intermediate multivariate separators; rank III (white)—poorest multivariate separators. For DFA (shape) (vectors 1-3), rankings for “shape-based-diagnostics” are: rank I (black)—trait is a rank I multivariate separator with either rank I or II shape variance; rank II (gray)—trait is a rank II multivariate separator with either rank I or II shape variance; rank III (white)—trait is a multivariate separator of any rank but has rank III shape variance, or trait is a rank III multivariate separator of any rank shape variance.

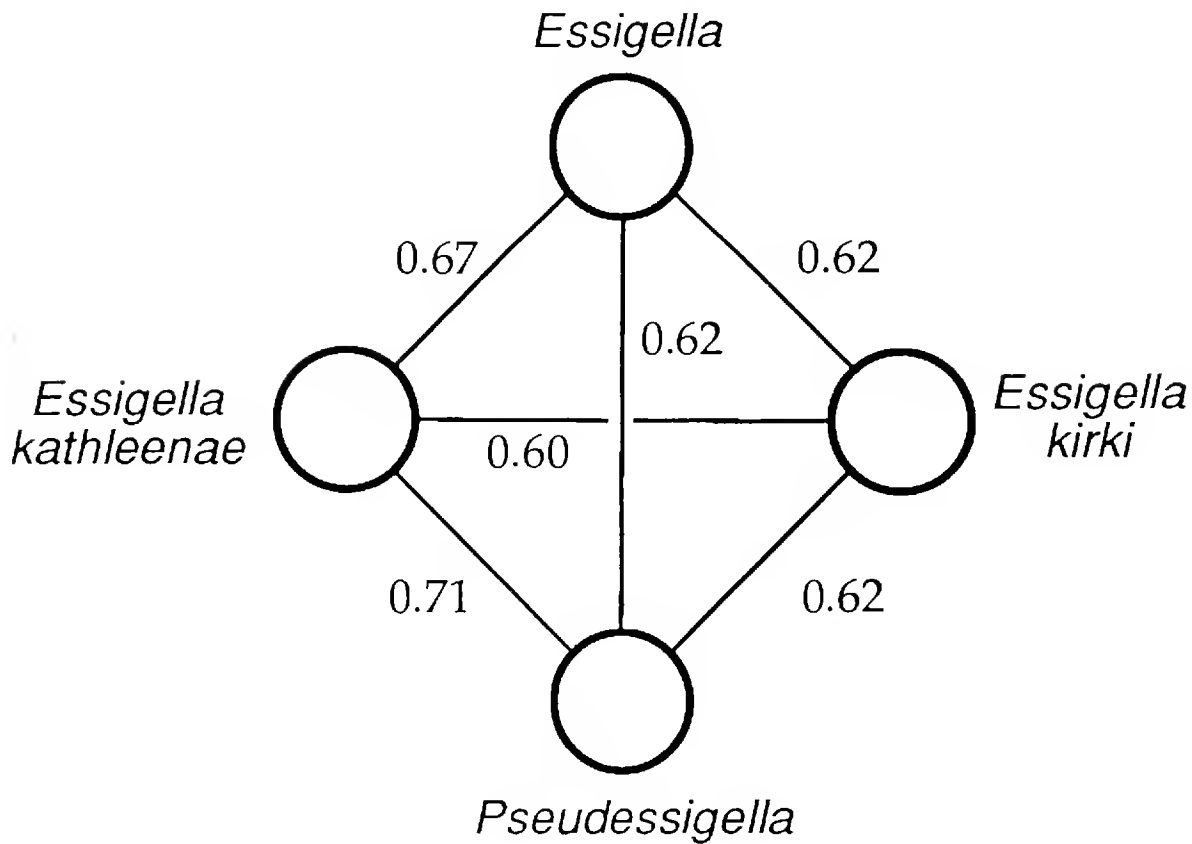


Figure 10. Similarity among the taxa, for shape components on PCA vectors 2/3. The similarity values (= 1 - distance) can be interpreted as an index of the stability of the relative rankings for the shape component of the traits on the two most dominant shape vectors.

had more shape selection imposed upon it than has *E. kathleenae*. It might be considered to be more “wayward” in shape, along a possible evolutionary “shape” continuum between the genera. This is despite previous findings that *E. kirki* was the closest in total anagenic distance to *Pseudessigella* on the phylogenetic network for these taxa and, therefore, represented the most primitive *Essigella* species (Sorensen 1987a).

The variance shown in shape stability between the taxa also indicates shape components may not, therefore, be as stable during multivariate evolution as might be thought, at least within the Eulachnina. Stabilizing and disruptive selection among the covariant character suites may be rather important during multivariate evolution, both within *Essigella* and between it and *Pseudessigella*. Because orthogonal shape is more theoretically conservative as a phylogenetic component during the evolution of a genus than is size (Leman & Freeman 1984), one would expect that shape variance should also be more important between differing groups of species, as clades, within a genus also (e.g., species-groups and monophyletic subgenera). Variance in shape components between species within a genus should occur mostly at the species-group level or above, because of the more significant evolutionary effort required to modify differing orthogonal character suites. In contrast, the differences between species within species-groups or complexes should most efficiently evolve by simple allometric change along their common general-size component; this would suggest that monophyletic species-groups should show mostly size differences between their closely related species, subspecies, etc.

This is not shown, however, between the group I species here. Using this logic, if *E. kathleenae* and *E. kirki* were parts of a tight monophyletic group, they should have shown a higher similarity in shape variance, with their major differences

occurring in general-size variance. Because group I of *Essigella* is paraphyletically defined and plesiomorphically sequestered within genus (Sorensen 1987a), however, the relatively low stability in shape between these species is not that surprising. They do not form a clade and because of their early "divorce" from each other and the remaining *Essigella* lineage(s), they have the least phyletic commonality of any pair of species in the genus. Although they are phenotypically quite similar, their similarity is largely based in plesiomorphy with reference to other *Essigella*.

Because both the size and shape components of traits should be important during radiant evolution of species within a genus, a DFA of all species of *Essigella* was conducted to explore which traits that are highest in shape variance are also the most multivariately important in differentiating monophyletic groups (clades) within the genus. Because the functions of DFA represent Landean minimum selective mortality measures (as: $[\nabla \ln \bar{W}]^T z$, sensu Lande 1979), they are parsimonious indices of the apomorphic anagenic distance that is necessary to account for the observed contemporaneous positions of the group centroids for the species in the n -dimensional space defined by the DFA vectors (Sorensen 1987a, b; Sorensen & Sawyer 1989). In this context, the vector loading coefficients of the characters on the functions determine the relative importance of each trait as a parsimonious contributor to the observed evolution (separation) of species for the matrix employed.

The results of the DFA are also shown in Fig. 9. Traits 1, 5, 8, 14–16, 22 and 25 in rank I have the highest multivariate contributions in optimally distinguishing (and evolving, sensu Lande 1979) *Essigella* species. Traits 2, 4, 7, 9, 10, 12, 13, 17, 24 and 26 show intermediate multivariate importance in rank II, and traits 3, 6, 11, 18–21 and 23 have the least importance in rank III. From these results, it is apparent that a mixture of traits that show their strongest variance in both size and shape seem important in the overall historical evolution of *Essigella* species.

To determine if traits with high shape variance (present criteria) best multivariately distinguish groups of species, as clades, within *Essigella* rather than individual species within such groups, a new set of rankings was created (shape-based-diagnostics) to reflect both the multivariate contribution of each trait as a diagnostic in DFA, and the relative importance of its shape contribution in *Essigella*. Three ranks were assigned (Fig. 9): rank I traits were the best (rank I) separators in DFA that also had either the highest or intermediate shape variance (ranks I or II) in PCA; rank II traits were intermediate separators (rank II) in DFA which also had either the highest or intermediate shape variance (ranks I or II) in PCA. Rank III traits were poor DFA separators (diagnostic rank III) of any shape rank, or were either the best or intermediate rank separators (diagnostic ranks I or II) that showed poor shape variance (shape rank III).

As rank I shape-based-diagnostics, traits 5, 8, 15 and 16 appear to best separate groupings of species within *Essigella* rather than simply individual species (Sorensen 1983). Trait 16, the number of dorsal setae on the terga of the anterior abdomen segments, separates the three major groupings of *Essigella* (Sorensen 1987a: groups I, II, III); groups II and III are clades, as is the combination of II + III. Trait 16 also differentiates *E. pini* Wilson homoplasiously from the monophyletic species-group involving *E. californica* and *E. hoernerii* (Sorensen

1987a: spp. H, A, B, respectively), within group III. Trait 8, a body width component, separates the monophyletic species complex involving *E. knowltoni* Hottes (Sorensen 1987a: spp. E, F, G) and to a lesser extent its monophyletic cohort *E. alyeska* Sorensen (Sorensen 1987a: sp. D), as a clade within group III; this assemblage involves a major portion of the orthogonal shape covariance shown among the species of group III. Trait 15, the maximal length of a set of sclerites that serve as muscle anchorages on the venter of the anterior abdominal segments, serves to separate many clades within *Essigella*, notably: group II, the *E. knowltoni* complex of group III, and the *E. californica* complex of group III. Trait 5, the length of the third antennal segment, shows both size and shape variance; it separates the *E. californica* complex as a clade, and also separates individual species within several other species-groups.

As rank II shape-based-diagnostics, traits 4, 7, 17 and 24 are less apparent in distinguishing groupings above the species level (Sorensen 1983). Trait 4, the length of the fourth antennal segment, behaves much as trait 3 in that some groupings of species show differential expression for the segment (e.g., group II, and some complexes within group III) to a degree, but the trait varies between species within some species-groups (e.g., the *E. knowltoni* complex of group III). Traits 7 and 24, the length of setae on the frons and ventral setae on the metatibia, are more difficult to interpret because of homoplasy and intraspecific variance. Both sets of setae have characteristic patterns of variance within species; they are always (plesiomorphically ?) short in some *Essigella* species (e.g., *E. kathleenae* and *E. kirki* of group I), but can vary widely in their lengths among individuals of other *Essigella* species (e.g., the *E. knowltoni* and particularly the *E. californica* complexes of group III) showing an apomorphically longer mean setal length for such species. Trait 17, the number of marginal setae on the anterior abdominal segments, parallels trait 16 and shows the same group defining properties, except that the variance in trait 17 is slightly more within several species.

Rank I shape-based-diagnostics, as a class, therefore, appear to best distinguish clades at various levels within *Essigella*, more than individual species within those groupings. Rank II shape-based-diagnostics, however, appear less evident in their separation of clades rather than individual species, and these traits tend to show variance that is either more homoplasious between species(-groups) or is subject to intraspecific variance in *Essigella*.

Traits within *Essigella* that are rank I diagnostics, exclusive of those that are also rank I or II shape-based-diagnostics, should be expected to portray higher levels of (homoplasious) importance in separating species within species-groups. Because the analysis of such size-based-diagnostics requires a local partitioning of the overall variance within *Essigella* at the level of its species, the examination of size-based-diagnostics will be treated elsewhere (unpublished data).

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ENTOMOPATHOGENIC FUNGI
(ZYGOMYCOTINA: ENTOMOPHTHORALES) INFECTING
CEREAL APHIDS (HOMOPTERA: APHIDIDAE)
IN MONTANA

MING-GUANG FENG,¹ ROBERT M. NOWIERSKI,
ALBERT L. SCHAREN,² AND DAVID C. SANDS³

Entomology Research Laboratory, Montana State University, Bozeman, Montana
59717

Abstract.—A field survey of dryland and irrigated crops of small grains was conducted in Montana during the 1990 growing season to search for entomopathogenic fungi for use in the biological control of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko). Dryland crops were heavily infested by *D. noxia*, but no evidence of fungal infection was found among the populations of this aphid species. *Diuraphis noxia* populations were undetectable on spring grains grown under irrigation. However, other cereal aphids, mainly *Metopolophium dirhodum* (Walker) and *Rhopalosiphum maidis* (Fitch), occurred abundantly. Mycoses caused by Entomophthorales were observed killing both aphid species from late July through August. Among 292 aphid cadavers collected during the occurrence of mycoses, 45.9% were killed by *Pandora neoaphidis* (Remaudière & Hennebert) Humber, 31.8% by *Conidiobolus obscurus* (Hall & Dunn) Remaudière & Keller, 21.6% by *Entomophthora planchoniana* Cornu, and 0.7% by *Zoophthora radicans* (Brefeld) Batko. Among the aphids killed by *C. obscurus*, the proportion of cadavers producing resting spores inside the body, rather than primary conidia on the body surface, increased quickly as the incidence of infection decreased on both aphid hosts. Distinguishing features of the two true *Entomophthora* species, *E. planchoniana* and *E. chromaphidis* Burger & Swain, infecting aphids in North America are discussed in comparison with information reported from different geographic areas. The four fungal species, plus *Conidiobolus thromboides* Drechsler, which was not found in 1990, but was successfully isolated from *Diuraphis tritici* (Gillette) in 1989, are new records as pathogens of cereal aphids for Montana.

Key Words.—Insecta, cereal aphids, Aphididae, Entomophthorales, aphid-pathogenic fungi, biological control agents

Aphids are often subject to attack by entomopathogenic fungi, including numerous species of Entomophthorales (Latgé & Papierok 1988, Waterhouse & Brady 1982) and at least two species of Hyphomycetes (Feng & Johnson 1990; Feng et al. 1990a, b; Hall 1981). These fungi are considered to have great potential as candidates for use in microbial control of various aphids (Latgé & Papierok 1988).

Fungal pathogens infecting cereal aphids have been reported in Europe (Dean & Wilding 1971, 1973; Dedryver 1983; Papierok & Havukkala 1986) and South America (Lássari 1985). Some regional lists of aphid fungi have also been published in Australia (Milner et al. 1980), Finland (Papierok 1989) and Israel (Ben-Ze'ev et al. 1984). In North America, five entomophthoralean species have been recorded from 34 aphid host species in the eastern United States and Canada

¹ Permanent address: China National Rice Research Institute, Hangzhou, Zhejiang Province, People's Republic of China.

² USDA-ARS, Department of Plant Pathology, Montana State University, Bozeman, Montana 59717.

³ Department of Plant Pathology, Montana State University, Bozeman, Montana 59717.

(Remaudière et al. 1978). Recently, Feng et al. (1990b) recovered 10 species of fungal pathogens from several species of cereal aphids infesting grain crops grown under irrigation in southwestern Idaho. One of these aphid hosts is the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), a recently-introduced, devastating pest of small grains in North America (Burton 1988). Microbial control, involving the use of entomopathogenic fungi, is one promising strategy that will contribute to the management of this pest in the future (Burton 1988, 1989).

This study surveyed for fungal pathogens of cereal aphids in dryland and irrigated small grains in Montana and generate regional strains for use in both laboratory and field studies.

MATERIALS AND METHODS

Field Survey.—A field survey conducted in Montana during the 1990 growing season included dryland and irrigated crops. The dryland crops were fall-sown winter wheat in two fields and spring-sown barley in one field located 25 or 35 km west of Billings. The irrigated crops were several small experimental plots of late-sown spring wheat and barley on the Montana State University campus in Bozeman. The survey was initiated in mid-May and continued through harvest. The fields were visited each week.

On each field date, numerous aphid colonies throughout each of the fields were examined carefully to determine if any aphids were infected with fungal pathogens. On the dryland crops, this examination was made while samples, ranging from 100 to 960 tillers (decreasing with increasing aphid density), were randomly taken in each field for purposes of estimating aphid population levels. Aphid cadavers, when found in the colonies, were placed in plastic vials in a cooler and transported to the laboratory for identification and isolation of fungal agents responsible for aphid mortality.

Identification of Aphid-Pathogenic Fungi.—External symptoms and fungal reproductive structures from each of the aphid cadavers were examined under a dissecting microscope as soon as possible following the collection (within the same day). Desiccated specimens were maintained in a moist chamber for several hours to allow for development of reproductive structures. Cadavers were then individually mounted on glass slides using cotton blue or aceto-orcein stains. Identification was based on external symptoms and the morphology of spores and sporulating structures (Waterhouse & Brady 1982). A recent revision of the classification for the Entomophthorales (Humber 1989) was used. The fungi associated with the cadavers were considered to have caused the death of their hosts if they had been previously documented as pathogens of aphids in the literature.

Isolation of Aphid-Pathogenic Fungi.—Saubouraud dextrose agar (DIFCO Laboratories, Detroit, Mich.) supplemented with 1% yeast extract (DIFCO, Laboratories, Detroit, Mich.) was used as a basic medium (SDAY) to isolate fungal pathogens from infected aphids. Some fresh aphid cadavers were individually attached to a small piece of double-faced sticky film in the center of a Petri dish cover. Cadavers were suspended over SDAY medium in the bottom of a Petri dish for a period of 10–20 h and then removed. Discharged spores from the cadaver would thus fall down to the medium for initiation of an in vitro culture. The Petri dishes containing inoculum were incubated at approximately 20° C with a photoperiod of 16:8 (L:D).

RESULTS AND DISCUSSION

The dryland crops were heavily infested by *D. noxia* during the 1990 growing season. Mean population densities (\pm SE) on average reached 14.4 (\pm 46.5) and 47.9 (\pm 87.4) aphids per tiller in the two winter wheat fields, respectively and 136.2 (\pm 102.9) on the spring barley. The percentage of tillers infested was 50%, 86%, and 96%, respectively. Other cereal aphids were occasionally found, but no consistent populations were detected. Despite the high levels of *D. noxia* populations on the dryland crops, no aphids were found to be infected by any fungal pathogens during the growing season.

Diuraphis noxia populations were undetectable on regularly sown grain crops in the Bozeman area during the growing season. However, other cereal aphids, including the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), and the rose-grass aphid, *Metopolophium dirhodum* (Walker), occurred abundantly in the small plots of late-sown spring grains grown under irrigation after early July. Mycoses induced by entomophthoralean fungi were observed killing both aphid species from late July through late August.

Four species of entomophthoralean fungi were identified from among the 292 cadavers of *M. dirhodum* and *R. maidis* collected during the four-week period of mycosis development. Nearly half of those cadavers (45.9%) were killed by *Pandora neoaphidis* (Remaudière & Hennebert) Humber, 31.8% by *Conidiobolus obscurus* (Hall & Dunn) Remaudière & Keller, 21.6% by *Entomophthora planchoniana* Cornu, and 0.7% by *Zoophthora radicans* (Brefeld) Batko. The identity and descriptions of these fungi are given separately below.

Conidiobolus spp.—Although only a single species, *C. obscurus*, was found among the *Conidiobolus*-killed aphids in the 1990 growing season, another fungus, *Conidiobolus thomboides* Drechsler, was successfully isolated from an infected individual of the western wheat aphid, *Diuraphis tritici* (Gillette), on winter wheat in Bozeman during the fall of 1989. Hence, these two species are listed here together as Montana records. *Conidiobolus obscurus* was recovered from 30 *M. dirhodum* and 63 *R. maidis* cadavers. Several isolates of *C. obscurus* have been obtained from both aphid hosts on SDAY and sent to ARSEF (USDA-ARS Collection of Entomopathogenic Fungal Cultures, USDA-ARS Plant Protection Research Unit, U.S. Plant, Soil and Nutrition Laboratory, Ithaca, New York) for permanent storage.

Aphids recently killed by *C. obscurus* were grey or grey-brown, and were attached to the plant by their probosces. Neither rhizoids nor cystidia were present. Conidiophores were simple, unbranched (Fig. 1a). Primary conidia containing many globules were nearly spherical (Fig. 1b), and measured as 33.8 (28.8–37.5) \times 28.0 (22.5–33.8) μm ($n = 100$). Secondary conidia formed from primary conidia by germination (Fig. 1c). Resting spores (Fig. 1d) were spherical with a diameter of 36.5 (27.5–45.0) \times 35.4 (27.5–43.8) μm ($n = 50$). No differences were significant in the dimensions of the primary conidia ($t_1 = 1.41$, $P > 0.10$; $t_2 = 0.53$, $P > 0.50$; $df = 98$) and resting spores ($t_1 = 1.10$, $P > 0.20$; $t_2 = 0.50$, $P > 0.50$; $df = 98$) between the two aphid hosts. However, the primary conidia [39.6 (28.8–33.7) \times 33.7 (25.0–44.3) μm , $n = 50$] and resting spores [38.9 (36.3–43.8) \times 37.4 (35.0–40.0) μm , $n = 15$] from in vitro cultures were significantly larger than the primary conidia ($t_1 = 10.03$, $P < 0.01$; $t_2 = 11.09$, $P < 0.01$; $df = 148$) and resting spores ($t_1 = 4.55$, $P < 0.01$; $t_2 = 3.74$, $P < 0.01$; $df = 113$) collected in vivo, respectively.

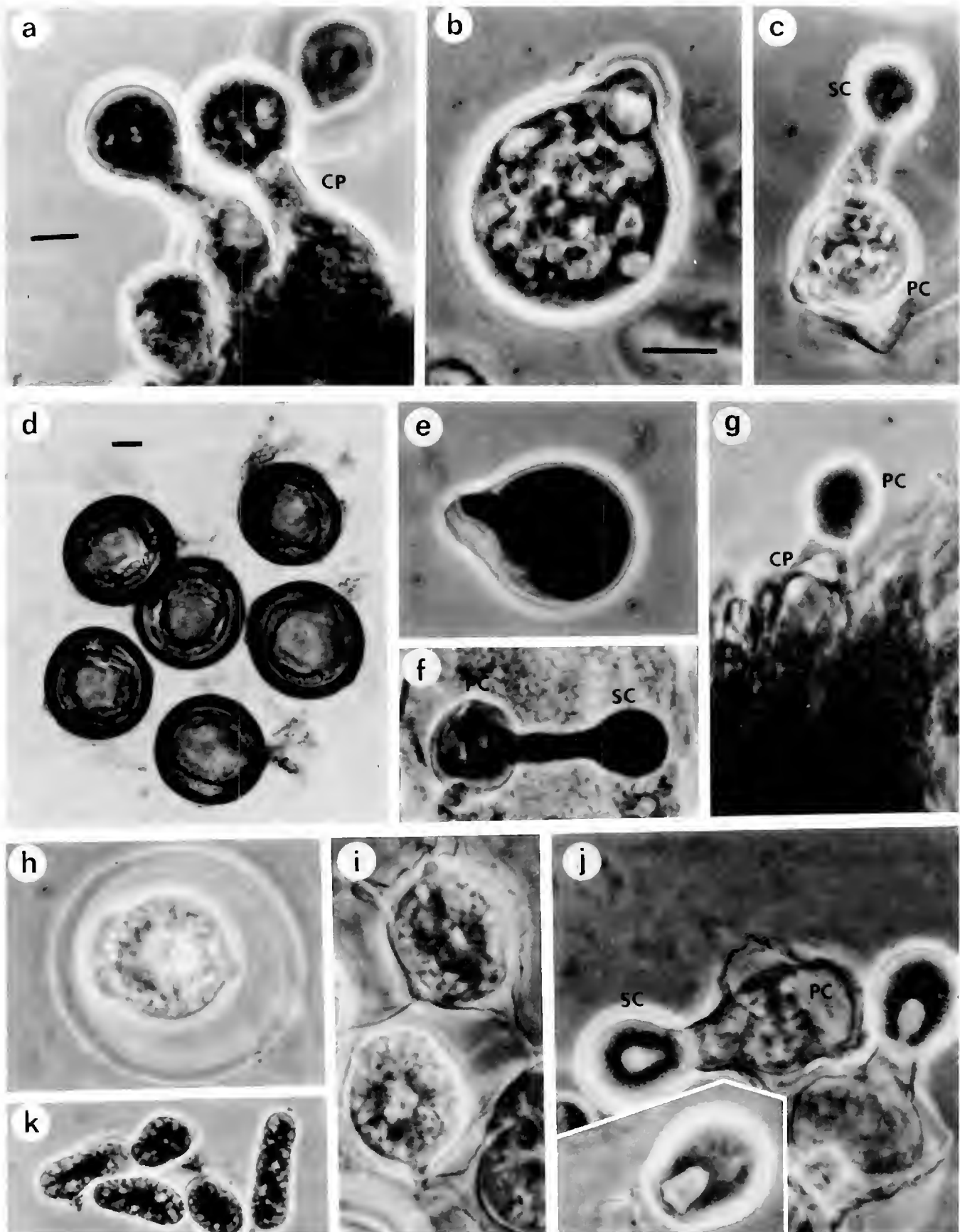


Figure 1. (a–d) *Conidiobolus obscurus*, (e–f) *C. thromboides*, and (g–k) *Entomophthora planchoniana*. (a) Developing conidiophores (CP). (b) A primary conidium. (c) A secondary conidium (SC) being produced from a primary conidium (PC). (d) Resting spores of *C. obscurus*. (e) A primary conidium. (f) A secondary conidium (SC) being produced from a primary conidium (PC) of *C. thromboides*. (g) A conidiophore. (h–i) Primary conidia imbedded in cytoplasm. (j) Secondary conidia (SC) being produced from primary conidia (PC). (k) Hyphal bodies germinated from conidia of *E. planchoniana*. Scale bars: 10 μm . The bar on (a) applies to (c) and (g); the bar on (b) applies to (e), (h–j); and the bar on (d) applies to (k).

The primary conidia of *C. thromboides* were subspherical, but smaller (Fig. 1e) than those of *C. obscurus*. The measurements from the in vitro culture were 26.4 (22.0–31.3) \times 20.9 (17.5–23.8) μm ($n = 50$). The resting spores were also similar in shape but smaller than those of *C. obscurus*.

Entomophthora planchoniana.—This fungus was recovered from 37 *M. dirhodum* and 26 *R. maidis* cadavers. No attempt was made to obtain a pure culture because true *E. planchoniana* has rarely been successfully cultured using an artificial medium.

Aphids killed by *E. planchoniana* were yellow-brown or brick brown and stuck to the plant by rhizoids in a thick bundle or several bundles forming a platform. Cystidia were absent. Conidiophores were unbranched (Fig. 1g). Primary conidia were typically discharged with a mass of cytoplasm creating a 'halo' (Fig. 1h, 1i). Primary conidia were bell-shaped and measured as $18.9 (15.0\text{--}22.5) \times 15.5 (12.0\text{--}17.8) \mu\text{m}$ ($n = 75$). Secondary conidia (Fig. 1j) that germinated from the primary conidia were more rounded and smaller than the primary conidia: $15.1 (13.3\text{--}17.5) \times 12.6 (10.8\text{--}14.8) \mu\text{m}$ ($n = 50$). No resting spores were observed from the materials examined.

There are only two true *Entomophthora* species that have been documented as aphid pathogens in the world: *E. planchoniana* and *E. chromaphidis* Burger & Swain. *Entomophthora planchoniana* is well known in Europe (Waterhouse & Brady 1982; Papierok 1989) and also has been reported in Israel (Ben-Ze'ev et al. 1984) and Australia (Milner et al. 1980). In North America, however, this species has been recorded only from two aphid cadavers of unknown identity that were collected from the eastern coast (Remaudière et al. 1978). On the other hand, *E. chromaphidis* was originally described from the walnut aphid, *Chromaphidis juglandicola* (Kaltenbach), in southern California (Burger & Swain 1918) and recently recovered from cereal aphids in southwestern Idaho (Feng 1990). The two species can be distinguished from each other by the size of primary conidia and the number of nuclei in each conidium (R. A. Humber, MGF, unpublished data). Primary conidia of *E. chromaphidis* contain 2–8 nuclei each and are generally smaller than those of *E. planchoniana*, which contain 2–6 nuclei (Waterhouse & Brady 1982). There was no significant difference in the size of the primary conidia from *M. dirhodum* and *R. maidis* cadavers, killed by *Entomophthora* in Montana, compared to those seen in other reports (Table 1) from Europe and Australia. However, the primary conidia of the *Entomophthora* from Montana are significantly larger than those of the real *Entomophthora* species reported from California and Idaho. The comparison did not include the materials from Israel (Ben-Ze'ev et al. 1984) and the east coast of North America (Remaudière et al. 1978) because the authors did not provide measurements. Unfortunately, our specimens were not stained well enough to allow the counting of the nuclei inside the conidia because almost all the primary conidia were imbedded in the cytoplasm. Even so, the Montana fungus could be *E. planchoniana* rather than *E. chromaphidis* because of the similarity to the European fungus in conidial size.

Pandora neoaphidis.—A total of 134 cadavers, including 115 *M. dirhodum* and 19 *R. maidis*, were attributed to infection by *P. neoaphidis*. No isolates were obtained using SDAY.

Aphids freshly killed by *P. neoaphidis* turned pale brown or yellow-brown and adhered to the plant by numerous rhizoids, each of which consisted of a thin stalk ending in a disk-like terminal expansion. Cystidia, present under moist conditions, were distally tapered, thicker than conidiophores, and extended far beyond them (Fig. 2a). Conidiophores were digitately branched at their apices (Figs. 2a, 2b). Primary conidia contained a single large nucleus, were ovoid to cylindrical in

Table 1. Comparison of the sizes of primary conidia of true *Entomophthora* species from aphids in Montana and other geographic areas.

Region	Fungus ^a	Primary conidia, μm			t^d	P	Reference
		L/W ^b	Mean ^c	Range			
Australia	<i>Epl</i>	L	(17.0)	14–20	1.61	>0.10	Milner et al. 1980
		W	(15.0)	13–18	0.47	>0.50	
England	<i>Epl</i>	L	19.0	14–23	–0.09	>0.50	Waterhouse & Brady 1982
		W	14.0	12–20	1.32	>0.10	
Finland	<i>Epl</i>	L	18.1	13–22	0.68	>0.40	Papierok 1989
		W	14.9	10–18	0.55	>0.50	
California	<i>Ech</i>	L	(12.5)	11–14	5.42	<0.01	Burger & Swain 1918
		W	(10.5)	10–11	4.33	<0.01	
Idaho	<i>Ech</i>	L	14.4	13–16	3.79	<0.01	Feng 1990
		W	12.3	10–13	2.82	<0.01	

^a *Epl* = *E. planchoniana*, *Ech* = *E. chromaphidis*.

^b L = length (including papillae), W = width.

^c Table entries in brackets estimated from the range of original measurements but not given directly by the authors.

^d t -test under null hypothesis $H_0: x_{\text{MT}} = y_{\text{COM}}$, where x_{MT} is the measurement from Montana material (L: 18.89 ± 1.17 ; W: 15.54 ± 1.16 ; $n = 75$), y_{COM} the measurement from the materials compared, and $t = (x_{\text{MT}} - y_{\text{COM}})/\text{SE}_x[(n + 1)/n]^{1/2}$ with $\text{df} = n - 1$.

shape (Fig. 2c) and measured $23.6 (18.8\text{--}30.0) \times 12.4 (10.0\text{--}15.0) \mu\text{m}$ ($n = 80$). Secondary conidia developed from primary conidia (Fig. 2d) and were similar in shape but smaller than the primary conidia. No resting spores were present in the specimens examined.

Zoophthora radicans.—This fungus was recovered from two *M. dirhodum* cadavers only. Because of the paucity of specimens, no attempt was made to isolate *Z. radicans*, although it usually grows quite well on SDAY.

Aphids killed by *Z. radicans* were pale brown or orange-brown. Rhizoids were present. Cystidia were also present, but were relatively few in number compared with those of *P. neoaphidis*. Conidiophores were branched (Fig. 2e). Primary conidia were uninucleate, long and ellipsoid in shape (Fig. 2f): $18.3 (15.3\text{--}21.3) \times 7.4 (6.5\text{--}8.8) \mu\text{m}$ ($n = 50$). Secondary conidia germinated apically or laterally from primary conidia and were similar to primary conidia. No capilliconidia and resting spores were observed in the limited number of specimens.

Development of Aphid Mycosis.—The relative proportion of infections by *P. neoaphidis* tended to increase during the 4 week period of mycosis development, whereas that of *C. obscurus* appeared to decrease (Fig. 3). The fungus, *Z. radicans*, was observed only at the beginning of the period. Thereafter, it remained undetected or possibly its influence on the aphids was masked by other fungi. The infection by *E. planchoniana* remained about the same among the aphids after early August (Fig. 3). More *M. dirhodum* cadavers were attributed to infection by *P. neoaphidis* than were *R. maidis* cadavers. The reverse was true for *C. obscurus*.

Many of the aphids killed by *C. obscurus* produced resting spores rather than primary conidia, which are the primary form infecting live aphids. As shown in Fig. 4, the proportion of cadavers containing resting spores in the field appeared to increase during the 4 week period, irrespective of the species of aphid host.

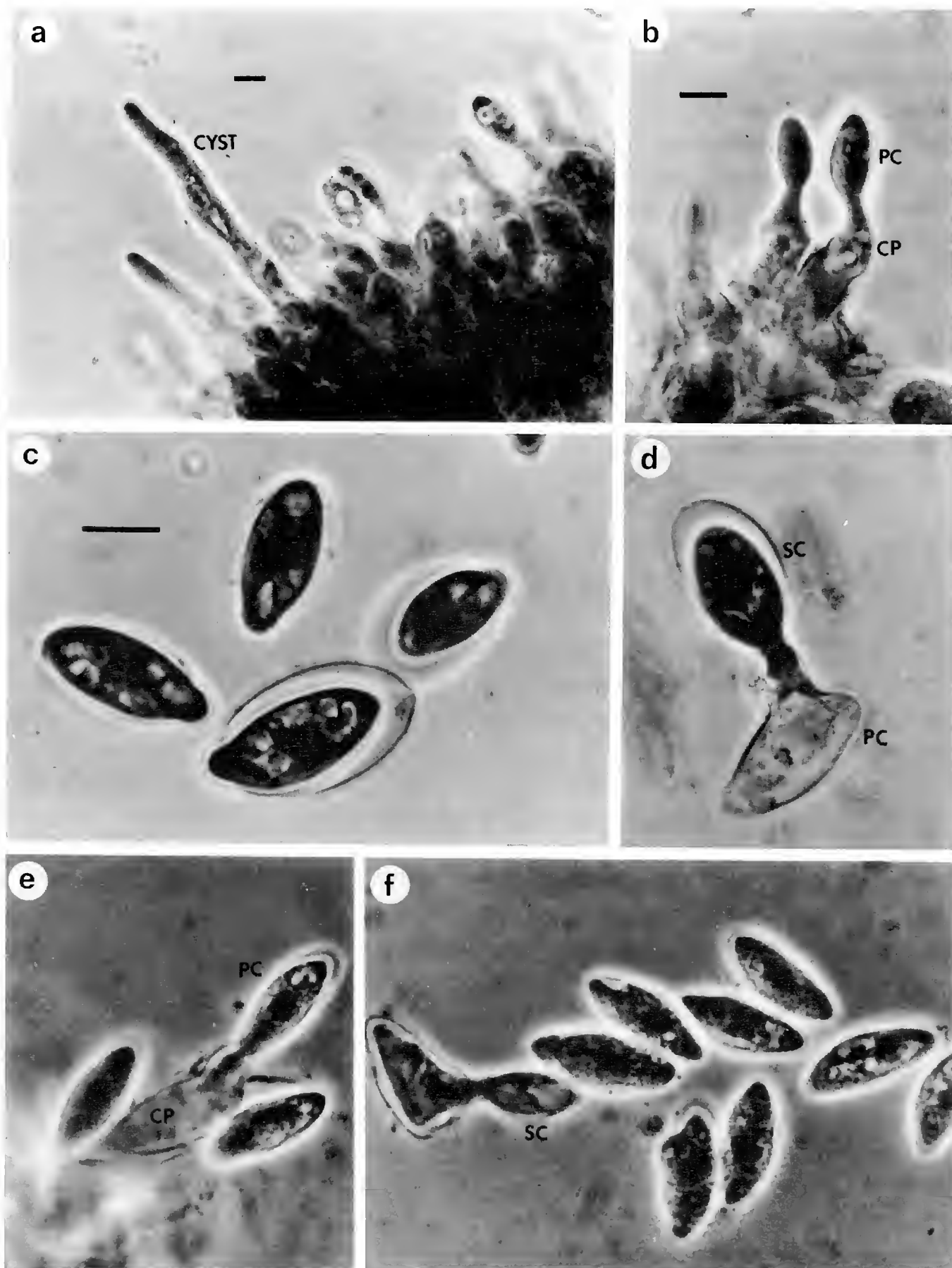


Figure 2. (a–d) *Pandora neoaphidis* and (e–f) *Zoophthora radicans*. (a) Cystidia (CYST). (b) Conidiophores. (c) Primary conidia. (d) A secondary conidium (SC) being produced from a primary conidium (PC). (e) Conidiophores. (f) Primary conidia and secondary conidium (SC). Scale bars: 10 μm . The bar on (c) applies to (d–f).

This phenomenon has not been reported by previous researchers (e.g., Feng et al. 1990b, Milner et al. 1980, Papierok 1989) although resting spores of *Conidiobolus* spp. from aphids are frequently observed from in vitro cultures. The production of resting spores is often thought to require a short photoperiod or low temperature or a combination of both for initiation (Wilding & Latteur 1987). However, during

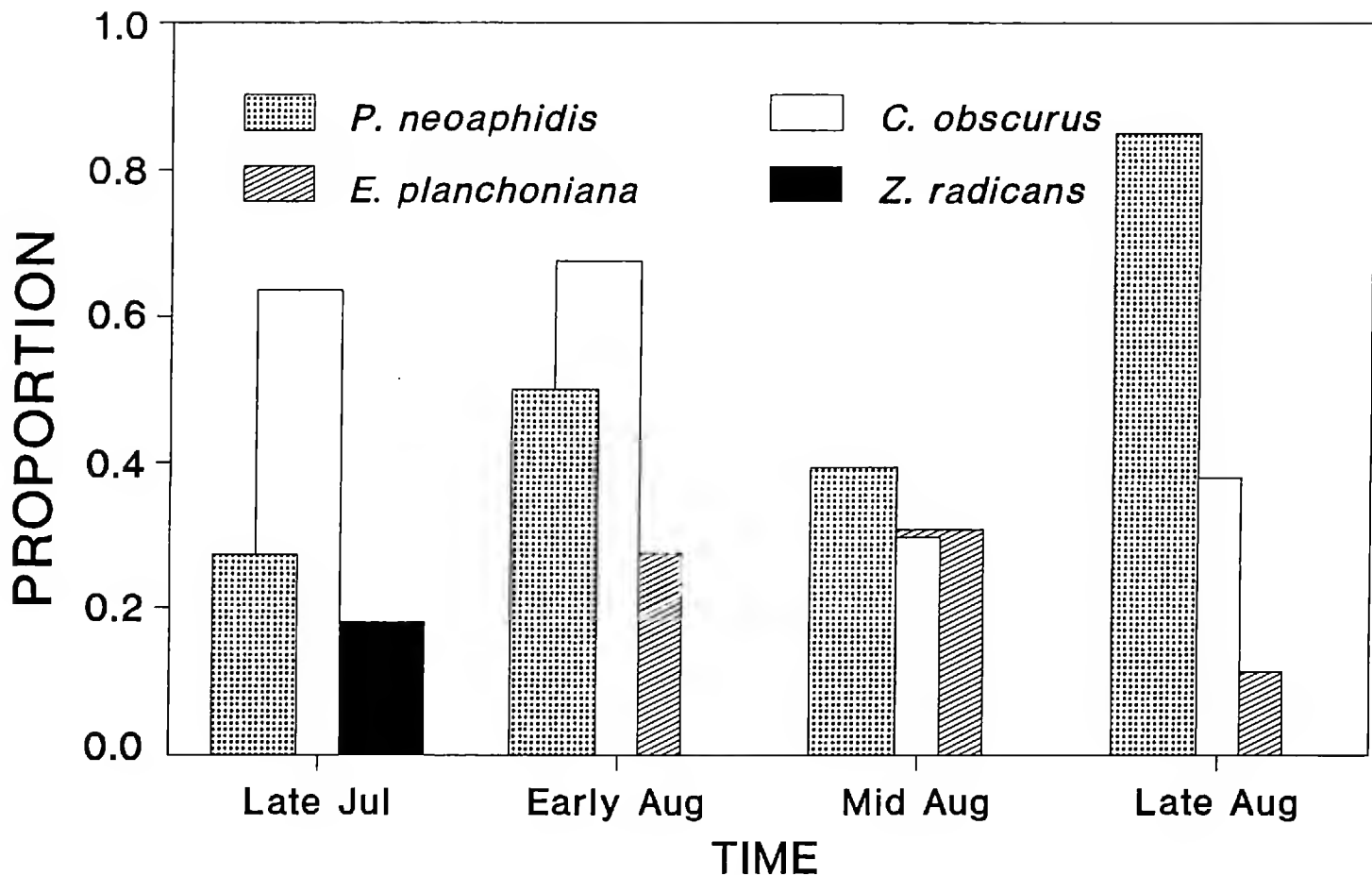


Figure 3. Proportion of each fungal pathogen among the cadavers of *M. dirhodum* and *R. maidis* in irrigated spring grains in Bozeman, Montana during the 1990 growing season.

the period from late July to late August in 1990, the natural photoperiod and temperature in Bozeman remained in a summer pattern: 14–15 h day length and mild temperature conditions; the monthly mean temperature for August was 19.4° C (11.0–27.9° C). It is unclear whether any other environmental factors may have been involved in this phenomenon.

The production of resting spores in the field implies an interruption of the fungal infection cycle, because generally following resting spore formation a minimum period of vernalization is required before germination is initiated (Wilding & Latteur 1987). This may explain why the level of infection by *C. obscurus* decreased among the aphids during the survey (Fig. 3). This also suggests that for *Conidiobolus* species to be successfully used against cereal aphids in Montana, additional understanding of the mechanisms for the production and germination of resting spores will be required.

The mortality of cereal aphids resulting from fungal infection in Bozeman was at low levels (< 10%) compared with those reported from cereal aphids in irrigated spring wheat in southwestern Idaho (up to 90%; Feng 1990). The frequent thundershowers from late July through early August as well as the irrigation water provided may have enhanced the development of fungal infection in the aphid populations in Bozeman. Arid weather (low moisture and high temperature) may have prevented fungal diseases from developing in the aphid populations on dryland crops.

The four species of Entomophthorales, found during the 1990 season, plus the *C. thromboides* isolate, obtained in the fall of 1989, are new records as pathogens of cereal aphids for Montana. *Entomophthora planchoniana* represents the first record from cereal aphids in North America.

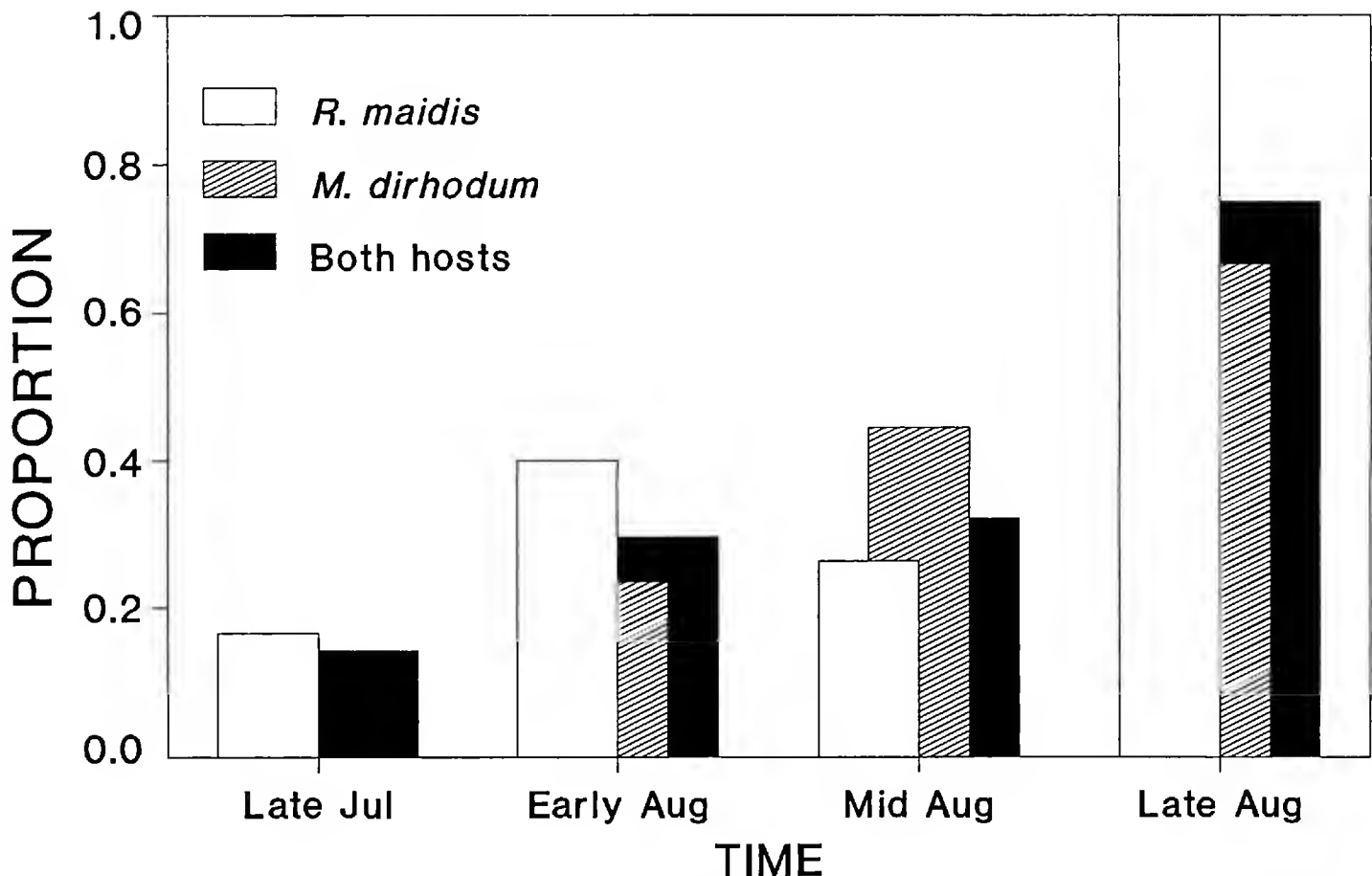


Figure 4. Proportion of aphid cadavers producing resting spores in irrigated spring grains in Bozeman, Montana during the development of mycosis.

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**NEW SPECIES OF *ASPIRHINA* KIRBY FROM THE
NEOTROPICAL REGION
(HYMENOPTERA: CHALCIDIDAE)**

JEFFREY A. HALSTEAD

296 Burgan, Clovis, California 93612¹

Abstract.—Four new *Aspirhina* Kirby are described from the Neotropical region: *A. alvarengai* NEW SPECIES, *A. bifurca* NEW SPECIES, *A. deceptor* NEW SPECIES, and *A. spinosa* NEW SPECIES. *Aspirhina dubitator* (Walker), the only previously described species, is redescribed and its female is described for the first time. Characters are presented to distinguish *Aspirhina* from other Neotropical Chalcididae. No biological information is known for members of the genus *Aspirhina*.

Key Words.—Insecta, *Aspirhina*, Neotropical, Chalcididae, Chalcidoidea, Hymenoptera

The genus *Aspirhina* was proposed by Kirby (1883) for a Brazilian species that Walker (1862) originally described as *Halticella* [correctly *Haltichella*] *dubitator*. Since then, no other species were added or described in *Aspirhina*. Four new species from the Neotropical region are described in this paper. A key to the species of *Aspirhina* and diagnostic characters for the genus are presented. No biological or host information is known for *Aspirhina*, and their potential as biological control agents is unassessed. Overall, a total of 25 specimens were examined, indicating that *Aspirhina* are rare in collections.

Aspirhina is distinguished from other genera of New World Chalcididae by the following character combination: hind tibia truncate apically, two apical spurs present (Haltichellinae); marginal vein reaching anterior margin of forewing, post-marginal and stigmal veins present (Haltichellini); vertex of head not produced into horns; preorbital carina strong, arch-like above anterior ocellus; pronotum with a carina along anterior margin except at median; forewing clouded, a darker spot under marginal vein; scutellum with a posteriorly projecting triangular to finger-like process, never with a small median tooth; tergum I dorsally with at least three longitudinal carinae at base, originating from a transverse carina.

Museum acronyms for specimen depositories are: American Museum of Natural History, New York (AMNH); British Museum of Natural History, London (BMNH); Canadian National Collection, Ottawa (CNC); Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Affairs, Gainesville (FSCA); J. A. Halstead, personal collection (JAHC); and U.S. National Museum of Natural History, Washington, D.C. (USNM). Abbreviations include "T" for tergum or terga (e.g., T1 for tergum I). Distributional information for paratypes and material examined is listed alphabetically by country and location, respectively.

¹ Correspondence: % Kings River Conservation District, 4886 E. Jensen Avenue, Fresno, California 93725.

KEY TO SPECIES OF *ASPIRHINA*

- 1 Tergum I dorsally punctate, with four longitudinal carinae (rarely five carinae) in which outermost carinae are about $0.5 \times$ length of innermost carinae (Fig. 1a); scutellar projection apically emarginate to forked (Figs. 12a, 12b) and dorsally punctate (Fig. 1b) *alvarengai* NEW SPECIES
- Tergum I dorsally smooth, with three or four longitudinal carinae of about equal length (Figs. 2a, 3a, 4a, 5a); scutellar projection usually not as above 2
- 2(1) Tergum I dorsally with three longitudinal carinae (Fig. 3a); scutellar projection apically rounded (Fig. 11) and dorsally striate (Fig. 3b) ..
..... *spinosa* NEW SPECIES
- Tergite I dorsally with four longitudinal carinae; scutellar projection not as above 3
- 3(2) Scutellar projection apically rounded (Fig. 14); hind femur with teeth on ventral margin extending $0.66 \times$ hind femur length (Fig. 9)
..... *dubitator* (Walker)
- Scutellar projection apically emarginate to forked (Figs. 13, 15); hind femur with teeth on ventral margin extending $0.5 \times$ or less hind femur length 4
- 4(3) Scutellar projection apically emarginate (Fig. 13) and dorsally punctate (Fig. 4b) *deceptor* NEW SPECIES
- Scutellar projection apically forked (Fig. 15) and dorsally striate (Fig. 5b)
..... *bifurca* NEW SPECIES.

ASPIRHINA DUBITATOR (WALKER)
(Figs. 2a, 2b, 9, 14)

Halticella dubitator Walker, 1862: 366.

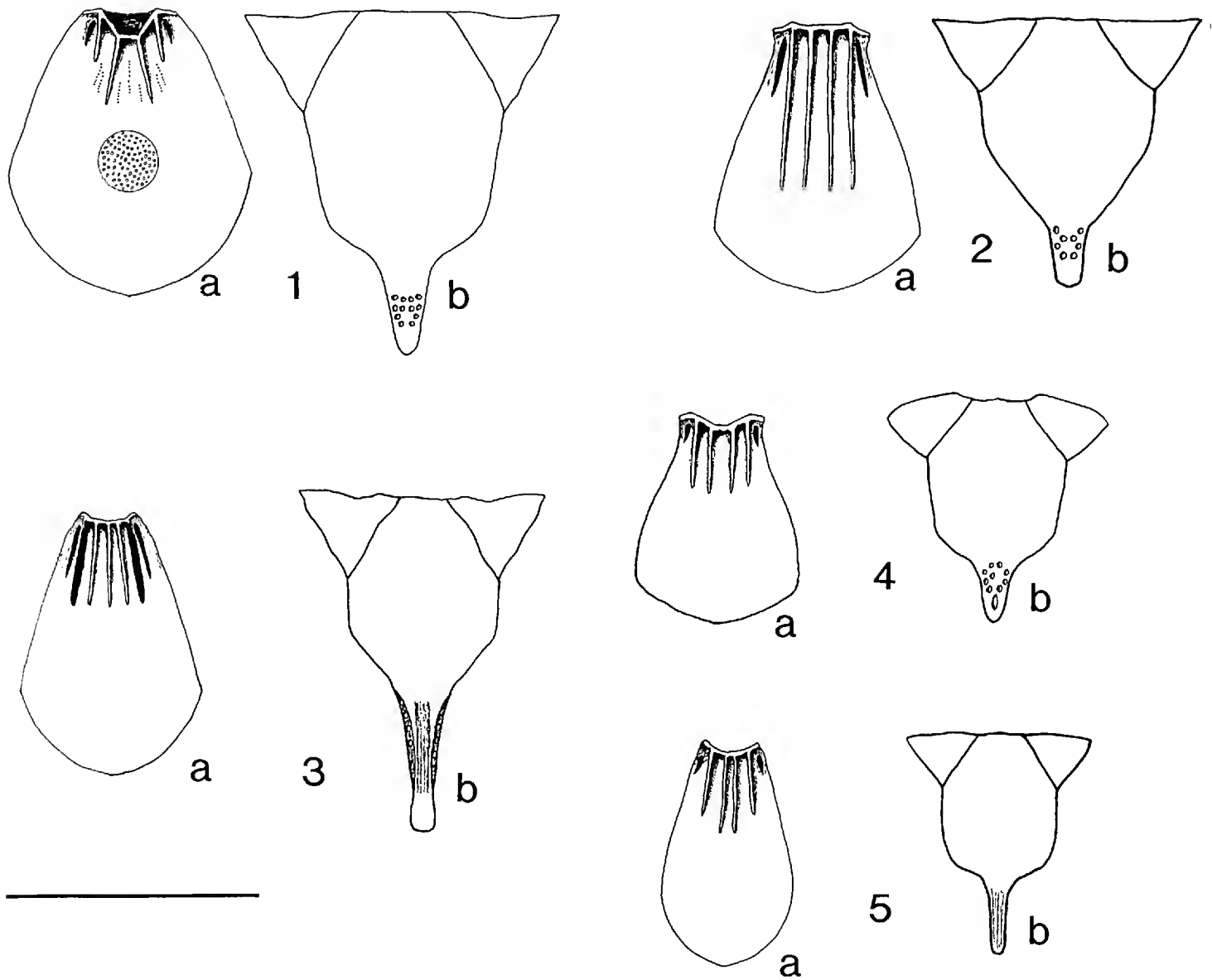
Aspirhina dubitator (Walker); Kirby 1883: 60.

Types. — Holotype, male; data: “Brazil, *Aspirhina dubitator* Walker, B.M. TYPE 5.555.” Examined by author. Holotype resides in the British Museum of Natural History, London.

Description. — *Male* (holotype). *Body length:* 5.2 mm. *Color:* black with tegula, fore leg, mid leg (except coxa), hind trochanter, and apical half of hind tibia orange. *Pronotum and Mesoscutum:* dorsally without a median carina. *Scutellum:* in lateral view with dorsal margin straight and apex of projection finger-like, blunt (Fig. 14); in dorsal view apical projection $0.25 \times$ maximum scutellar length (Fig. 2b); sculptured with oval setigerous punctures separated by 0.5 to $1.0 \times$ puncture diameter; 16 punctures along midline between base and apex; integument smooth and polished except weakly coriaceous basally, apical projection punctate except at apex. *Hind femur:* oval; teeth on ventral margin extending $0.66 \times$ hind femur length (Fig. 9). *Gaster:* pubescence silver on T1–2, remainder of terga with gold pubescence. *T1:* dorsally with four longitudinal carinae, extending $0.66 \times$ T1 length (Fig. 2a), integument polished.

Female. Like male, but pubescence of gaster entirely silver and hind tibia and hind femur (basally and apically) orange.

Diagnosis. — *Aspirhina dubitator* may be distinguished from other *Aspirhina* by its unique combination of the characters: tergum I dorsally smooth and with four longitudinal carinae which are about equal in length (Fig. 2a), scutellar projection



Figures 1–5. *Aspirhina* spp., males. Tergum 1 (a) and scutellum (b), dorsal views. Sculpture of apical projection of scutellum and punctation of tergum 1 (circle insert) illustrated. 1. *A. alvarengai* NEW SPECIES. 2. *A. dubitator*. 3. *A. spinosa* NEW SPECIES. 4. *A. deceptor* NEW SPECIES. 5. *A. bifurca* NEW SPECIES. Scale line 1.0 mm.

apically rounded (Fig. 14) and dorsally punctate (Fig. 2b), and teeth on ventral margin of hind femur extending $0.66 \times$ hind femur length (Fig. 9).

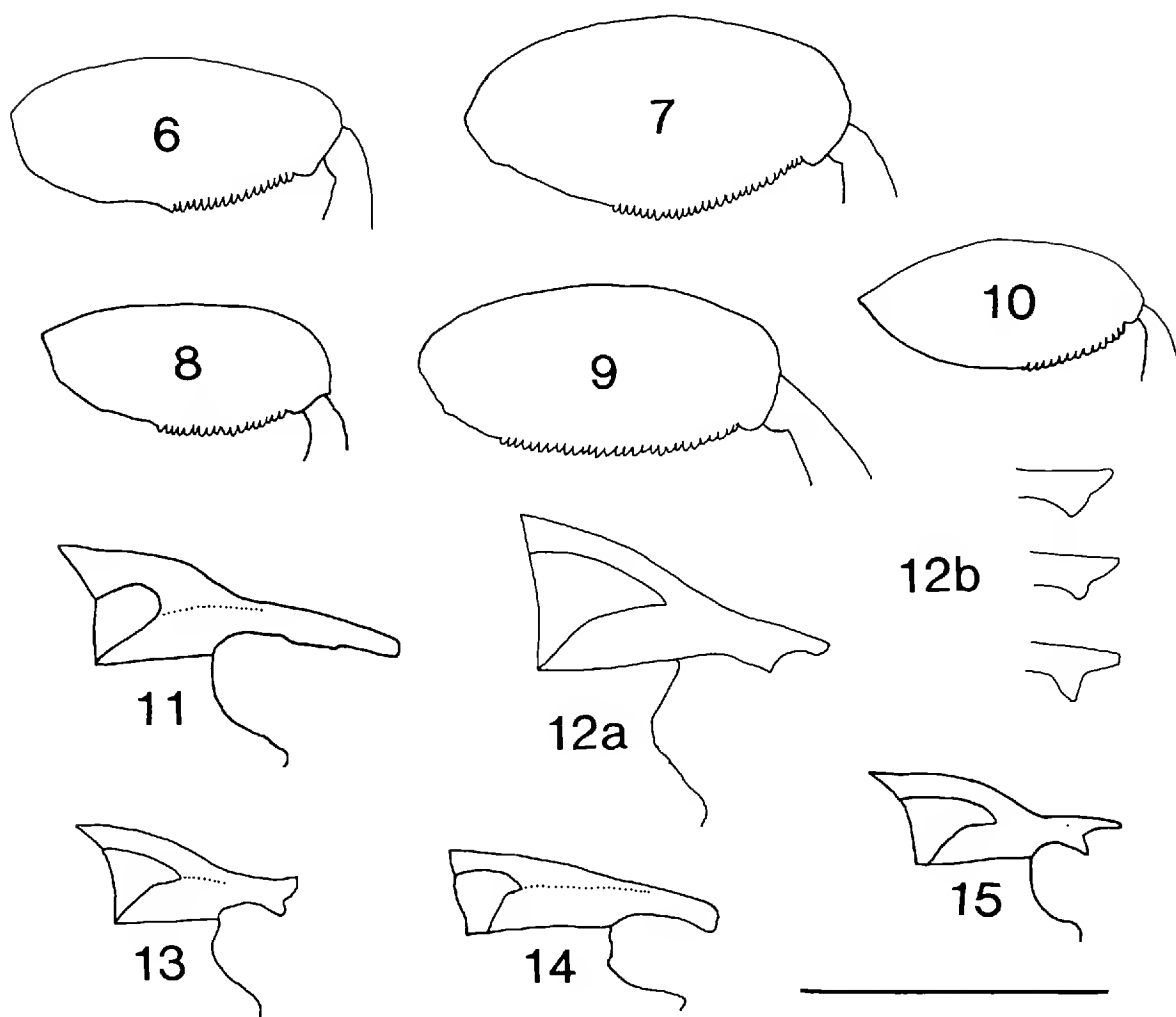
Variation.—*Male.* Longitudinal carinae of T1 vary in length from 0.6 to $0.8 \times$ T1 length. Two specimens with only fore and mid leg brown and tarsi orange. One specimen with hind leg (except coxa and central area of outside of femur) orange. *Female.* Known only from specimen described, which is deposited in the AMNH.

Distribution.—Brazil.

Material Examined.—BRAZIL. AMAZONAS ESTIRAR DE EQUADOR: Rio Javari, Sep 1979, M. Alvarenga, 4 males (CNC). MATO GROSSO: Sinop, Oct 1974, Malaise trap, M. Alvarenga, 1 male (JAH). RODONIA: Rio Guapore opposite mouth of Rio Baures, 1–5 Oct 1964, Bouseman and Lussenhop, 1 female.

ASPIRHINA BIFURCA HALSTEAD, NEW SPECIES
(Figs. 5a, 5b, 10, 15)

Types.—Holotype, male; allotype, female; data: “BOLIVIA, Beni: Rio Itenez opposite Costa Marques (Brazil), Sept. 4–6, 1964, Bouseman & Lussenhop.” Holotype and allotype reside in the American Museum of Natural History, New



Figures 6–15. *Aspirihina* spp., males. Figs. 6–10. Hind femur, lateral view. Figs. 11–15. Scutellum, lateral view. 6, 11. *A. spinosa* NEW SPECIES. 7, 12a, 12b. *A. alvarengai* NEW SPECIES, 12b-variation in apex of scutellum. 8, 13. *A. deceptor* NEW SPECIES. 9, 14. *A. dubitator*. 10, 15. *A. bifurca* NEW SPECIES. Scale line 1.0 mm.

York. *Paratypes*: 1 male with same data and depository as holotype; BRAZIL. GOIAS: Jatai, Nov 1972, F. M. Oliveira, 1 male (USNM). COSTA RICA. San Isidro de General, 700–800 m, Aug 1980, N.L.H. Krauss, 1 male (JAHC, from AMNH). ECUADOR. PICHINCHA: 47 km S of Santo Domingo Rio Palenque Station, 21–25 Feb 1979, S. and J. Peck, 1 male (CNC).

Description. — *Male* (holotype). *Body length*: 3.8 mm. *Color*: black with tegula and legs (except central area of outside of hind femur) orange; antenna, apical projection of scutellum, hind femur centrally, and hind coxa brown. *Pronotum and Mesoscutum*: dorsally without a median carina. *Scutellum*: in lateral view with dorsal margin convex and apex of projection forked (Fig. 15); in dorsal view apical projection $0.35 \times$ maximum scutellar length (Fig. 5b); sculptured with oval setigerous punctures separated by 0.12 to $0.33 \times$ puncture diameter; 12 punctures along midline between base and apex; integument sculpture coriaceous, anterior projection faintly striated to apex. *Hind femur*: oval; teeth on ventral margin extending $0.42 \times$ hind femur length (Fig. 10). *Gaster*: pubescence silver on T1–2, remainder of terga with gold pubescence. *T1*: dorsally with four longitudinal carinae, extending $0.4 \times$ T1 length (Fig. 5a), integument polished.

Female (allotype). Like male, but body length 4.2 mm, legs completely orange, and antenna slenderly filiform.

Diagnosis. — *Aspirihina bifurca* may be distinguished from other *Aspirihina* by its unique combination of the characters: tergum I dorsally smooth and with four longitudinal carinae which are about equal in length (Fig. 5a), scutellar projection apically forked (Figs. 15) and dorsally striate (Fig. 5b), and teeth on ventral margin of hind femur extending $0.42 \times$ length of hind femur (Fig. 10).

Variation.—*Male.* One paratype with hind femur completely orange; another paratype with hind femur completely brown. Apical projection of scutellum varies slightly in length and width. Some specimens with striation on projection confined to apical half. *Female.* Known only from allotype.

Distribution.—Bolivia, Brazil, Costa Rica, and Ecuador.

Etymology.—The specific name (Latin) refers to the forked apical projection of the scutellum.

Material Examined.—This species is known only from the type specimens.

ASPIRHINA ALVARENGAI HALSTEAD, NEW SPECIES
(Figs. 1a, 1b, 7, 12a, 12b)

Types.—Holotype, male; data: "BOLIVIA: Dept. Beni, Romansos, 1 km. N. Junction Rio Itenez & Rio Paragua, VII-30-1964, J. K. Bouseman and L. Lussenhop Collectors." Holotype resides in the American Museum of Natural History, New York. *Paratypes:* BOLIVIA. SANTA CRUZ: Gral. Saavedra Est. Experimental, Aug 1973, Malaise trap, C. Porter and L. Stange, 1 male (FSCA). BRAZIL. Pedra Azul, M. Gerais, Nov 1972, Seabra and Oliveira, 1 male (CNC). CEARA: Brasalha, May 1969, M. Alvarenga, 1 male (CNC). RONDONIA: Rio guapore opposite mouth of Rio Baures, 1–5 May 1964, Bouseman and Lussenhop, 1 male (AMNH). BAHIA: Encruzilhada, 960 m, Nov 1974, M. Alvarenga, 1 male (CNC). PANAMA. Barro Colorado Island Canal Zone, 14 Mar 1956, C. W. and M. E. Rettenmeyer, 1 male (USNM). SURINAME. Saramaca, Prov. Raleigh Vallen N. P. Foengoe Is., 22–31 Jan 1985, T. Thormin, 1 male (JAHC, from CNC).

Description.—*Male* (holotype). *Body length:* 6.0 mm. *Color:* black with apices of tibia and tarsus of fore and mid legs orange. *Pronotum and Mesoscutum:* dorsally without a median carina. *Scutellum:* in lateral view with dorsal margin nearly straight but steeply angled and apex of projection longer dorsally than ventrally (Fig. 12a); in dorsal view apical projection $0.29 \times$ maximum scutellar length (Fig. 1b); sculptured with oval setigerous punctures separated by 0.25 to $0.5 \times$ puncture diameter; 14 punctures along midline between base and apex; integument sculpture coriaceous, apical projection punctate except at apex. *Hind femur:* oval; teeth on ventral margin extending $0.52 \times$ hind femur length (Fig. 7). *Gaster:* pubescence silver on T1–2, remainder of terga with gold pubescence. *T1:* dorsally with four longitudinal carinae, extending $0.33 \times$ T1 length (Fig. 1a), sculpture punctate.

Female. Unknown.

Diagnosis.—*Aspirhina alvarengai* may be distinguished from other *Aspirhina* by its unique combination of the characters: tergum I dorsally smooth and with four longitudinal carinae in which the outermost carinae are about $0.5 \times$ length of innermost carinae (Fig. 1a), scutellar projection apically emarginate to forked (Figs. 12a, 12b) and dorsally punctate (Fig. 1b), and teeth on ventral margin of hind femur extending $0.52 \times$ length of hind femur (Fig. 7).

Variation.—*Male.* Apical projection of scutellum varies from weakly to strongly emarginate (Figs. 12a, 12b). Outermost longitudinal carina of T1 rarely shorter than the innermost carinae. Tergum I commonly smooth and polished at base. Two paratypes with punctures of T1 vague (Panama) to absent (Bolivia); integument smooth and polished though indications of punctures evident. One paratype (Bolivia) with five longitudinal carinae on T1.

Distribution.—Bolivia, Brazil, Panama, and Suriname.

Etymology.—Named for M. Alvarenga who collected much of the *Aspirhina* material.

Material Examined.—This species is known only from the type specimens.

ASPIRHINA SPINOSA HALSTEAD, NEW SPECIES
(Figs. 3a, 3b, 6, 11)

Types.—Holotype, male; data: "BRAZIL, Serrade Bocaina S. Paulo, XI-1968, 1600 m, M. Alvarenga." Holotype resides in the Canadian National Collection, Ottawa. *Paratype*: 1 male with same data and depository as holotype.

Description.—*Male* (holotype). *Body length*: 4.5 mm. *Color*: black with apices of tibia, tarsus of fore and mid legs, and club of antenna orange. *Pronotum and Mesoscutum*: dorsally with a median carina. *Scutellum*: in lateral view with dorsal margin convex and apex of projection rounded (Fig. 11); in dorsal view apical projection $0.4 \times$ maximum scutellar length (Fig. 3a); sculptured with oval setigerous punctures separated by 0.12 to $0.17 \times$ puncture diameter; 10 punctures along midline between base and apex; integument sculpture coriaceous; apical projection with a median, striated carina, punctate laterally below carina. *Hind femur*: oval; teeth on ventral margin extending $0.37 \times$ hind femur length (Fig. 6). *Gaster*: pubescence silver on T1–2, remainder of terga with gold pubescence. *T1*: dorsally with three longitudinal carinae, extending $0.33 \times$ T1 length (Fig. 3b), integument polished; on each side of lateral carina a long furrow extending length of longitudinal carinae; T1 somewhat fused with T2 but separation between them evident.

Female. Unknown.

Diagnosis.—*Aspirhina spinosa* may be distinguished from other *Aspirhina* by its unique combination of the characters: tergum I dorsally smooth and with three longitudinal carinae which are about equal in length (Fig. 3a), scutellar projection apically rounded (Fig. 11) and dorsally striate (Fig. 3b), and teeth on ventral margin of hind femur extending $0.37 \times$ length of hind femur (Fig. 6).

Variation.—Paratype male with antenna brown, hind tarsus orange, and median carina on mesoscutum vague.

Distribution.—Brazil and Bolivia.

Etymology.—The specific name (Latin) refers to the long, slender apical projection of the scutellum.

Material Examined.—This species is known only from the type specimens.

ASPIRHINA DECEPTOR HALSTEAD, NEW SPECIES
(Figs. 4a, 4b, 8, 13)

Types.—Holotype, male; data: "BOLIVIA, Beni: Rio Itenez opposite Costa Marques (Brazil), Sept. 4–6, 1964, Bouseman & Lussenhop." Holotype resides in the American Museum of Natural History, New York.

Description.—*Male* (holotype). *Body length*: 4.1 mm. *Color*: black with antenna, tegula, and legs brown. *Pronotum and Mesoscutum*: dorsally without a median carina. *Scutellum*: in lateral view with dorsal margin convex and apex of projection slightly incised (Fig. 13); in dorsal view apical projection $0.29 \times$ maximum scutellar length (Fig. 4b); sculptured with oval setigerous punctures separated by 0.12 to $0.5 \times$ puncture diameter; nine punctures along midline between base and apex; integument sculpture coriaceous, apical projection punctate to apex. *Hind femur*: oval; teeth on ventral margin extending $0.5 \times$ hind femur length (Fig. 8). *Gaster*: pubescence silver on T1–2, remainder of terga with gold pubescence. *T1*: dorsally with four longitudinal carinae, extending $0.33 \times$ T1 length (Fig. 4a), integument polished.

Female. Unknown.

Diagnosis.—*Aspirhina deceptor* may be distinguished from other *Aspirhina* by its unique combination of the characters; tergum I dorsally smooth and with four longitudinal carinae which are about equal in length (Fig. 4a), scutellar projection apically emarginate (Fig. 13) and dorsally punctate (Fig. 4b), and teeth on ventral margin of hind femur extending $0.5 \times$ length of hind femur (Fig. 8).

Variation.—Unknown. Species known only from type specimen.

Distribution.—Bolivia.

Etymology.—The specific name (Latin) refers to this species' ability to elude collectors.

Material Examined.—This species is known only from the type specimen.

ACKNOWLEDGMENT

I thank the staff of the museums listed for the opportunity to examine their specimens; Gary Gibson and John Huber (CNC) for gathering chalcidid material; Z. Boucek for assistance identifying the genus *Aspirhina*, and J. S. Noyes (British Museum of Natural History, London) for loaning the type of *A. dubitator*; K. J. Woodwich for the use of his drawing tube to prepare the figures, and D. J. Burdick (California State University, Fresno) for the use of laboratory facilities and for reviewing this paper. I thank also two anonymous reviewers for their editorial comments which improved this manuscript.

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Scientific Note

FIRST RECORD OF THE AUSTRALIAN PSYLLID *BLASTOPSYLLA OCCIDENTALIS* TAYLOR (HOMOPTERA; PSYLLOIDEA) ON *EUCALYPTUS* (MYRTACEAE) IN MEXICO

The occurrence of Australian Myrtaceae-feeding psyllids, including *Blastopsylla occidentalis* Taylor, has recently been reported from California on introduced but long-established host plants such as *Eucalyptus spathulata* Hooker and *Lophostemon confertus* R. Brown (Taylor, K. 1985. J. Aust. Entomol. Soc., 24: 17–30; Taylor, K. 1987. J. Aust. Entomol. Soc., 26: 229–233).

It has generally been assumed that these records represent recent direct introductions from Australia. However, *Blastopsylla occidentalis* is also well established in Mexico. Large populations were discovered on mature *Eucalyptus* trees growing 1 km south of San Juan Carapan, Michoacan on 12 Feb 1989, raising the possibility that Californian infestations may have originated from within the New World.

A number of pest species of psyllid have recently extended their ranges over considerable distances (Hodkinson, I. D. 1988. New Scientist, 118: 47–51). For example, the *Leucaena* psyllid, *Heteropsylla cubana* Crawford, has spread, over the last few years, from an origin in Central America, throughout the Pacific Basin as far as India. Psyllids can form a significant element of the aerial plankton (Spalding, J. B. 1979. Arctic Alpine Res., 11: 83–94) and wind dispersal or passive transport in or on aircraft have been suggested as mechanisms of spread, in addition to the dissemination of infested plant materials. The potato psyllid, *Paratrioza cockerelli* Sulc is already known to disperse seasonally on prevailing winds from breeding areas in northern Mexico, New Mexico, Arizona and Texas into the central states of the U.S.A. (Wallis, R. L. 1955. U.S. Dept. Agric., Tech. Bull., 1107). The normal direction of the prevailing winds, however, poses a greater obstacle to direct wind-assisted dispersal flights by *B. occidentalis* from Mexico to California, although more roundabout routes remain a distinct possibility. The importance of Central America as a potential source of psyllid infestation cannot be overstated. The recent introduction into Honduras (Burckhardt, D. & M. Martinez. 1989. Bull. Soc. Entomol. Fr., 94: 65–66) of a major disease vector of citrus, the Asian citrus psyllid, *Diaphorina citri* Kuwayama, raises the spectre of a rapid northwards expansion into the major citrus growing areas of the U.S.

I. D. Hodkinson, *School of Natural Sciences, Liverpool Polytechnic, Liverpool, L3 3AF, United Kingdom.*

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Scientific Note

**LOCATION OF HOLOTYPE OF *ARAEOSCHIZUS*
ANTENNATUS BLAISDELLI PAPP
(COLEOPTERA: TENEBRIONIDAE)**

Charles S. Papp recently described two new *Araeoschizus* from our Baja California, México collections (Papp, C. S. 1989. Notes on the Stenosini genus *Araeoschizus* LeConte from Baja, [sic] California, Mexico. (Coleoptera: Tenebrionidae.) Entomography, 6: 335–340). Papp (p. 338) incorrectly listed deposition of the holotype of *Araeoschizus antennatus blaisdelli* Papp as “In the Natural History Museum of the College of Idaho, Caldwell, Idaho” [CIDA]. Since we do not retain primary types, the specimen has been forwarded to the California Academy of Sciences as Type #16623. The holotype of *Araeoschizus antennatus clarki* Papp is also at the collection of the California Academy of Sciences (Papp, p. 335) as Type #16624. Additional specimens of both taxa are also deposited in CIDA.

William H. Clark, *Orma J. Smith Museum of Natural History, College of Idaho, Caldwell, Idaho 83605.*

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Scientific Note

**NEW HOST FOR *ACANTHOSCELIDES AUREOLUS* HORN
(COLEOPTERA: BRUCHIDAE)**

Acanthoscelides aureolus Horn forms a species-complex (Johnson, C. D. 1970. Biosystematics of the Arizona, California, and Oregon species of the seed beetle genus *Acanthoscelides* Schilsky (Coleoptera: Bruchidae). Univ. Calif. Publ. Entomol., 59; Johnson, C. D. 1983. Misc. Publ. Entomol. Soc. Amer., 56) of small (< 3 mm) beetles that range from the Alberta and Manitoba to Chiapas, Mexico, and from California to Minnesota and Nebraska. It commonly feeds on several species of *Astragalus* (Leguminosae).

I discovered a new host for *Acanthoscelides aureolus* at a record high elevation of 3620 m (11,800 ft) in White-Inyo Range of Mono Co., California. The new host is *Astragalus kentrophyta* Gray var. *implexus* (Canby) Barneby, an unusual species of *Astragalus* with fruits that rarely contain more than one seed (though

there are an average of six ovules per pistil). Its seeds are small, averaging 0.0018 g (SD = 0.0005 g), and typically mature in late August and early September. Adults of the beetle have been reared from laboratory stored seeds of the plant one or two months after collection. Adults have been observed emerging yearly from seeds collected between 1987 and 1990.

Voucher specimens of the beetle are deposited at Northern Arizona University, Flagstaff, Arizona, and the California Department of Food and Agriculture, Sacramento. Specimens of *A. kentrophyta implexus* are deposited at the Department of Botany Herbarium, University of California, Davis.

Material Examined.—CALIFORNIA. MONO Co.: White-Inyo Range, Sheep Mountain, alpine dolomite barrens above Patriarch Grove, 3620 m (11,880 ft) W. R. Owen, *Astragalus kentrophyta* Gray var. *implexus* (Canby) Barneby.

Acknowledgment.—I thank C. D. Johnson (Northern Arizona University, Flagstaff) for confirming the identification of *A. aureolus* and T. N. Seeno (California Department of Food and Agriculture, Sacramento).

Wayne R. Owen, *White Mountain Research Station, University of California, Los Angeles* and *Graduate Group in Ecology, University of California, Davis 95616*.

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Book Review

Oman, P. W., W. J. Knight & M. W. Nielson. 1990. Leafhoppers (Cicadellidae): a Bibliography, Generic Check-List and Index to the World Literature 1956-1985. CAB International, Wallingford, Oxon, United Kingdom, 368 p. (ISBN 0-85198-690-0).

One problem in systematics, as an academic field, is its rigorous dependence upon both information and priority. A systematist without a set of references on the taxonomic nomenclature and bibliography of his group is as handicapped as a lawyer without access to a legal library. Fortunately for leafhopper workers, a monumental catalogue for the cicadellids was published in several parts, largely by Z. P. Metcalf, and later by V. W. Burnside (e.g., [in part], Metcalf, Z. P. 1962-68. General catalogue of the Homoptera. Fascicle VI. Cicadelloidea. Parts 1-17. U.S. Dept. Agric., Agric. Res. Service, Washington D.C.). Metcalf's historic work provided an information base for leafhopper systematics that covered 200 years, ending in 1955. During the last 35 years, cicadellid researchers have severely felt the absence of Metcalf's coverage.

The current, very credible and welcomed volume by Oman, Knight and Nielson correct the deficient of easily accessible information since Metcalf. The work was largely compiled by Paul Oman over the years, and was completed when W. J. Knight and M. W. Nielson came to his aid to finish the formidable volume. These workers form the planet's most impressive and illustrious team in leafhopper taxonomy to date. Oman has achieved the position of world patriarch in cicadellid systematics; his catalogue of the genera of North America (Oman, P. W. 1949. The Nearctic leafhoppers [Homoptera: Cicadellidae], a generic classification and checklist. Mem. Entomol. Soc. Wash., 3) remains the taxonomic "bible." Knight and Neilson both have extensive experience and major systematic works to their credit; Neilson's compendium on leafhopper vectors (Neilson, M. W. 1968. The leafhopper vectors of phytopathogenic viruses [Homoptera, Cicadellidae]. Taxonomy, biology, and virus transmission. U.S. Dept. Agric. Tech. Bull., 1382) is a staple for the field of plant disease vectors.

The present work continues Metcalf's broad based bibliography through 31 Dec 1985, and covers all fields that are relevant to leafhopper biosystematics in its broadest sense, from behavior and biogeography to natural enemies and vector/pathogen interaction. The 7000 citations (all 164 pages of them in double bed, quarto format) contained in it were gathered both manually, and by computer searches of the Abstracts of Entomology, the Bibliography of Agriculture, Biological Abstracts, Entomology Abstracts, the Review of Applied Entomology and Zoological Record. The format employed assigns each citation an author-year-letter designation (i.e., "Bairyamova, V. 1970b"), as did Metcalf; this allows authors to make their literature citations in reference to this volume, rather than having to provide complete bibliographic information in their articles.

The taxonomic portion of the work covers 8000 new species and 1100 new genera. It provides information on: the family-group names proposed between 1956-1985, and the use of such names in the Cicadellidae during that period; a

provisional classification for the family; misassigned generic names; misidentified type-species; names placed on the official lists for generic names and family-group names in zoology; and names placed on the official index of rejected and invalid family-group names in zoology. It also provides an annotated, alphabetical checklist of the names at and above the generic level within the family. This information is indispensable, and will prove invaluable to leafhopper taxonomists, and anyone doing work on biodiversity.

Because of the wealth of important information that this tome contains, my criticisms of the volume are few; I'm sure, however, that some taxonomists will have individual points of contention with particular taxonomic treatments that are listed (all taxonomists seldom think completely alike). Diacritical marks have been omitted throughout the book; an unfortunate, but not major, problem for such a reference. Although the format is attractive and book is easily used, it might have been physically produced with a more archival quality in mind; especially because it will serve as a reference for generations. For example, I find no mention that the paper used is acid-free. Because of marketability, however, books today are seldom made to better standards.

If you work on leafhoppers, particularly their systematics, you cannot afford to be without this volume, which retails for \$86.50 US (£49.50 UK).

John T. Sorensen, *Insect Taxonomy Laboratory, California Dept. of Food & Agriculture, 1220 N Street, Sacramento, California 94815.*

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PACIFIC COAST ENTOMOLOGICAL SOCIETY
STATEMENT OF INCOME, EXPENDITURES AND
CHANGES IN FUND BALANCES

YEARS ENDED 30 SEPTEMBER 1989 AND 1988

	1989	1988
Income		
Dues and subscriptions	\$ 11,762	\$ 11,555
Reprints and miscellaneous	14,296	13,110
Sales of Memoirs	0	11
Interest	5,720	4,643
Dividends	576	544
Increase (Decrease) in value of capital stock:		
American Telephone & Telegraph Company	1,510	(620)
Pacific Telesis Group	3,705	(363)
Total Income	\$ 37,659	\$ 28,880
Expenditures		
Publication costs—Pan-Pacific Entomologist	\$ 45,718	\$ 20,141
Postage, newsletter and miscellaneous expenses	1,789	2,827
	\$ 47,507	\$ 22,968
Increase (Decrease) in fund balances	(\$ 9,848)	\$ 5,912
Fund balances October 1, 1989 and 1988	110,709	104,797
Fund balances September 30, 1989 and 1988	\$100,861	\$110,709

STATEMENT OF ASSETS
30 SEPTEMBER 1989 AND 1988

	1989	1988
Cash in bank		
Commercial account	\$ 16	\$ 11,161
Undeposited checks	0	140
Savings accounts & Certificates of Deposit		
General Fund	12,876	20,727
Charles P. Alexander Fund	41,819	39,520
Fall Memoir Fund	30,647	28,963
Total cash in bank	\$ 85,358	\$100,511
Investment in 80 shares of American Telephone & Telegraph Co. common stock and 264 shares of Pacific Telesis Group at market value	\$ 15,503	\$ 10,198
	\$100,861	\$110,709

See accompanying notes to the financial statements.

PACIFIC COAST ENTOMOLOGICAL SOCIETY

NOTES TO THE FINANCIAL STATEMENTS

YEAR ENDED SEPTEMBER 30, 1989

SUMMARY OF SIGNIFICANT ACCOUNTING POLICIES.

Accounting Method: Income and expenses are recorded by using the cash basis of accounting.

Capital Expenditures: Annual capital expenditures of \$5,000 or less are charged to expense.

Marketable Securities: American Telephone & Telegraph Co. and Pacific Telesis Group common stock are carried at market value. Increases and decreases in value are reflected in income.

Income Tax: The Society is exempt from Federal income and California franchise tax.

As Chairman of the Auditing Committee, and in accordance with its bylaws, I have reviewed the financial records of the Society.

During the course of this review nothing was noted which indicated any material inaccuracy in the foregoing statements.

H. Vannoy Davis
Chairman of the Auditing Committee

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Ferrari, J. A. & K. S. Rai. 1989. Phenotypic correlates of genome size variation in *Aedes albopictus*. Evolution, 42: 895-899.
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THE PAN-PACIFIC ENTOMOLOGIST

Volume 67

January 1991

Number 1

Contents

Pacific Coast Entomological Society, articles of incorporation and bylaws	1
ASQUITH, A. & J. D. LATTIN— <i>Omanonabis</i> : a new genus of Nabidae (Heteroptera) from western North America, with a review of <i>Nabis edax</i> Blatchley	7
KAMM, J. A.—Larval development of <i>Dargida procincta</i> (Grote) (Lepidoptera: Noctuidae) in the pacific northwest	20
TSAUR, S. C. & F. J. LIN—A new <i>Drosophila</i> species in the <i>montium</i> Meijere subgroup of the <i>melanogaster</i> Meigen species-group in the subgenus <i>Sophophora</i> Sturtevant from Taiwan (Diptera: Drosophilidae)	24
SORENSEN, J. T.—Phylogenetic character responses for shape component variance during the multivariate evolution of eulachnine aphids: redescription of <i>Pseudessigella</i> Hille Ris Lambers (Homoptera: Aphididae: Lachninae)	28
FENG, M. G., R. M. NOWIERSKI, A. L. SCHAREN & D. C. SANDS—Entomopathogenic fungi (Zygomycotina: Entomophthorales) infecting cereal aphids (Homoptera: Aphididae) in Montana	55
HALSTEAD, J. A.—New species of <i>Aspirhina</i> Kirby from the Neotropical region (Hymenoptera: Chalcididae)	65
SCIENTIFIC NOTES	
HODKINSON, I. D.—First record of the Australian psyllid <i>Blastopsylla occidentalis</i> Taylor (Homoptera: Psylloidea) on <i>Eucalyptus</i> (Myrtaceae) in Mexico	72
CLARK, W. H.—Location of holotype of <i>Araeoschizus antennatus blaisdelli</i> Papp (Coleoptera: Tenebrionidae)	73
OWEN, W. R.—New host for <i>Acanthoscelides aureolus</i> Horn (Coleoptera: Bruchidae)	74
BOOK REVIEW	
SORENSEN, J. T.—Oman, P. W., W. J. Knight & M. W. Nielson. 1990. Leafhoppers (Cicadellidae): a bibliography, generic-check-list and index to the world literature 1956–1985. CAB International, Wallingford, Oxon, United Kingdom, 368 p.	75
Sponsoring members of the Pacific Coast Entomological Society: 1989	77
Pacific Coast Entomological Society, financial statement for 1988, 1989	78
Announcement—publications of the Pacific Coast Entomological Society	80

The
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MATERNAL EFFECTS AND EGG HATCHABILITY IN *MELANOPLUS* (ORTHOPTERA: ACRIDIDAE)

W. CHAPCO AND P. W. RIEGERT

Department of Biology, University of Regina,
Regina, Saskatchewan, S4S 0A2, Canada

Abstract.—Continuous culturing of nondiapause strains of *Melanoplus* is possible because eggs are able to hatch within a short period of time and without the requirement of cold exposure. Analysis of intercross data involving field and nondiapause strains reveals that the proportion of eggs with this property is under maternal influence and, in some cases, a function of the egg's genotype. The problem of loss of genetic variation that is often associated with laboratory strain maintenance is discussed and a solution that capitalizes on maternal effects is offered.

Key Words.—Insecta, Orthoptera, Acrididae, *Melanoplus*, hatchability, maternal effects

The central and desirable feature of the much used nondiapause strain of *Melanoplus sanguinipes* Fabr., developed by Pickford & Randell (1969), and of the recently established nondiapause strain of *M. differentialis* (Thomas) (Oma et al. 1990), is the ability of eggs to hatch in a relatively short period of time (about 21 days at 30° C for *M. sanguinipes*) without the requirement of cold treatment. In this paper the term "egg hatchability" is restricted to this usage, which in reality is equivalent to the proportion of nondiapausing eggs; indeed, it is this trait that was selected for by the developers of these nondiapause cultures. There is no doubt that egg hatchability has a heritable basis, and although the mode of inheritance is presently unknown, polygenic inheritance is likely involved judging from the slow responses to selection for the trait (Slifer & King 1961). Environmental factors, such as temperature and photoperiod (Oma et al. 1990), can also influence hatchability; these agents probably interact with genotype to account for latitudinal variations in voltinism that are observed in the United States. Maternal effects, genic or nongenetic (mediated, for example, through maternal nutrition), result in offspring with phenotypes more similar to those of the female parent than to those of the male parent (Mather & Jinks 1982). Such effects were recently suspected during hybridization experiments (WC, unpublished data) when the species status of distant populations of *M. sanguinipes* and the nondiapause strain noted were examined. To support the claim for maternal effects, an analysis of these data and results collected 27 years ago (PWR, unpublished data) on *M. sanguinipes* and *M. packardii* Scudder is presented.

MATERIALS AND METHODS

Data were gathered separately by the authors. In studies by WC, the following field populations were sampled. Fourth and fifth instars of *M. sanguinipes* were collected near Bethune, Saskatchewan (Bet); Rigaud, Quebec (Que); and Green Mountain Road, British Columbia (BC) during the spring and summer of 1981. Insects were sexed, separated and allowed to mature in laboratory cages until commencement of matings. Adult *M. sanguinipes* were sampled from West Lafayette, Louisiana (Lo); Trinity Texas (Tx1); Oakhurst, Texas (Tx2); and Prescott, Arizona (Az) during the spring and summer of 1980. Insects were allowed to

Table 1. Mean (\pm SE) hatchability of field strains and of crosses with nondiapause strains of *Melanoplus sanguinipes* (NDwc and NDpr) and *M. packardii* (NDpr-pac).

Strain	Strain values	Crossed with ND ♀♀	Crossed with ND ♂♂
NDwc	78.8 \pm 2.4 (111) ^a	—	—
Bet	0.3 \pm 0.3 (22)	87.2 \pm 3.4 (26)	22.4 \pm 5.9 (31)
Que	2.6 \pm 1.3 (36)	54.0 \pm 5.1 (43)	0.0 \pm 0.0 (11)
BC	25.2 \pm 4.5 (49)	79.4 \pm 6.3 (24)	5.1 \pm 2.8 (7)
Lo	30.4 \pm 6.4 (38)	55.3 \pm 5.9 (42)	42.7 \pm 8.6 (24)
Tx1	38.9 \pm 6.9 (21)	50.7 \pm 8.2 (14)	21.7 \pm 13.6 (5)
Tx2	30.6 \pm 13.6 (7)	70.5 \pm 7.6 (21)	9.7 \pm 7.6 (8)
Az	38.7 \pm 6.8 (34)	91.8 \pm 2.6 (22)	43.1 \pm 7.4 (28)
NDpr	81.7 \pm 2.7 (100)	—	—
Wyn	NA	83.5 \pm 2.7 (61)	23.1 \pm 2.3 (168)
NDpr-pac	76.4 \pm 1.5 (305)	—	—
Dav	26.2 \pm ^b (49)	68.9 \pm 4.9 (53)	25.8 \pm 3.4 (67)

^a n = number of pods.

^b—no standard error because pods hatched in groups.

NA—not available.

deposit eggs in cages available in the laboratories of resident colleagues (see Acknowledgment). Harvested eggs (F_1 of field animals) were sent to the University of Regina and the emergent offspring used for these studies. All strains were crossed reciprocally with the nondiapause strain (NDwc) developed by Pickford & Randell (1969) beginning with material collected near Delisle, Saskatchewan (Pickford 1958). In addition, two of the above field populations, Que and BC, were mated reciprocally. Experimental conditions were essentially the same as those in Chapco (1984). About 10 pairs of virgin adults were introduced into standard Hunter-Jones cages. Dead insects were removed and replaced with virgins, if available. Egg pods were collected daily until most or all egg layers were dead and then individually transferred to shell vials with moistened vermiculite and incubated at 30° C for a maximum of 50 days, a length well beyond the period required for the nondiapause strain. Hatchlings were counted daily and removed. Hatchability for each pod was obtained by dividing hatchling number by the total number of eggs, determined by summing the former figure and the number of unhatched eggs.

In studies by PWR, fifth instars of *M. sanguinipes* and *M. packardii* were sampled from Wynyard (Wyn) and Davidson (Dav), Saskatchewan, respectively and allowed to mature in the laboratory. The former was crossed reciprocally (14 pairs) with Pickford and Randell's nondiapause strain (in its 45th generation of selection at the time of the study) and the latter (10 pairs) with a nondiapause strain (in its seventh generation of selection for nondiapause) initiated by PWR. To avoid confusion with NDwc used by WC, the nondiapause strains of PWR are labelled NDpr and NDpr-pac, respectively. Experimental conditions were the same as those of WC except that egg pods were transferred to petri dishes containing moistened filter paper.

Statistical significance of reciprocal differences and of other linear contrasts (see below) was assessed by a modified t -test that takes into account unequal sample variances (Zar 1984), which is the case here. Nonparametric tests of significance

Table 2. Analysis (*t*-tests) of reciprocal differences (maternal effects) and homogenic vs heterogamic mating differences (egg effects).

Strain	Reciprocal differences	ND strain vs ND ♀♀ × field ♂♂	Field strain vs field ♀♀ × ND ♂♂
Bet	***	*	***
Que	***	***	ns
BC	***	ns	***
Lo	ns	***	**
Tx1	ns	**	ns
Tx2	***	ns	ns
Az	***	***	ns
Wyn	***	ns	—
Dav	***	ns	—

ns—not significant.

*— $P < 0.05$.

**— $P < 0.01$.

***— $P < 0.001$.

(Campbell 1967) essentially yielded the same conclusions as the *t*-tests, attesting to the robustness of the latter.

RESULTS AND DISCUSSION

Mean percent hatchabilities along with standard errors are presented in Table 1 for the field strains and reciprocal crosses with nondiapause strains. Hatchabilities for the WC field material ranged from almost 0 (Bet) to 39% (Tx1), far below the value for the nondiapause strain, 79%. A comparison of values for reciprocal crosses suggests a maternal influence on the trait. In general, hatchabilities of eggs laid by nondiapause females mated with field males are consistently greater (significantly so in 5 cases; Table 2) than values for the reciprocal crosses. For example, the hatchability of eggs produced by the cross, NDwc ♀♀ × Bet ♂♂, exceeds the value for Bet ♀♀ × NDwc ♂♂ by about 65%. The phenomenon is apparently not restricted to the nondiapause strain. Que and BC are two field strains that differ in hatchability and exhibit significant reciprocal differences ($P < 0.01$): values for Que ♀♀ × Bet ♂♂ and Bet ♀♀ × Que ♂♂ are 0.7 ± 0.7 (10) and 39.2 ± 9.9 (9), respectively. Analysis of the PWR data on *M. sanguinipes* and *M. packardii* also reveals significant differences between reciprocal crosses (Table 2) adding further support to the claim for maternal effects. It is difficult to assess what these effects really represent. Had all strains been reared under the same conditions, the claim could be made that maternal effects are genotypically mediated on the female parent's side. This conclusion may be valid for the southern populations since insects were uniformly treated (at the University of Regina) and reared from eggs that had been sent although transgenerational effects are not unknown (Sander et al. 1985). In any case, the experimental design precludes a proper separation of genetic and environmental factors that underly the maternal effects.

Despite the ambivalence regarding inheritance and hatchability at the maternal level, a genetic analysis is possible, but at the level of the egg. The availability, on the whole, of two sets of homogamic and heterogamic crosses permits an examination of the possible role of the egg's genotype on hatchability. If maternal

effects, genic or nongenetic, were entirely responsible for the trait, then it would be expected that values would be the same irrespective of the source of the male. To test this possibility, differences between means for crosses with the same maternal type were examined (Table 2, last two columns). Out of a total of nine contrasts involving nondiapause females, there were five significant differences and out of a total of seven contrasts involving field females, there were three significant differences. The magnitude of these differences varies. To illustrate, in the Quebec study, the hatchability of eggs laid by NDwc females mated to Que males is in the same direction as that for the NDwc strain (i.e., indicating a maternal effect), but the value (54%) is significantly less than the value for NDwc (79%). In a few situations the hatchability of F_1 eggs is greater than the corresponding parental value, a result that suggests heterotic effects. For instance, the hatchability associated with the cross, NDwc ♀♀ × Az ♂♂, is 92%, a value significantly greater than the figure for NDwc. It would appear, therefore, that the genotype of the egg can, in some cases, influence its hatchability.

The findings with respect to maternal effects are germane to those wishing to maintain cultures of nondiapause grasshoppers that serve as model systems for purposes of investigating natural populations. It is not uncommon for laboratory strains to experience a reduction in numbers and a subsequent loss of genetic variation, or experience inadvertent selection as a result of adaptation to laboratory conditions. After a number of generations, a laboratory strain may no longer be representative of its species. The problem can be ameliorated to some extent by mating virgin females from the nondiapause strain with field-caught males thereby increasing the storehouse of genetic variation. By virtue of the maternal influence revealed in this paper, the inconvenience that diapause would otherwise present can be circumvented. Indeed, two such "hybrid strains" had been successfully propagated with the Louisiana and Arizona materials for seven generations, when they were terminated.

ACKNOWLEDGMENT

We thank M. Dakin of the University of Southwestern Louisiana, J. R. Hilliard of Sam Houston State University, and R. N. Foster and B. Thornley of USDA, Phoenix, Arizona for their unselfish help in the collecting of grasshoppers. Financial support from the Natural Sciences and Engineering Research Council (Strategic Grant G-0399 to WC) is gratefully acknowledged.

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**LIFE HISTORY AND DESCRIPTIONS OF IMMATURE
STAGES OF *TEPHRITIS BACCHARIS* (COQUILLET)
ON *BACCHARIS SALICIFOLIA* (RUIZ & PAVON)
PERSOON IN SOUTHERN CALIFORNIA
(DIPTERA: TEPHRITIDAE)**

RICHARD D. GOEDEN AND DAVID H. HEADRICK
Department of Entomology, University of California,
Riverside, California 92521

Abstract.—*Tephritis baccharis* (Coquillett) is bivoltine and monophagous on *Baccharis salicifolia* (Ruiz & Pavon) Persoon in southern California. The egg, second and third instar larvae, and puparium are described and illustrated. Eggs are inserted singly into terminal buds of main and axillary branches in late winter or early spring. First instar larvae hatch and tunnel into the pith just basad to the apical bud where they initiate gall formation. Gall and larval growth continue slowly into the fall, when pupation occurs. Most F₁ flies emerge, mate, and after about one week begin oviposition. Some F₁ flies that emerge in the fall may overwinter as adults; however, a few F₁ individuals may not emerge and instead overwinter as pupae in puparia in mature galls. Second and third instar, F₂ larvae also overwinter in developing galls. Flies were long-lived under laboratory conditions; males and females lived an average of 140 days and 83 days, respectively. This longevity and the long fecundity period of females allow *T. baccharis* to attack the new buds and branch growth produced by *B. salicifolia*, because this phraetophyte is capable of protracted, nearly year-round vegetative growth and flowering in southern California.

Principal natural enemies of *T. baccharis* include three, solitary, primary, parasitoids, *Pnigalo* sp. (Hymenoptera: Eulophidae), *Halticoptera* sp. and *Pteromalus* sp. (Hymenoptera: Pteromalidae), and unidentified birds as important predators on overwintering larvae in galls.

Key Words.—Insecta, biology, gall, parasitoids, bird predation, mating behavior, chemosensilla

Among 18 described species of *Tephritis* indigenous to North America (Foote 1960, Stolfus 1977, Foote & Blanc 1979, Jenkins & Turner 1989), only the biology of *T. stigmatica* (Coquillett) on *Senecio* spp. heretofore was well known (Tauber & Toschi 1965, Goeden 1988a). This paper details the biology of a second Nearctic species, *T. baccharis* (Coquillett), on *Baccharis salicifolia* (Ruiz & Pavon) Persoon [= *B. glutinosa* Persoon and *B. viminea* deCandolle (McVaugh 1984)], Asteraceae in southern California.

Interest has been expressed in the biological control of *B. salicifolia* (Boldt & Robbins 1990), other *Baccharis* spp. (Boldt & Robbins 1987, Boldt et al. 1988), and other indigenous weeds (Pemberton 1985) in the U.S. with natural enemies obtained from South America. Also, stenophagous *Baccharis*, feeding insects from North America have been imported to Australia for the biological control of *B. halimifolia* L. (Palmer 1987, Julien 1987, Palmer & Bennett 1989).

MATERIALS AND METHODS

Field observations, laboratory examination, and the rearing of field collected galls from several locations (see below) in southern California during 1983-1990 provided most of the information reported herein. These field data were supplemented by laboratory cagings, in 1989, of single males and females or paired reared adults of opposite sex. The adults were reared in 850 ml, clear plastic cages

fitted with screened lids for ventilation and basal water reservoirs in which absorbant cotton wicks and bouquets of excised vegetative branches of *B. salicifolia* were emersed through a hole in each cage bottom. Honey striped with a bulb and syringe on the underside of the lids provided food for the flies. Flies or parasitoids were reared from larvae and puparia dissected from galls held separately in cotton-stoppered, glass, shell vials within humidity chambers at 22–24° C and 76% RH.

Plant names follow Munz (1974) and McVaugh (1984); tephritid names follow Jenkins & Turner (1989). Voucher specimens of *T. baccharis* from each study site are located in the research collection of RDG (Department of Entomology, University of California, Riverside). RDG also has established a separate collection of hymenopterous parasitoids of California Tephritidae; DHH has established a separate collection of immature Tephritidae.

Immature stages were described from two eggs dissected from buds (laboratory cagings), a second and third instar larva, and a puparium dissected from galls. Larvae and eggs were treated for scanning electron microscopy (SEM) as described in Headrick & Goeden (1990a). Specimens were examined and micrographs prepared at 15 kV accelerating voltage, using Polaroid SS P/N film on a JEOL JSM-C35 SEM, located in the Department of Nematology, University of California, Riverside. The third instar larva is described in detail using the nomenclature and format adopted by Headrick & Goeden (1990a); the second instar larva description is limited to observed differences. Means \pm SE are provided throughout the paper.

TAXONOMY

Coquillett (1894) described *T. baccharis* as a *Trypeta*. Jenkins & Turner (1989) revised the *Baccharis*-infesting tephritids of North America, reviewed the taxonomy, designated the lectotype, illustrated and measured ova, and described and illustrated important characters of adult *T. baccharis*.

Egg.—Five eggs dissected from oviposition punctures (Fig. 1A) were white, fusiform, 0.68 ± 0.02 mm long and 0.26 ± 0.01 mm wide. The chorion is reticulated and the apex bears a 0.04 mm button-like, honey-combed pedicel (Fig. 2A). Polygonal reticulation of the chorion (Fig. 2B) is common to all eggs of Tephritidae examined to date (by DHH), but is highly developed in *Tephritis* species, especially *T. baccharis* (Jenkins & Turner 1989). An unusual feature of the reticulation is its differential complexity. The end embedded in plant tissue has more shallow fenestrations (Fig. 2C), which increase in height and become topped with papillae toward the heavily ridged pedicel (Fig. 2D). The plant itself may provide some measure of protection for the smooth end of the egg, which probably has little gas exchange function for the developing embryo, because it is inside plant tissue. The polygonal reticulation strengthens the exposed chorion, protecting not only the embryo, but also the pedicel through which most gas exchange probably takes place (as seen in a more exaggerated form in the eggs of *Paracantha gentilis* Hering [Headrick & Goeden 1990a]).

Third Instar Larva.—A single third instar larva measured 5.3 mm long and 2.5 mm wide (Fig. 3A). It is creamy white, superficially smooth, elongate, cylindrical, tapered and bluntly rounded anteriorly, and gradually increasing in width to its truncate posterior end.

The gnathocephalon is less conical and more reduced, and the rugose pads are

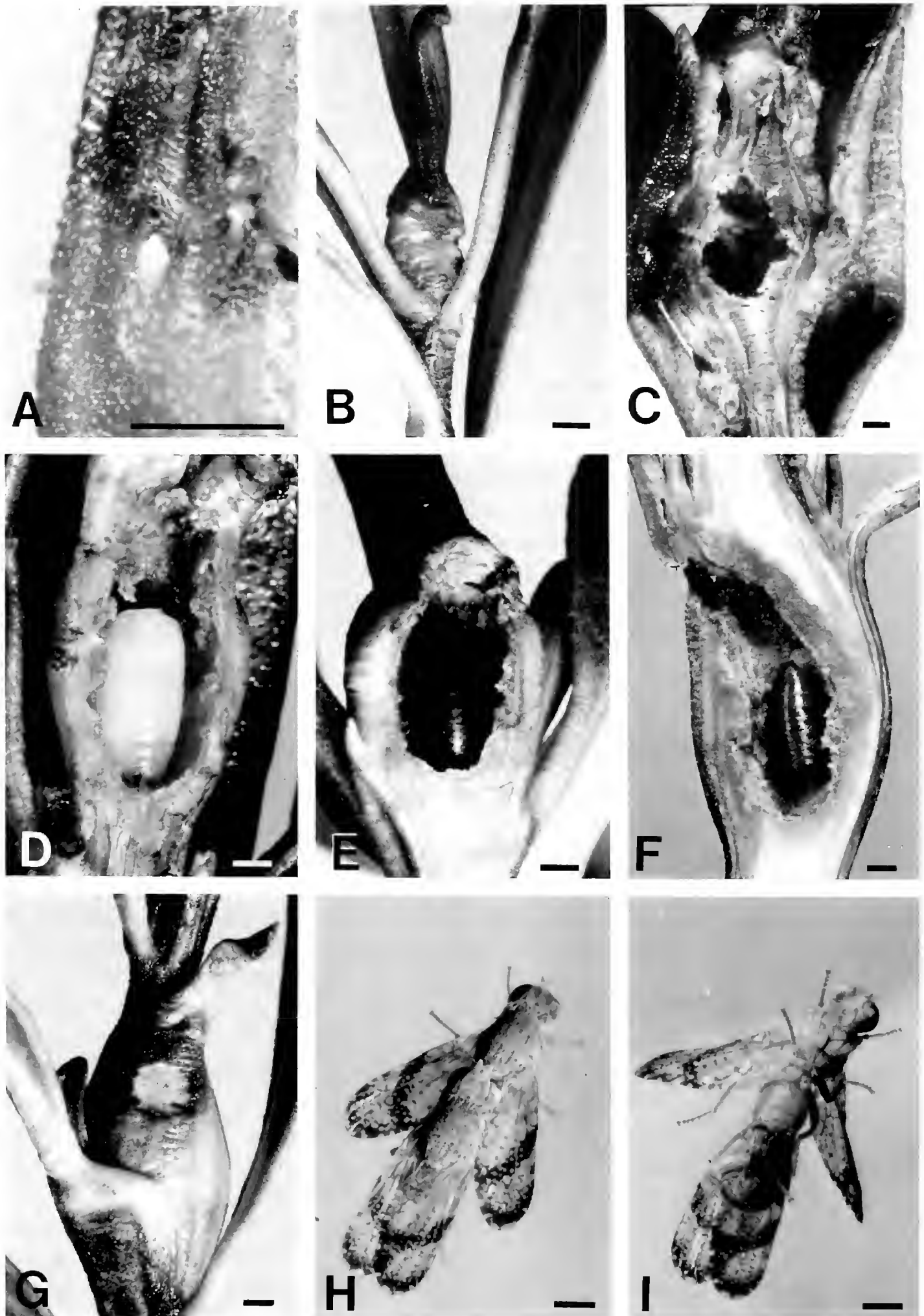


Figure 1. Life stages and galls of *Tephritis baccharis* on *Baccharis salicifolia*: (Bar = 1 mm) (A) egg protruding from ovipositional puncture in bud; (B) lateral view of small, immature gall; (C) sagittal section through small immature gall exposing feeding chamber; (D) third instar larva in feeding chamber in full-size gall; (E) gall with apical meristem killed by larval feeding; (F) puparium in feeding chamber below exit tunnel for adult; (G) lateral view of mature gall with round window through which adult emerges; (H) mating adults, dorsal view; (I) mating adults, ventral view.

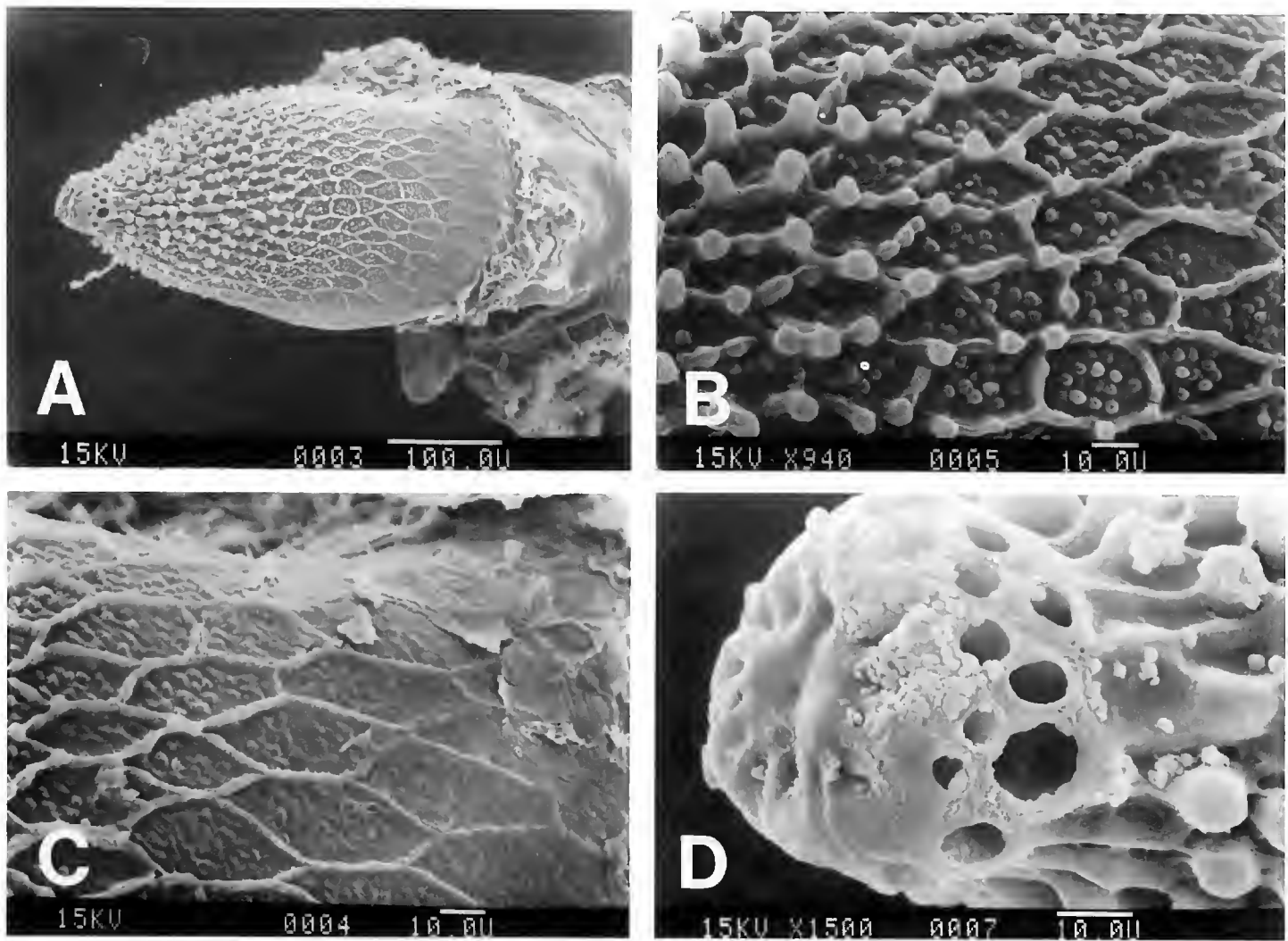
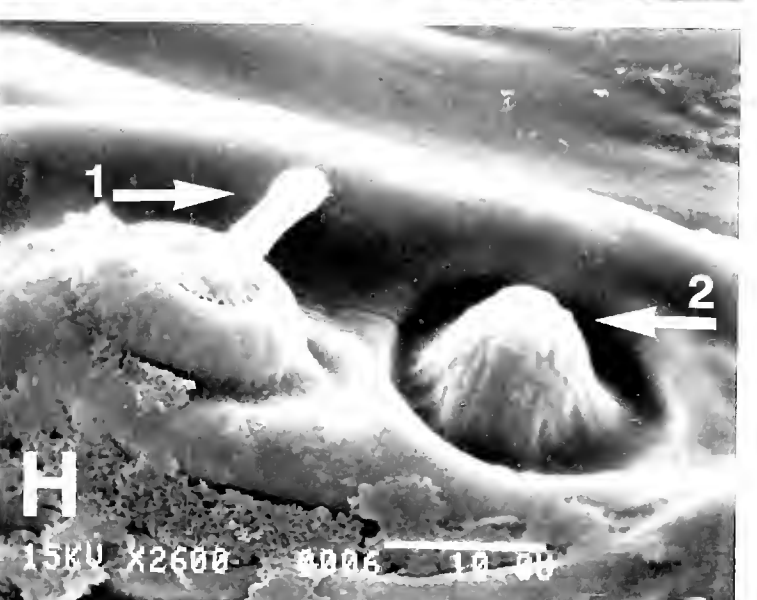
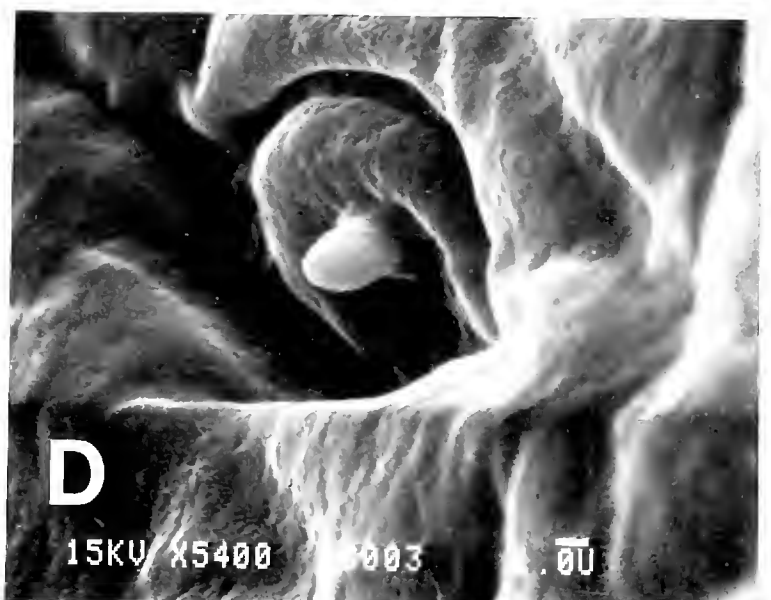
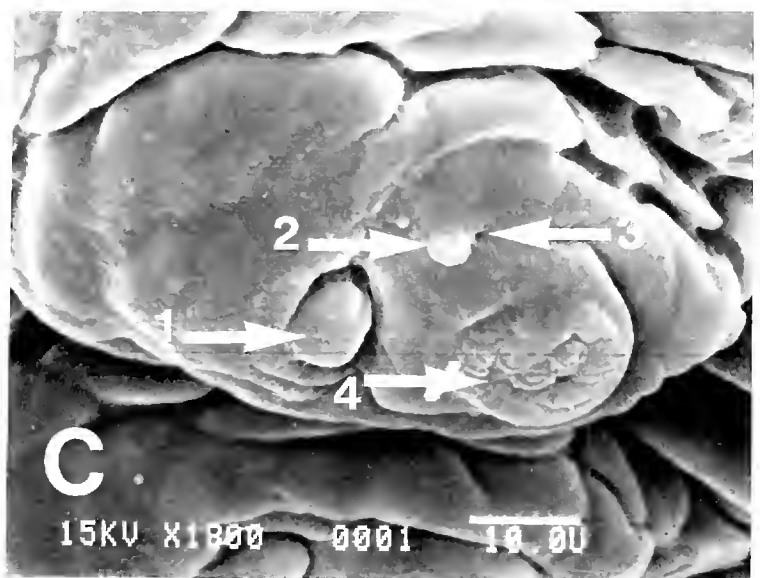
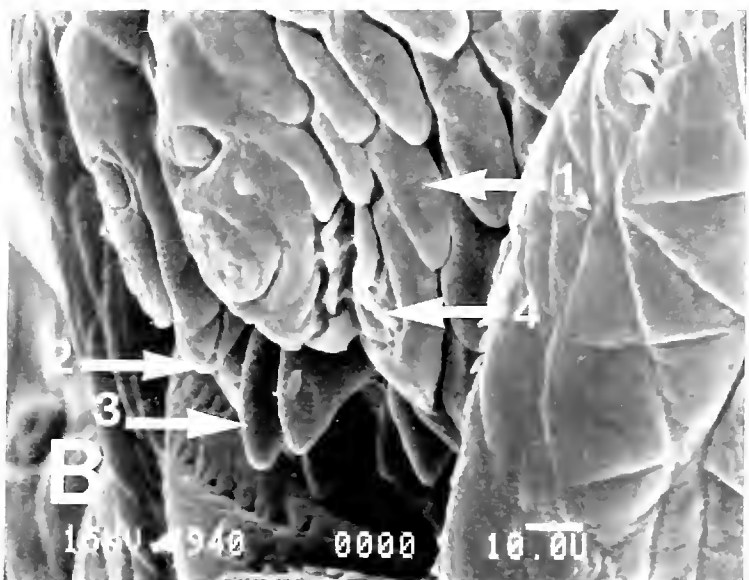


Figure 2. Egg of *T. baccharis*: (A) habitus, dissected from *B. salicifolia*; (B) detail of polygonal reticulation; (C) detail of point of insertion into plant tissue; (D) pedicel at exposed end of egg.

more dorsoventrally elongate than in most species of tephritid larvae examined by us to date (Fig. 3B: 1). The gnathocephalon bears flattened anterior sensory lobes separated by a medial depression (Fig. 3C). The paired dorsal sensory organs lie just dorsad of the anterior sensory lobes and are composed of a single papilla (Fig. 3C: 1). The sensory lobes bear the lateral sensory organ, the pit sensory organ and the terminal sensory organ (Fig. 3C: 2, 3, 4), which share the same structure and placement as with other tephritid larvae examined to date (DHH, unpublished data). The integumental petals which surround the mouth lumen (Fig. 3B: 2) are much reduced in comparison with other tephritid larvae (e.g., *Stenopa affinis* Quisenberry [Goeden & Headrick 1990]). The mouth hooks are heavily sclerotized and tridentate. The teeth are stout and bluntly conical (Fig. 3B: 3). A median oral lobe, which was not visible with SEM, was observed with a dissecting microscope; this brings the total number of nonfrugivorous tephritid larvae with a median oral lobe to 15 species (Headrick & Goeden 1990a; Goeden & Headrick 1990; DHH, unpublished data). Lateral lobes bearing several sensilla were located dorso-laterally on the edge of the mouth lumen (Fig. 3B: 4), are similar in placement, and share similar types of sensilla to those observed in *S. affinis* (Goeden & Headrick 1990).

The prothorax is smooth and bears several flattened sensilla. Larvae of Tephritidae typically have flattened sensilla on the prothorax (Foote 1967, Headrick & Goeden 1990a); however, *T. baccharis* has at least four sensilla, each with a finger-like projection surrounded by a collar. These sensilla may be mechanically



stimulated by deflection (Fig. 3D). The anterior thoracic spiracle is located dorso-laterad on the posterior margin and bears four papillae, each in turn topped with a distinct, smooth, rounded smaller papilla (Fig. 3E).

The succeeding segments are superficially smooth and demarcated by a depression that circumscribes the body. The integument adjacent to the segmental line is reticulated with shallow depressions and has intersegmental bands of minute acanthae (Fig. 3F: 1). Each segment bears a group of three sensilla arranged in a vertical row, posterior to the segmental line on the lateral aspect of the body (Fig. 3F: 2). The sensilla are smooth with a central pore, and are similar in shape and placement to the lateral sensilla described for *S. affinis* (Goeden & Headrick 1990).

The caudal segment bears the posterior spiracular plates composed of three elongate oval rimae about 0.07 mm long (Fig. 3G: 1), and four interspiracular processes with two to five branches; the longest process measured 0.03 mm in length (Fig. 3G: 2). The caudal segment also has the typical arrangement of sensory papillae that includes dorsal, lateral and ventral pairs of finger-like projections in a basal collar located on the posterior margin of the body (Fig. 3H: 1). A tuberculate chemosensillum is associated with each of the two dorsal sensilla in a shallow depression (Fig. 3H: 2). On the apex of the chemosensillum is a raised crown that bears several open pores. This sensillum has not been observed or described for any other tephritid larva to date (DHH, unpubl. data).

Second Instar Larva.—A second instar larva dissected and examined from an overwintering gall measured approximately 3.5 mm long and 1.5 mm wide (Fig. 4A). It is a translucent white, cylindrical, with a cone-shaped gnathocephalon, and rounded posteriorly. Most structures were similar in shape and placement to those of the third instar larva. The gnathocephalon is slightly rugose, with elongate pads as seen in the third instar. The anterior lobe is flattened and bears all three sensory organs as well as the closely associated dorsal sensory organ. The mouth hooks are bidentate and not bluntly rounded at the apex as in the third instar larva. The caudal segment has dorsal, lateral and ventral finger-like sensilla around the posterior margin. The posterior spiracular plates bear three rimae and interspiracular processes with one or two blades about 0.01 mm in length.

Puparium.—Fifty-two of 61 puparia of *T. baccharis* dissected from galls averaged 1.99 ± 0.03 (range, 1.50–2.31) mm in widest width, and 40 of these that were intact averaged 4.37 ± 0.07 (range, 3.34–5.59) mm in length. The puparia are superficially smooth, distinctly segmented, elongate ellipsoidal, anteriorly rounded, and slightly flattened posteriorly and dorsoventrally. The anterior end bears the invagination scar of the mouth and the anterior thoracic spiracles (Fig. 4B: 1, 2). The posterior end is finely wrinkled without protruding spiracular plates (Fig. 4C). One of 61 puparia dissected from galls was mostly unpigmented and black only at both ends; all other puparia were uniformly black. Goeden (1988a)

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Figure 3. Third instar larva of *T. baccharis*: (A) habitus, anterior end at left; (B) detail of gnathocephalon, 1—rugose pads, 2—integumental petals, 3—mouth hooks, 4—lateral sensory lobes; (C) anterior sensory lobes (dorsal at left), 1—dorsal sensory organ, 2—lateral sensory organ, 3—pit sensory organ, 4—terminal sensory organ; (D) sensillum on anterior of prothorax; (E) anterior thoracic spiracles; (F) lateral aspect of the body, 1—acanthae, 2—lateral sensilla; (G) posterior spiracular plate (dorsal at right), 1—rimae, 2—interspiracular processes; (H) posterior sensilla, 1—finger-like process, 2—dome sensillum.

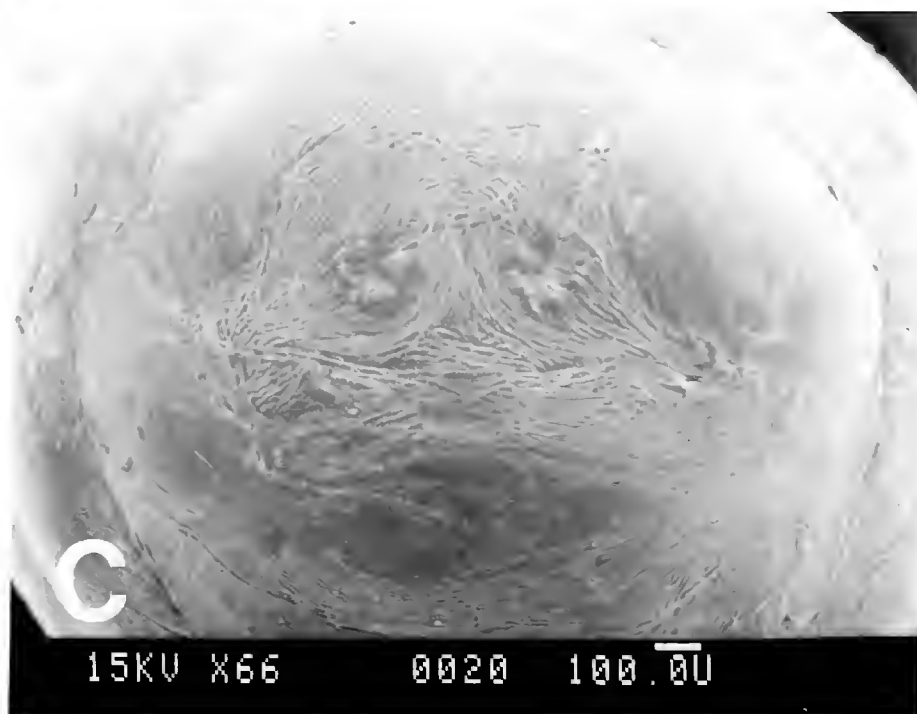
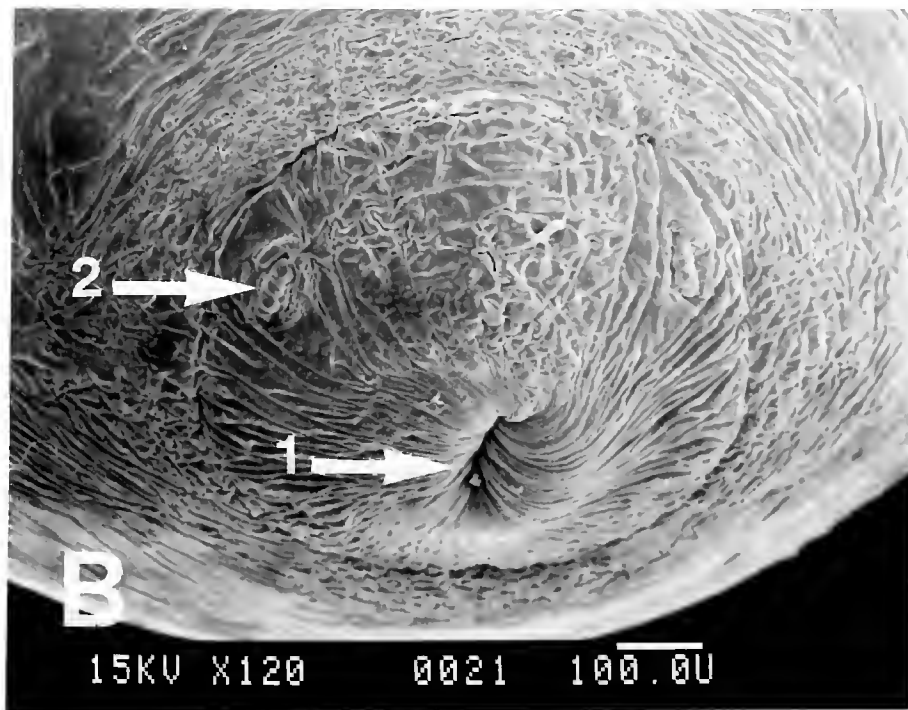
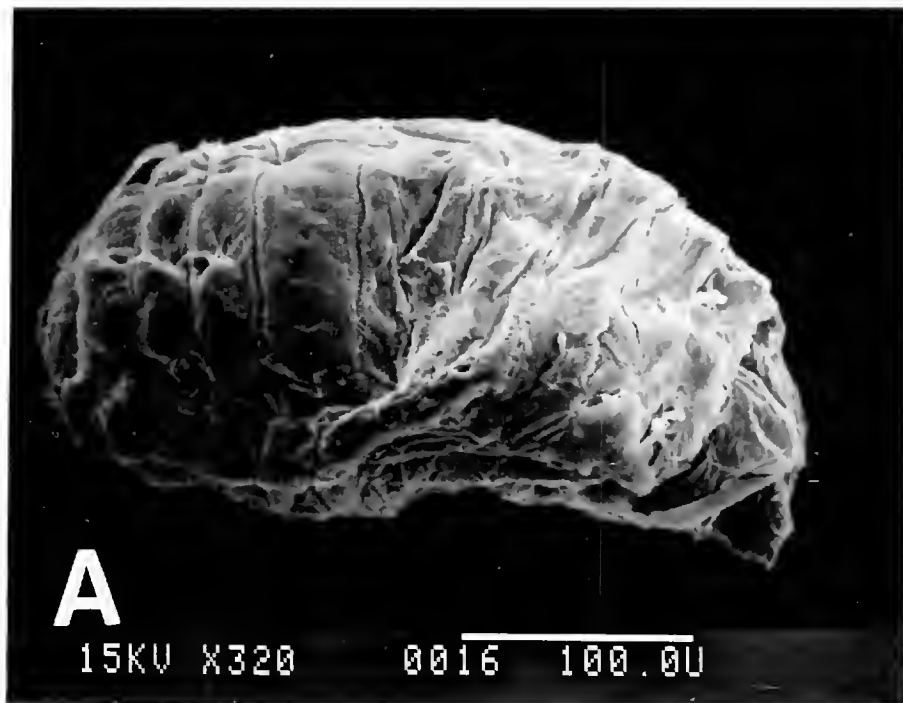


Figure 4. Second instar larva and puparium of *T. baccharis*: (A) habitus, second instar (anterior at right); (B) anterior end of puparium, 1—mouth invagination, 2—anterior thoracic spiracles; (C) posterior end of puparium.

reported incomplete pigmentation of some *T. stigmatica* puparia. This color variation also has been observed among some flower head infesting *Trupanea* (Goeden 1988b), gallicolous *Procecidochares* spp. (RDG, unpublished data), and was reported by Headrick & Goeden (1990a) among puparia of *Paracantha gentilis* Hering.

DISTRIBUTION, HOST, AND STUDY SITES

Jenkins & Turner (1989) described the range of *T. baccharis* as "eastcentral Mexico northwest to westcentral California." The distribution of its only known host plant, *B. salicifolia* (Wasbauer 1972, Jenkins & Turner 1989) was described by Boldt & Robbins (1990) as "common along waterways in the southwestern United States and northern Mexico as well as western and southern South America."

Tephritis baccharis has been reared only from bud galls on *B. salicifolia*, never from capitula of this or any other species of *Baccharis* or Asteraceae widely sampled throughout California since 1980 (RDG, unpublished data). Nearctic species of *Tephritis* are either obligate or facultative gall formers on branches or stems, or ovule feeders in capitula (Foote 1960; Tauber & Toschi 1965; Jenkins & Turner 1989; Goeden 1988a; RDG, unpublished data). *Tephritis baccharis* is a monophagous, obligate gall former.

Our field study locations for flies and galls augment the California and southwestern U.S. distributions plotted by Foote & Blanc (1963) and Jenkins & Turner (1989), respectively: W end of Central Valley, Laguna Canyon, and Cebada Canyons (Goeden 1983), Santa Cruz Island, Santa Barbara Co., 8–13 Oct 1983; Big Morongo Canyon, Riverside Co., 7 Mar 1985, 3 Apr 1986, 23 Jan 1989, 30 Jan 1990; Oriflamme Canyon, NW San Diego Co., 8 Mar 1989. Additional locations where the characteristic galls on *B. salicifolia* were observed or collected included: Canebrake Creek, N of Spring Canyon, NW Kern Co., 3 Mar 1987; Mission Canyon, Riverside Co., 2 Apr 1987; Scissors Crossing, NW San Diego Co., 19 Dec 1989 and 9 Jan 1990. This fly, like *B. salicifolia*, is widely distributed in riparian habitats in southern California; however, its galls were not observed at many other locations where flower heads of this dioecious shrub sampled yielded other Tephritidae (Goeden 1983; RDG, unpublished data).

Biology

Egg. — In laboratory cagings, eggs were inserted for all or most of their lengths, mainly into apical buds, and a few into axillary buds. Only the highly reticulated, pedicellar ends slightly projected beyond or below the edges of the longitudinal egg punctures (Fig. 1A). Three egg punctures measured 0.55 mm long by 0.15 mm wide. The long axes of the egg bodies, buds, and branches were parallel. Bud tissues turned necrotic in areas immediately surrounding the eggs, as reported for *Eutreta diana* (Osten Sacken), another gallicolous tephritid (Goeden 1990). One unhatched egg contained an embryo with its partly pigmented cephalopharyngeal skeleton located at the pedicellar end; however, the first instar larva always ecloses through a slit in the chorion near the end opposite the pedicel, and immediately begins tunneling basipetally. Apparently the embryo of *T. baccharis* turns 180° just before eclosion, like several other species of nonfrugivorous Tephritidae (Varley 1937, Cavender & Goeden 1982, Goeden 1987, Goeden et al. 1987). This

behavior apparently evolved to allow instant entry by the delicate, newly eclosed first instar larvae into moist, host plant tissues, and also to accommodate embryo respiration via the exposed pedicel (Headrick & Goeden 1990a).

All galls examined contained only one larva or puparium, indicative of only one egg having been oviposited in each bud in nature; however, in cagings, where ovipositional sites were scarce, as many as 10 eggs were inserted in a single apical bud. Similarly, in the field, most current generation galls were solitary at ends of separate branches; only one branch from Oriflamme Canyon bore two similar aged galls connected by a narrow neck of ungalled internode. Both sexes of *B. salicifolia* bore galls of *T. baccharis*.

Larva. — Two newly hatched larvae averaged 0.49 mm in length. The first instar tunneled until it reached the pith of the branch just basad to the apical meristem. The necrotic tunnel of one first instar was traced for 9 mm from this incipient gall site distally to its empty egg chorion. The young larva settles, molts, and initially excavates a small ellipsoidal cell about 3 mm long and <2 mm wide in the juvenile gall, evidenced externally as only a slight swelling of a branch terminal (Figs. 1B, 1C). Here, it feeds and develops (perhaps sporadically) through the summer or the following fall and winter, depending upon which generation it represents, F_1 or F_2 , respectively (see below). The molt to the second instar could be ascertained by the presence of a small, intact, cephalopharyngeal skeleton discarded at one end of the cell. Once plant growth begins in mid-winter to early spring, or is triggered once again later in the year by late summer rainfall as sometimes occurs in southern California, gall and larval growth are accelerated and proceed concurrently.

Twenty (87%) of 23 fully formed F_2 galls of the previous year's overwintering generation sampled at Oriflamme Canyon were fusiform; the remaining galls, subovoidal. The former shape resulted from continued growth of the bud at each gall apex; whereas, the latter shape resulted from death of the terminal bud from larval feeding by *T. baccharis*. Such intragenerational differences in shape also were noted among galls of *T. stigmata* by Goeden (1988a), and the causes for this difference were discussed relative to galls of *E. diana* by Goeden (1990). The galls of *T. baccharis*, like those of *T. stigmatica*, are shortened, thickened, succulent terminal parts of main or axillary branches (Figs. 1D, 1E). The 23 mature galls incorporated an average of 3.8 ± 0.3 (range, 1–6) nodes, and were smooth surfaced, light green and longitudinally striped or unilaterally colored red-purple when occupied. When empty, the galls turned tan, shriveled, and dehisced, or became woody and persisted as branch swellings. Externally, the 23 galls averaged 13.1 ± 0.5 (range, 8–19) mm in length, and 5.6 ± 0.2 (range, 4–7) mm in width. The larva feeds on the expanded pith parenchyma which comprises the bulk of the gall (Figs. 1C, 1D). The feeding larva eventually hollowed out an ellipsoidal, central, longitudinal, basally rounded cavity. This open feeding cavity was irregularly surfaced with yellow-white callose tissue, and averaged 5.5 ± 0.2 (range, 4.4–7.8) mm in length and 2.7 ± 0.1 ($n = 23$; range, 2.1–3.5) mm in width (Fig. 1D).

Twenty (66%) of 30, F_1 galls collected on Santa Cruz Island were fusiform; the remainder, subovoidal. These 30 galls incorporated 3.8 ± 0.1 (range, 3–5) axils and externally measured 20.4 ± 1.0 (range, 12–33) mm long by 8.3 ± 0.3 (range, 6–13) mm wide.

When fully grown, the larva extends the feeding cavity into an exit tunnel 1.7 ± 0.1 ($n = 23$; range, 0.8–3.2) mm long, which may end apically (and thus kill the terminal bud, Fig. 1E), or more commonly ends subapically (Fig. 1F) in an oval to round, thin, cuticular window 1.6 ± 0.1 (range, 1.1–2.1) mm in diameter (Fig. 1G).

Puparium.—Pupation occurs in the feeding chamber with the posterior end of the puparium resting on, or up to, about 1 mm above the bottom of the feeding chamber. The anterior end of the puparium normally faces the window to allow egress of the emerging adult (Fig. 1F).

Adult.—Five males and five females (F_1) emerged between 13 Nov and 6 Dec 1985 from galls collected on Santa Cruz Island during the previous October. Six males and three females emerged from 22 Mar to 5 Apr (overwintered F_2) from galls collected in Oriflamme Canyon in Mar 1989. Both sexes emerged throughout the emergence periods. Also, two females emerged from F_1 galls collected at Big Morongo Canyon on 23 Jan 1985. One male and one female emerged on 15 Jan 1990 from F_1 galls apparently containing these individuals as fully developed pupae within puparia collected at Scissors Crossing on 9 Jan 1990. These latter two rearing records demonstrate that some F_1 individuals also overwinter as puparia in galls.

Apparently females are polygamous, males are polyandrous. Females began to mate in laboratory cagings ($n = 3$) 1 to 2 days after their emergence. Pairs mated repeatedly; one pair mated on at least 17 different days, and for the last time when the female was 121 days old. Another pair caged together at emergence mated on each of the first 7 consecutive days after they emerged. Mating by virginal males and females in laboratory cagings was protracted, involving little courtship behavior and no apparent postmating behavior. The male mounted the female after a short period of mutual recognition evidenced when the flies stood face-to-face and alternately, slowly waved their wings three to seven times. The anal edge of each wing was turned downward as each wing was brought forward until nearly perpendicular to the substrate in supination (Headrick & Goeden 1990b). The male then jumped over and atop the female or mounted her from one side, forcibly spread her wings, and rapidly initiated coitus. The mating posture (Figs. 1H, 1I) was much like that illustrated and described by Tauber & Toschi (1965) for *T. stigmatica*. The hind tarsi of the male rest on the substrate or move back and forth along the oviscape to help position the female's terminalia, his midtarsi grasp the middle of her abdomen laterally, and his foretarsi clasp her abdomen at its juncture with the thorax. The mouthparts of the male are positioned above her scutellum; the mouthparts of both flies pump rapidly during copulation (four to five pumps/sec). The wings are held parallel to the substrate. The wings of the female are spread at about 80° and centered over her abdomen; those of the male are overlapped atop his dorsum or are spread up to about 30° (Figs. 1H, 1I). Except for their mouthparts, both flies generally remain motionless during copulation, although the female may groom her head and mouthparts with her foretarsi, occasionally bring one wing forward, or even walk about while carrying the male with his hind tarsi on or off the substrate. Matings were observed throughout the daylight hours, and in one instance was extended over 2 days and nights under artificial lighting. To avoid mating, a nonreceptive female turned in tight circles, flew at the male, or turned and walked away. Males also mounted,

rode, but did not couple with nonreceptive females. For example, one male daily mounted and remained in a mating posture atop a nonreceptive female for up to 6 h on each of 4 consecutive days after they last mated, but without coupling with her.

Females began oviposition in bouquets in cages 1–2 weeks after emergence. Probing did not always result in oviposition. An average of about one egg per day was laid by each of seven females (range, 0.4–2 eggs daily). The oldest female was 65 to 72 days old when she last oviposited. Five males lived an average of 140 (range, 58–196) days; three females, 83 (range, 38–142) days. Tauber & Toschi (1965) reported the laboratory longevity of *T. stigmatica* adults when fed water, sugar, and enzymatic protein hydrolysate of yeast as 6 to 187+ days. Long-lived adults occur more widely among nonfrugivorous Tephritidae than is generally recognized (Christenson & Foote 1960, Freidberg 1984). Whether longevity among nonfrugivorous species correlates with the presence or absence of symbionts in the adult as suggested by Harris (1989) remains to be addressed experimentally.

Seasonal History.—*Tephritis baccharis* usually is bivoltine on *B. salicifolia* in southern California, but may be univoltine at some desert locations during dry years, as reported with *Procecidochares* sp. by Silverman & Goeden (1980). *Tephritis baccharis* does not additionally reproduce in capitula of the same host species or of an alternate host, as do *T. stigmatica* (Coquillett) (Tauber & Toschi 1965, Goeden 1988a), *T. arizonaensis* Quisenberry (Goeden 1983; Jenkins & Turner 1989; RDG, unpublished data), *T. palmeri* Jenkins, and *T. subpura* (Johnson) (Jenkins & Turner 1989). However, the combination of long-lived adults and long-fecund females in *T. baccharis* and a host phraetophyte capable of nearly year-round growth and flowering under southern California conditions (Munz 1974), can lead to localized overlapping and obscuring of fly generations. This reproductive flexibility on the part of *T. baccharis* facilitates utilization of buds and new branch growth on its host plant, which itself shows reproductive flexibility, traits useful for survival in drainages with high water tables and riparian habitats in otherwise harsh, arid environments.

Natural Enemies.—Three species of chalcidoid Hymenoptera were reared from *T. baccharis* during this study. Three females of *Pteromalus* sp. (Pteromalidae) were recovered from puparia as solitary endoparasitoids. Two males of *Halticoptera* sp. (Pteromalidae) were reared as solitary, larval ectoparasitoids. One female of *Pnigalo* sp. (Eulophidae) was recovered from a small gall as a solitary, ectoparasitoid of an early stage larva of *T. baccharis*.

Large holes in the sides of empty galls matched symptoms of predation by birds, probably bush tits, *Psaltriparus* sp., recently documented for galls of *Eutreta diana* (Goeden 1990). Five (14%) of 35 galls sampled from Oriflamme Canyon yielded parasitoids; five more galls suffered bird predation. Fifty-nine (69%) of 86, mainly F₂ galls of all sizes collected in Big Morongo Canyon on 30 Jan 1990 had been opened by birds and the larvae within removed.

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**PARASITOIDS OF BLACK SCALE IN CALIFORNIA:
ESTABLISHMENT OF *PROCOCOPHAGUS PROBUS*
ANNECKE & MYNHARDT AND *COCCOPHAGUS RUSTI*
COMPERE (HYMENOPTERA: APHELINIDAE)
IN OLIVE ORCHARDS**

K. M. DAANE, M. S. BARZMAN, C. E. KENNETT,
AND L. E. CALTAGIRONE

Division of Biological Control, Department of Entomology,
University of California, Berkeley, California 94720

Abstract. — A survey of the parasitoid species of black scale, *Saissetia oleae* (Olivier), in California central valley olive orchards revealed that two recently imported parasitoids, *Prococcophagus probus* Annecke & Mynhardt and *Coccophagus rusti* Compere, have become established. These South African parasitoids were released from 1979 to 1983. During the release period, neither parasitoid was recovered. However, subsequent to the release, surveys of distribution of these species revealed that both had become established. In the first survey (1984–1987), 23 commercial olive orchards located in Tehama, Glenn, Madera, and Tulare Counties, were sampled. A second survey (1988–1990) included seven olive orchards located in Tehama and Madera Counties, and black scale infestations on selected ornamental olive and oleander plants in Tehama, Colusa, Sutter, Glenn, and Butte Counties. *Prococcophagus probus* and *C. rusti* were reared from black scale infested olive and oleander plants in Tehama County. Recovery of these species, over the three years after the last release, provides evidence of their establishment in the Sacramento Valley.

Key Words. — Insecta, Aphelinidae, *Prococcophagus*, *Coccophagus*, Homoptera, *Saissetia oleae*, olive, biological control

Black scale, *Saissetia oleae* (Olivier), believed native to South Africa (De Lotto 1976), is found throughout the tropical and subtropical regions of the world. It is a very polyphagous species with a host range that includes such common plants to California as oleander (*Nerium oleander* L.), pepper tree (*Schinus molle* L.), coyote brush (*Baccharis pilularis* Wolf), and toyon (*Heteromeles arbutifolia* Lindahl) (Argyriou 1963). In California, *S. oleae* has been a pest of olive (*Olea europaea* L.) and *Citrus* spp. since the 1880s. As a result of its wide host range and high reproductive rate, the scale has spread throughout California and is ubiquitous in the state's central valley olive orchards, resulting in frequent infestations.

Black scale is exotic to most olive growing regions and has been the target of numerous classical biological control programs (Bartlett 1978). Studies of population dynamics in the Mediterranean region have attributed significant scale mortality to natural enemies (Argyriou & Katsoyannos 1976, Monaco 1976, Parasakakis et al. 1980, Roberti 1981). In California, biological control programs against *Saissetia oleae* began in 1891 and natural enemies have been imported since from Asia, Africa, Australia, Central and South America, Europe, and the Middle East (Bartlett 1978, Kennett 1986). Parasitoid importation and establishment in California resulted in relatively successful control of black scale on ornamentals and citrus in coastal regions. However, parasitoid establishment in the central valley

has not been as successful. Over 50 natural enemies of black scale have been introduced in California and less than 15 have become permanently established in the central valley (Table 1).

Establishment of black scale parasitoids is best understood in light of the population dynamics of their host. Seven black scale stages can be differentiated from egg to adult (Argyriou 1963), although most black scale parasitoids are specific to only two or three consecutive host stages (Smith & Compere 1928, Compere 1940). Thus, it is difficult for some parasitoids to become established where scale development is univoltine and synchronous because of the long periods in which suitable host stages are not commonly found. Due to harsh climate in the central valley, black scale development there is more synchronous than in coastal California (Daane 1988). For example, *Metaphycus lounsburyi* (Howard) is abundant at coastal locations but is rarely found in the interior valleys (Kennett 1986).

Further, many of the initial attempts to establish imported species of black scale parasitoids failed because of inadequate biological information (Bartlett 1978). For example, until the 1930s many primary parasitoids with obligatory male hyperparasitic habits were discarded as undesirable secondary parasitoids. Differences between parasitoid biotypes may also affect establishment. Panis & Marro (1978) showed that there were sufficient behavioral differences between two biotypes of *Metaphycus lounsburyi* (Howard) for them to be used in the same orchard for biological control.

We report here the establishment of two black scale parasitoid species, *Prococcophagus probus* Annecke & Mynhardt and *Coccophagus rusti* Compere, in olive orchards in the Sacramento Valley, where they were previously thought to have failed to become established. *Prococcophagus probus* was first released in California in 1979. *Coccophagus rusti* was first released in 1937 and was reported as established (Flanders 1952) in coastal locations, but not within the central valley. It was imported from South Africa again in 1978 and released in central valley olive orchards in 1980.

MATERIALS AND METHODS

Parasitoid Release.—From 1979 to 1982, five parasitoid species were imported to California from South Africa. *Prococcophagus saissetiae* Annecke & Mynhardt, *P. probus*, *C. rusti*, *Aloencyrtus saissetiae* (Compere), and *Metaphycus inviscus* Compere were collected by S. Naser (South African Ministry of Agriculture) and sent to the quarantine station at the Division of Biological Control, University of California, in Albany. After release from quarantine, colonies were established in the insectary on black scale reared on oleander. From 1979 to 1983, 1180 *P. probus* (67% female), 3265 *P. saissetiae* (59% female), 535 *C. rusti* (88% female), 265 *A. saissetiae* (98% female), and 1352 *M. inviscus* were released at five olive orchards in the central valley (three orchards near Corning, Tehama County, one near Parlier, Fresno County, and one near Porterville, Tulare County) and on selected ornamental host plants of the black scale in the east bay region of the San Francisco Bay area (Alameda and Contra Costa Counties). Releases were concentrated in the fall of each year when the proper black scale host stages were most common.

Recovery Attempts.—During the parasitoid release period (1979–1983), olive twigs infested with black scale were collected at each release site in the fall and

Table 1. A partial list of introduced primary black scale parasitoids (source: Smith & Compere 1928, Bartlett 1978, Kennett 1986).

Species	Origin	Date introduced	Established
Aphelinidae			
<i>Aneristus ceroplastae</i> Howard	Taiwan	1933, 1952	no
<i>Coccophagus anthracinus</i> Compere	South Africa	1923	no
<i>Coccophagus baldassarii</i> Compere	Eritrea	1953	no
<i>Coccophagus basalis</i> Compere	Brazil	1958	no
<i>Coccophagus capensis</i> Compere	South Africa	1924	yes
<i>Coccophagus caridei</i> (Brethes)	Brazil, Argentina	1934, 1935	no
<i>Coccophagus cowperi</i> Girault	East Africa	1937	yes
<i>Coccophagus eleaphilus</i> Silvestri	Eritrea, Morocco	1953, 1953	no
<i>Coccophagus hawaiiensis</i> Timberlake	Taiwan	1951	no
<i>Coccophagus japonicus</i> Compere	Japan	1951	no
<i>Coccophagus lycimnia</i> (Walker)	Africa	1900s (accidental)	yes
<i>Coccophagus lycimnia</i> (Walker) ^a	Brazil, Argentina	1935, 1935	no
	Australia	1972	no
	Africa, Mexico	?	no
<i>Coccophagus mexicensis</i> Girault	Mexico	1956	no
<i>Coccophagus nigrinus</i> Compere	Eritrea	1954	no
<i>Coccophagus ochraceus</i> Howard	Africa	1990s (accidental)	yes
<i>Coccophagus eritreaensis</i> Compere	South Africa	1925, 1937	no
<i>Coccophagus rusti</i> Compere	Kenya, Uganda	1937	yes
	South Africa	1932, 1981	yes
<i>Coccophagus scutellaris</i> (Dalman)	Africa	1900s (accidental)	yes
<i>Lounsburyi trifasciatus</i> (Compere)	South Africa	1924	yes
<i>Prococcophagus saissetia</i> Annecke & Mynhardt	South Africa	1978	no
<i>Prococcophagus probus</i> Annecke & Mynhardt	South Africa	1978	yes
Encyrtidae			
<i>Aloencyrtus saissetia</i> (Compere)	South Africa	1979	no
<i>Anicetus annulatus</i> Timberlake	Australia, Taiwan	1931, 1951	no
<i>Coccidoxenus niloticus</i> Compere	Kenya	1937	no
<i>Diversinervus elegans</i> Silvestri	Eritrea, Lebanon	1953, 1964	yes
<i>Diversinervus smithi</i> Compere	South Africa	1937	no
<i>Encyrtus fuliginosus</i> Compere	South Africa	1937	no
<i>Encyrtus infelix</i> Embelton	Hawaii	1921	yes
<i>Metaphycus angustifrons</i> Compere	Taiwan	1952, 1957	no
<i>Metaphycus bartletti</i> Annecke & Mynhardt	South Africa	1956	yes
<i>Metaphycus citrinus</i> Compere	Eritrea	1953	no
<i>Metaphycus flavus</i> (Howard)	Spain	1954, 1955	no
<i>Metaphycus gilvus</i> Compere	North Africa	1953	no
<i>Metaphycus helvolus</i> (Compere)	South Africa	1937	yes
<i>Metaphycus lichtensiae</i> Compere	South Africa	1958	no
<i>Metaphycus lounsburyi</i> (Howard)	Australia	1916–1918	yes
<i>Metaphycus luteolus</i> (Timberlake)	Mexico	1954, 1955	yes
<i>Metaphycus stanleyi</i> Compere	South Africa	1937	yes
<i>Metaphycus zebratus</i> Mercet ^b	Spain	1986	?
<i>Microterys flavus</i> (Howard)	Pakistan	1957	no
<i>Microterys okitsuensis</i> Compere	China, Japan	1951, 1952	no
<i>Microterys saissetiae</i> Compere	Uganda	1937	no
<i>Microterys tricoloricornis</i> (DeSoto)	Mexico	1956	no
Eupelmidae			
<i>Lecanobius utilis</i> Compere	Brazil, Argentina	?	yes

Table 1. Continued.

Species	Origin	Date introduced	Established
Pteromalidae			
<i>Anysis saissetiae</i> (Ashmead)	China, Pakistan	1924, 1957	no
<i>Lecaniobus cockerelli</i> Ashmead	West Indies	1913, 1915, 1940	no
<i>Mesopelittita atrocyanea</i> (Masi)	East Africa	1937	no
	South Africa	1957	no
	Mexico	1958	no
<i>Scutellista caerulea</i> (Fonscolombe)	South Africa	1901-1902	yes
<i>Scutellista cyanea</i> Motschulsky (red larval race)	Taiwan	1952	no

^a *Coccophagus lycimnia* has been introduced from a number of countries, however, establishment of this species may be from accidental introductions prior to importation efforts.

^b *Metaphycus zebratus* has been recovered continually since its release; documentation of permanent establishment is in progress.

spring of each year. Samples were brought into the laboratory and held in glass-topped sleeve cages from four to six weeks. Emerging parasitoids were collected three times a week and stored in 70% ethanol for later identification. These samples were taken as part of a central and northern California survey of black scale parasitoids that included a majority of the counties within the Sacramento and San Joaquin valleys and several coastal counties extending from Napa County to San Luis Obispo County (Kennett 1986). Nearly 70% of the samples were taken from urban and rural landscapes (olive; *Citrus* cultivars of grapefruit, orange; Modesto ash, *Fraxinus velutina* var. *glabra* Rehder; English holly, *Ilex aquifolium* L.), 20% from natural stands of native shrubs (coyote brush and toyon), and 10% from commercial olive orchards. Detailed results from these collections were reported by Kennett (1986).

From 1984 to 1987, a separate parasitoid survey was conducted in conjunction with a black scale population dynamics study on olive. All samples were taken from commercial olive orchards located in the central valley: seven orchards near Corning, Tehama County; one near Orland, Glenn County; one near Madera, Madera County; one near Parlier, Fresno County; and 11 near Lindsay, one near Strathmore, and one near Exeter, Tulare County. Included in this 23 orchard study were four of the five orchards that received the five imported black scale parasitoid species from 1979 to 1983. The release orchard in Porterville was removed in 1984 and is, therefore, not included in the survey. Likewise, the orchard in Parlier was removed in 1986 and data presented for parasitoids collection in 1987 does not include this orchard.

In each orchard sampled, except in Glenn County, collections were made every six to eight weeks. In the Glenn County orchard, samples were taken each fall and spring, when black scale parasitoids were most common. Olive twigs infested with black scale were collected and the scales were counted and recorded by developmental stage (first, second, third, pre-ovipositional, and adult) and condition (alive or parasitized). Infested twigs were placed in parasitoid emergence containers and held between 22 and 24° C for three to four weeks. Emerging parasitoids were collected and later identified.

From 1987 to 1989, seven orchards (five near Corning and two near Madera) were sampled, as described above, in each season of each year. An additional

survey for parasitoids on black scale infested olive and oleander plants was carried out in the spring of 1990 at seven sites in the Sacramento Valley: Red Bluff, Tehama County; Willows, Glenn County; Yuba City, Sutter County; Zamora, Yolo County; and Williams and Maxwell, Colusa County. Infested twigs were taken to the laboratory and parasitoids reared from the material as described above.

RESULTS AND DISCUSSION

New Parasitoids.—Of the five parasitoid species released, only *P. probus* and *C. rusti* were found to have become established in central valley olive orchards. Establishment is defined here as parasitoid recovery three years after the last insectary release.

Prococcophagus probus was collected in 1985 and 1986 in two of the four original release orchards. Both orchards were located near Corning, Tehama County. *Prococcophagus probus* comprised 0.7% of the total parasitoids collected between 1984 and 1987 (Table 2). It was most commonly found in winter samples. In one orchard, *P. probus* comprised 8.0% ($n = 274$) and 1.1% ($n = 1235$), respectively, of parasitoids in November and December collections combined for 1985 and 1986. It was not recovered from any orchards in Glenn, Madera, or Tulare Counties, nor was it recovered from any orchards other than the original release sites. This suggests that *P. probus* did not disperse from the release areas.

Coccophagus rusti was collected from orchards near Corning, Tehama County from 1985 to 1987. The parasite was most commonly reared from third instar and pre-ovipositional stage scale, collected in spring and early summer months. Overall, this parasitoid comprised only 0.4% of the total parasitoids collected between 1984 and 1987 (Table 2). When considering release orchards only, the percent species composition of *C. rusti* was often higher. In one release orchard, *C. rusti* comprised 8.2% ($n = 205$) of the parasitoids reared from two collections in June and July, 1987. *Coccophagus rusti* was also recovered from two nonrelease sites: 1986, in an olive orchard over 1 km from the nearest release site, and 1990, in Red Bluff on oleander over 64 km from the nearest known release site. At the latter site, *C. rusti* accounted for 58%, the greatest number, of 19 parasitoids reared. This suggests that it either is increasing its geographic distribution or that a population has been present, without detection, in some central valley locations since the releases in 1937. Although *C. rusti* has not previously been found in the central valley, Flanders (1952) reported it to have been established in California at coastal locations, on ornamental plants. Its low numbers in California, contrasts reports that it was the most abundant and widely distributed of black scale parasitoids collected in 1937 in South Africa, Uganda, and Kenya (Compere 1940).

Neither *P. saissetiae* nor *A. saissetiae* were recovered in the 1984 to 1987 or 1988 to 1990 surveys. *Metaphycus inviscus* was not recovered in either the 1984 to 1987 or the 1988 to 1990 surveys. These findings differ somewhat from those of the 1979 to 1983 survey (during the release period) when *M. inviscus* was the only newly released parasitoid to show continued and strong evidence of establishment (Kennett 1986). *Metaphycus inviscus* is morphologically similar to *Metaphycus bartletti* Howard, a commonly collected parasitoid, and can be easily overlooked when large numbers of *M. bartletti* are present.

Abundance.—Relative to the other parasitoid species collected, both *P. probus*

Table 2. Rankings (in parenthesis) and percent total parasitoid abundance of primary and secondary parasitoids reared from black scale samples taken in Tehama, Madera, and Tulare County olive orchards between 1985 and 1987.

Species	Percent Parasitoid Abundance			Total
	Sacramento Valley	San Joaquin Valley		
	Tehama	Madera	Tulare	
<i>Metaphycus bartletti</i> ^a	42.9 (1)	27.1 (2)	51.9 (1)	43.2 (1)
<i>Metaphycus helvolus</i> ^a	25.6 (2)	48.7 (1)	35.4 (2)	29.2 (2)
<i>Scutellista cyanea</i> ^a	13.6 (3)	12.0 (3)	0.2 (10)	11.7 (3)
<i>Coccophagus lycimnia</i> ^{a,b}	4.1 (4)	5.3 (4)	7.9 (3)	4.8 (4)
<i>Metaphycus zebratus</i> ^a	3.6 (5)	1.1 (7)	0.4 (8)	3.1 (5)
<i>Cheiloneurus inimicus</i> ^c	3.2 (6)	1.5 (6)	0.6 (7)	2.7 (6)
<i>Marietta mexicana</i> ^c	2.2 (7)	3.6 (5)	0.6 (6)	2.2 (7)
<i>Coccophagus ochraceous</i> ^a	2.0 (8)	0.1 (10)	1.5 (5)	1.8 (8)
<i>Coccophagus scutellaris</i> ^{a,b}	1.7 (9)	0.2 (9)	2.7 (4)	1.7 (9)
<i>Tetrastichus minutum</i> ^c	0.9 (10)	0.6 (8)	0.2 (9)	0.8 (10)
<i>Cheiloneurus noxius</i> ^c	0.7 (11)	—	—	0.5 (11)
<i>Prococcophagus probus</i> ^a	0.7 (12)	—	—	0.5 (12)
<i>Coccophagus rusti</i> ^a	0.5 (13)	—	—	0.4 (13)
<i>Metaphycus luteolus</i> ^a	<0.1 (14)	—	—	<0.1 (14)
<i>Moranila californica</i> ^{a,c}	<0.1 (15)	—	—	<0.1 (15)
	<i>n</i> = 8290	<i>n</i> = 936	<i>n</i> = 2469	<i>n</i> = 10,593

^a Primary parasitoids

^b Males developed as a secondary parasitoid on some similar species

^c Secondary parasitoid

^d Only one specimen found.

and *C. rusti* were not common, ranking 12th and 13th and comprising only 0.5 and 0.4%, respectively, of the total parasitoids collected (Table 2). The most abundant parasitoids in the collections were *Metaphycus bartletti* Annecke & Mynhardt and *Metaphycus helvolus* (Compere). The widespread distribution and abundance of *M. bartletti* reveals its increasingly important economic role since its introduction (Kennett 1980). *Scutellista caerulea* (Fonscolombe) (= *Scutellista cyanea* Motschulsky) ranked third in abundance.

The remaining parasitoid species were found in low numbers, often sporadically in time and space. Together, *P. probus*, *C. rusti*, *Metaphycus luteolus* (Timberlake), and *Moranila californica* Howard comprised less than 1% of the total parasitoids recovered. *Metaphycus luteolus* may have been underrepresented because of their small number and close similarity to *M. bartletti*. Because only one specimen of *M. californica* was found, while a colony was kept at the Division of Biological Control insectary, contamination of the field emergence container may have occurred despite housings in separate buildings.

Metaphycus zebratus (Mercet), imported from Spain in 1985 and released from 1986 to 1988 (Daane & Caltagirone 1989), was recovered in Tehama, Madera, and Tulare Counties. It ranked fourth in parasitoid species collected, despite being released in large numbers in orchards being sampled. The parasitoid was recovered in lower numbers each subsequent year after releases were discontinued.

Distribution. — Greater diversity and abundance of parasitoid species were found in the Sacramento Valley than the San Joaquin Valley (Table 2), due, in part, to

differences in the synchronization of scale development found in the central valley. Cultural practices typically used in the San Joaquin Valley exacerbate climatic mortality and promote a more synchronous scale population than in the Sacramento Valley (Daane 1988). For *S. caerulea*, there is strong evidence that scale phenology is limiting in the species abundance. Although the third most commonly collected parasitoid in Tehama County, *S. caerulea* was rarely reared from black scale collected on olive in Tulare County. Moreover, it has been found in moderate numbers, in Tulare County, on oleander, where the scale has a less synchronous development pattern (D. Bromberger, personal communication). It is, therefore, not surprising that *P. probus* and *C. rusti*, as well as a number of lesser abundant primary and secondary parasitoids, were found in the Sacramento Valley rather than in the San Joaquin Valley.

Biology.—Documenting black scale parasitoid distribution and establishment is often difficult because of the low number of specimens recovered and the morphological similarity of other parasitoid species. Brief biological descriptions and morphological diagnoses of *P. probus* and *C. rusti* are provided because of the difficulty in identifying these two relatively unknown parasitoid species in California.

Prococcophagus probus was described by Annecke & Mynhardt (1979) as a solitary, primary parasitoid of black scale. Its reproductive biology is probably similar to that of *Prococcophagus varius* Silvestri & *P. saissetiae*, two black scale parasitoids that are morphologically very close to *P. probus*. In those species, both male and female are primary parasitoids, but the diploid female larva develops as an endoparasitoid, while the haploid male larva develops as an ectoparasitoid (Mazzone & Viggiani 1983). The validity of *Prococcophagus*, as a genus separate from *Coccophagus*, has been questioned by Mazzone & Viggiani (1984). Nevertheless, *Prococcophagus* can be distinguished from *Coccophagus* by its ventrally expanded antennal scape, laterally compressed funicle, and usually largely infuscated fore wings. The antennal scape of the female is more than twice as long as wide, with two dark streaks on the outer surface; the first antennal funicle segment is the longest, with rhinaria (Annecke & Mynhardt 1979). Superficially, *P. probus* is similar to *M. bartletti* in color and size. In samples with many parasitoids, misidentification can easily occur.

Coccophagus rusti is a solitary endoparasite of third instar and preovipositional adult black scale (Flanders 1952). The male is hyperparasitic, developing as a direct endoparasite of some primary parasitoids of black scale and other hosts. This species can also develop in soft brown scale, *Coccus hesperidum* L. (Compere 1940). *Coccophagus rusti* is easily distinguished from other black scale parasitoids by the following characters: the scutellum has three pairs of setae, the abdomen is entirely black, the thorax is yellow-brown, the pedicel is shorter than first funicle segment, and the forewing has an infuscation with a pale diagonal streak (Smith & Compere 1928). The male differs from the female, with its whole body black or brown-black (Annecke 1964).

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**DESCRIPTION OF A NEW SPECIES OF *EPIBLEMA*
(LEPIDOPTERA: TORTRICIDAE: OLETHREUTINAE)
FROM COASTAL REDWOOD FORESTS IN
CALIFORNIA WITH AN ANALYSIS OF
THE FOREWING PATTERN**

RICHARD L. BROWN¹ AND JERRY A POWELL²

¹Department of Entomology, Drawer EM, Mississippi State, Mississippi 39762;

²Department of Entomological Sciences, University of California,
Berkeley, California 94720

Abstract.—*Epiblema deverrae* R. Brown, NEW SPECIES, is described from Monterey and Sonoma Counties, California and is differentiated from the sympatric species, *E. hirsutana* (Walsingham) and *E. radicana* (Walsingham), and from similar allopatric species. A description of its forewing pattern is based on an analysis of fasciae, color fields, and strigulae in the Olethreutinae.

Key Words.—Insecta, Tortricidae, Eucosmini, *Epiblema deverrae*, forewing pattern, strigulae, Asteraceae, *Madia*

An inventory of the Lepidoptera at the Landels-Hill Big Creek Reserve, Monterey County, California, has been conducted during the past decade (JAP, unpublished data). This is the first attempt to census the entire fauna of moths and butterflies at any locality in western North America. The Big Creek Reserve, one of 27 areas maintained by the Natural Reserve System (UCNRS) of the University of California, is situated about 30 km southeast of Big Sur, in the Santa Lucia Mountains, which end abruptly at the Pacific coast. The reserve encompasses 1550 ha, rising from sea level to 1200 m elevation (900 m in the areas surveyed). Rugged coastal mountains rise abruptly from the shoreline and are dominated by narrow ridges separated by deep, V-shaped canyons with walls that rise steeply from narrow streamside terraces. Vegetation types include coastal scrub, California sage scrub, *Ceanothus* and chamise chaparral, redwood forest, mixed hardwood forest, ponderosa pine-manzanita woodland, and sparse chaparral on rocky montane ridges (buckwheat [*Eriogonum*], yerba santa [*Eriodictyon*], and *Yucca whipplei* Torrey).

The reserve has been surveyed on more than 80 dates, using three approaches: diurnal net collecting, larval sampling and rearing, and blacklight attraction at sheets and traps. To date about 650 species have been differentiated, of which 26% are represented by larval collections. Based on comparisons with the numbers of flowering species (326) (Bickford & Rich 1984), as well as butterflies at Big Creek (57), and macro moths known at other stations in coastal California (McFarland 1965; Opler & Buckett 1971; JAP, unpublished data), a census of 800–850 species of Lepidoptera at Big Creek is anticipated.

The survey has yielded several species of moths that were previously unknown in the central coast ranges and at least three undescribed species of microlepidoptera in better studied families (Momphidae, Tortricidae), including a distinctive new

species of *Epiblema*. The genus *Epiblema* includes more than 100 species in the Holarctic region and southern Asia. Of these, 39 occur in America, north of Mexico (Blanchard 1979, 1985; Powell 1983; Miller 1985). *Epiblema* appears to be related to *Eucosma*, *Pelochrista*, *Sonia*, and other eucosmine genera that include species with larvae boring in stems and roots of Asteraceae. The description of this new *Epiblema* is facilitated with selected information from a recent analysis of forewing patterns in Tortricidae (RLB, unpublished data).

METHODS AND MATERIALS

A stereomicroscope with an ocular micrometer was used to examine and measure specimens. Specimens of all species mentioned in the diagnosis were examined except *E. simploniana* (Duponchel), of which figures were examined. The forewing length was measured from base to apex, including the fringe. Cornuti of the aedeagus were counted by examination of their sockets with a compound microscope. Valval length was measured as a straight line from the ventral, proximal corner of the sacculus to the apex of the cucullus. Colors were described with the standards of Kornerup & Wanscher (1983). The forewing description is based on a comparative study of pattern elements in more than 600 tortricid species representing all tribes defined by Horak & Brown (in press). The following abbreviations are used for depositories: Mississippi Entomological Museum, Mississippi State University (MEM); University of California, Berkeley (UCB).

FOREWING PATTERN ELEMENTS IN *EPIBLEMA*

Nijhout (1978) provided the following terminology for the five major types of pattern elements on Lepidoptera wings, as described by Süffert (1929): ripple patterns, dependent patterns, crossbands (fasciae), eyespots (ocelli), and color fields. These types, except ripple patterns, are present in *Epiblema*, including the species described here.

Fasciae occur on ontogenetically determined areas of the wing (Nijhout 1978, 1990) and generally are more darkly pigmented than the surrounding ground color. The areas between fasciae here are termed interfascial areas. The distinctiveness of fasciae is dependent on both the number of scales that are darkly pigmented (degree of expression) and the degree to which dark pigment is lacking in the interfascial areas. Based on an analysis of forewing patterns in the Tortricidae, the ancestral pattern is interpreted to include six fasciae: basal, subbasal, medial, postmedial, subterminal, and terminal. These fasciae, except for the terminal, previously have been identified in the tortricine tribe Cochylini (Bradley et al. 1973). In the Olethreutinae, the basal and subbasal fasciae are often confluent to form a basal patch; the median fascia usually is well expressed, although often broken near CuA_2 to form a separate pretornal spot; the postmedian fascia (termed the preapical fascia by some authors) is expressed usually as one or more spots, the largest and most anterior being the postmedian spot (termed the preapical spot by some authors); and the subterminal and terminal fasciae are either not expressed or are represented by narrow umbrae or small spots (Fig. 1).

Color fields have been defined as large areas of the wing surface that contrast in coloration with other areas and are not a fascia or other pattern element (Nijhout 1978). Süffert (1929) and Nijhout (1978) noted that "color fields" represented a lumping of more than one type of pattern element, and that little effort had been

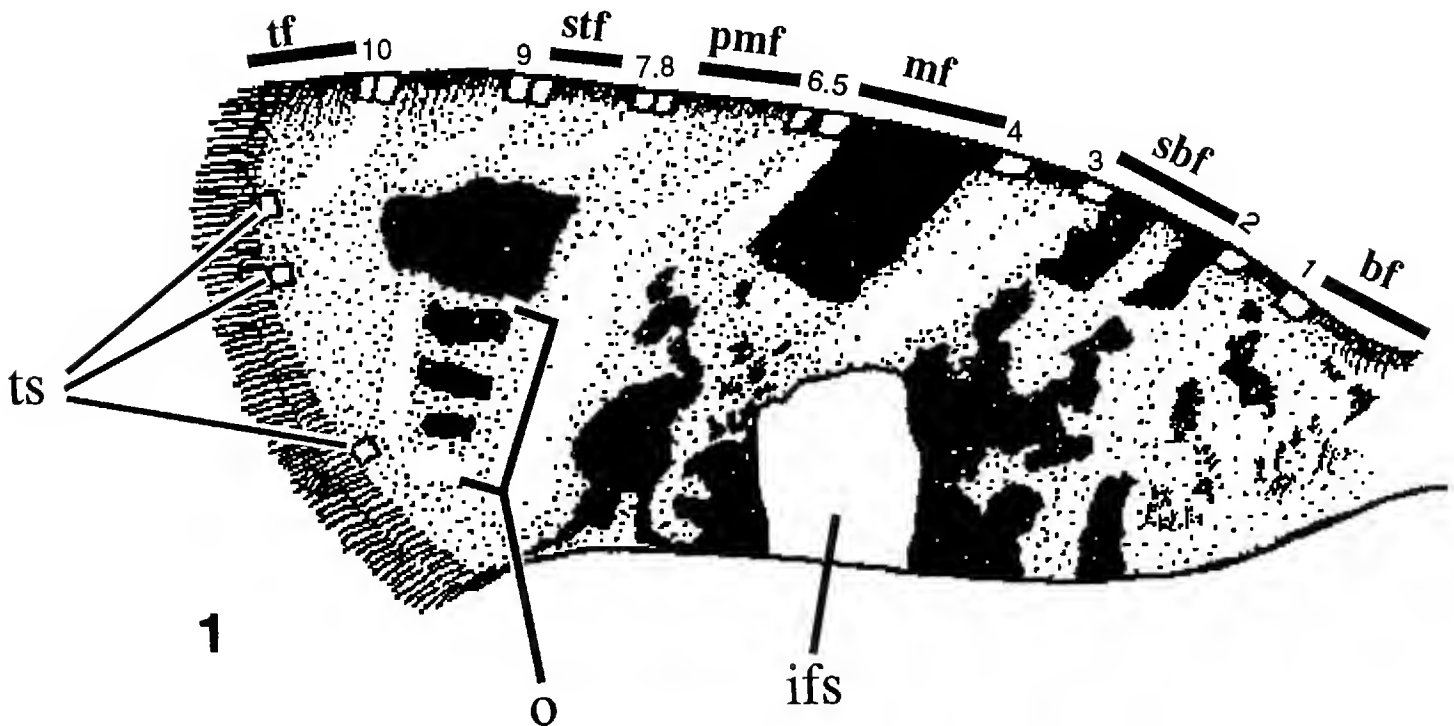


Figure 1. *Epiblema deverrae*, forewing pattern indicating positions of expressed and nonexpressed fasciae relative to coastal strigulae 1–10. ifs—interfascial spot, mf—median fascia, o—ocellus, pmf—postmedian fascia, sbf—subbasal fascia, stf—subterminal fascia, tf—terminal fascia, ts—terminal strigulae.

made in the analysis of the various types of color fields. Two types of color fields commonly occur in the Tortricidae, and here these are termed “patches” and “spots.” The term patch is used to describe a color field that differs from the ground color and that covers at least one fascia and one interfascial area. Although patches include several subgroups, depending on their position and size, patches often involve the expression of fasciae only on the costal or inner margins of the wing and the intervening interfascial area. The term spot is used for contrasting pigmentation that is confined either to a restricted portion of a fascia (i.e., pretornal spot) or to a restricted portion of an interfascial area (i.e., interfascial spot).

Interfascial spots are present on the inner margin (dorsum) between the subbasal and median fasciae in many species of the Olethreutinae, including the *Epiblema* described here (Fig. 1). Patches are common on the inner margin in generalized genera in the Eucosmini, especially in *Ancylis* and *Epinotia* (e.g., *E. solandriana* (L.)) (Bradley et al. 1979: pl. 32, Figs. 5–8) and on the costa in various unrelated genera (e.g. *Ancylis*, *Pseudexentera* and *Acleris*) (Bradley et al. 1973: pl. 40, Figs. 10–11). Although interfascial spots are present in many species of *Epiblema*, *Eucosma*, and related genera, patches have not been detected in any representative of this derived group of Eucosmini.

Strigulae, or short transverse marks, are present on the costa of most Olethreutinae, some Chlidanotinae, and some generalized Tortricinae (e.g., Phricanthini) (Horak & Brown in press). These strigulae appear to be dependent patterns, as they occur on the inner and outer margins of fasciae. In addition, strigulae apical to R_2 occur between the veins at the wing margin. Danilevski & Kuznetsov (1968) and Kuznetsov (1978) recognized seven pairs of costal strigulae, and these were numbered one to seven from apex to base. Examinations of species in the tribes Gatesclarkeanini, Phricanthini, and Chlidanotini by RLB indicate that the ancestral condition is the presence of ten costal strigulae between the wing base and R_5 ; these are numbered here 1–10 from wing base to apex. Strigulae are not limited

to the forewing costa; among various Tortricidae, a strigula may be present between each pair of adjacent veins on the termen, and here these are termed terminal strigulae.

Each of the costal strigulae in the Olethreutinae has a narrow stria extending towards the inner or outer margin, and these striae, which often are a shade of gray, appear to be silver when viewed through the microscope at an angle to the light. Each of the ten costal strigulae are paired in representatives of primitive taxa, but some are single in derived taxa. In derived taxa, some strigulae (e.g., numbers five and six in the species described here) are approximate or confluent (Fig. 1). Confluence of two independent strigulae to form what appears to be a single or paired strigula usually can be determined by examinations of related species or the detection of two silver striae arising from one apparent strigula.

Süffert (1929), as translated by Nijhout (1978), recognized four classes of ocelli, or eyespots, on Lepidoptera wings. Of these, band ocelli are present in the Olethreutinae, especially in the Grapholitini and derived Eucosmini. These ocelli are formed from the fragmentation of fasciae, usually the postmedian fascia, and the resulting fascial spots are accentuated by the gray striae, often widened, that originate from costal strigulae (Fig. 1).

EPIBLEMA DEVERRAE R. BROWN, NEW SPECIES

Types.—Holotype, male, data: "CALIF: Monterey Co., Landels-Hill Big Creek Res., 5 mi. N. Lucia, 4–6 June 1982; J. Powell, collector"; deposited at the University of California, Berkeley. The holotype is in excellent condition except for missing meso- and metathoracic legs on the right side. Paratypes, deposited as noted in parentheses: USA. CALIFORNIA. *MONTEREY Co.*: same data as holotype, 2 females, 4 males (genitalia slide JAP 5121) (UCB), 1 female (genitalia slide R. L. Brown 1321) (MEM); Big Creek Reserve, UCNLWR, Brunette Creek, 60–180 m el, redwood-hardwood, 26–28 May 1987, J. Powell, 1 female, 3 males (UCB); Big Creek Reserve, UCNLWR, headquarters, coastal to confluence area, 0–60 m, 26–28 May 1987, J. Powell, 1 female (UCB); Big Creek Reserve, UCNLWRS, Brunette Creek, 60–180 m el, redwood-hardwood, 5–8 Jun 1989, Y-F. Hsu and J. Powell, 1 female, 1 male (UCB), 1 male (MEM); Big Creek Reserve, UCNRS, Devils Creek Flat, 120 m el, 7 Jun 1989, J. Powell, 1 male (UCB). *SONOMA Co.*: Cazadero, 6 Jun 1979, J. Powell, 1 female (UCB).

Description.—*Head:* vertex and upper frons brown, brown-orange, or gray-brown, darker brown between antennae in some specimens; labial palpus with basal one-half orange-white or orange-gray, apical one-half brown or light brown. *Mesonotum:* brown to dark brown; tegulae brown to dark brown basally, brown or brown intermixed with gray-orange apically. *Forewing* (Figs. 1, 2): Forewing length 5.3–7.1 mm in males, 5.5–7.0 in females; male costal fold extending from base to proximal margin of median fascia, length of fold 0.33–0.40 forewing length. Upperside ground color brown to gray-brown intermixed with orange, with orange increasing in apical one-half; pattern elements including indistinct, broken, dark brown fasciae, white to orange-white interfascial spot on inner margin, white to orange-white costal strigulae, and white terminal strigulae. Basal and subbasal fasciae not forming distinct basal patch; basal fascia indistinct, basal area with small spots and broken, narrow umbrae; subbasal fascia reduced to broken umbrae, umbrae broad and confluent near midwing and inner margin, distal margin of fascia angled at midwing, extending to costa at about 0.30× the forewing length; median fascia broken by orange or brown near midwing into large spot on costa and large spot on inner margin, some specimens with inner marginal portion of fascia broken by orange or brown into small proximal spot and larger distal spot; postmedian fascia represented by large postmedian spot (appearing as two or three spots in some rubbed specimens) near apex of discal cell and three



Figure 2. *Epiblema deverrae*, female, Sonoma Co., California.

small bars, three bars bordered by subequal, gray (silver when viewed at an angle to the light) spot on inner margin near tornus and by broad, transverse, gray (silver) lines proximally and distally to form ocellus; subterminal fascia indistinct; terminal fascia represented by small spot at wing apex in some specimens. Interfascial spot present between subbasal fascia and median fascia, extending from inner margin to Cu_2 , subquadrate with proximal margin longer than distal margin. Costa with four to six conspicuous strigulae, strigulae one and two confluent with each other or indistinct; strigula three single, marking distal margin of subbasal fascia; strigula four single, marking proximal margin of median fascia, separated from strigula three by small dark brown spot, strigulae three and four indistinct in some specimens, each strigula with a gray (silver) stria extending posteriorly, striae becoming confluent at discal cell and extending to interfascial spot; strigulae five and six approximate at distal margin of median fascia, appearing as a single paired strigula, strigula five with gray (silver) stria extending to midwing, strigula six with gray (silver) stria extending to near tornus, becoming broad at midwing; strigulae seven and eight apparently confluent, appearing as single strigula in some specimens, with single gray (silver) stria extending to proximal margin of postmedian spot; strigula nine single or paired, with gray (silver) stria extending to distal margin of postmedian spot; strigula ten paired, with strigulae separated by dark brown spot, with gray (silver) stria extending to M_1 at termen; strigulae 5-6, 7-8, 9, and 10 bordered by orange or dark brown, separated from each other by dark brown spots. Termen with small strigulae between R_5 and M_1 , M_1 and M_2 , and CuA_1 and CuA_2 , some specimens with orange-white, attenuate, fringe scales arising from strigulae. Proximal fringe scales attenuate, short, brown with white to orange-white apices; distal fringe scales attenuate, long, gray-brown. Forewing underside brown except white to orange-white costal strigulae and area of hindwing overlap posterior to CuP . *Hindwing*: Upperside uniformly brown except area of forewing overlap anterior to $Sc+R_1$; underside uniformly brown, concolorous with forewing underside. *Male genitalia* (Fig. 3): Uncus reduced to rounded lobe, densely setose dorsally; socii slightly flattened, moderately setose posteriorly; gnathos arising from triangular projections of tegumen; aedeagus with patch of 13 or 14 cornuti on vesica; anellus with pointed anterior ventral corners; valva with sacculus moderately setose, clasper at base near dorsal margin with flat medial surface and beset with group of short, moderately stout setae, a second clasper-like, rounded projection near sacculus with sparse, slender, short to long setae, ventral margin of neck without setae, cucullus large relative to valva, length of cucullus $0.60 \times$ length of valva (one preparation examined). *Female genitalia* (Fig. 4): Sternum VII with moderately dense scales throughout, posterior one-half with sparse, short setae, becoming dense on posterolateral corners; tergum VIII with moderately dense, long setae on posterior fourth and on triangular, lateral extensions, scales absent; papillae anales densely setose, without rugae or papillose projections; lamella postvaginalis with dense microtrichia medially, with sparse, long setae on lateral rims; lamella antevaginalis reduced to lightly sclerotized, smooth rim; ductus bursae weakly spiraled, with moderately sclerotized colliculum posterior to inception of ductus seminalis; signa flat, blade-like, bases with shallow invaginations (one preparation examined).

Diagnosis.—*Epiblema deverrae* is superficially similar to *E. hirsutana* (Walshingham), which was described from Sonoma Co., California. In *E. hirsutana*,

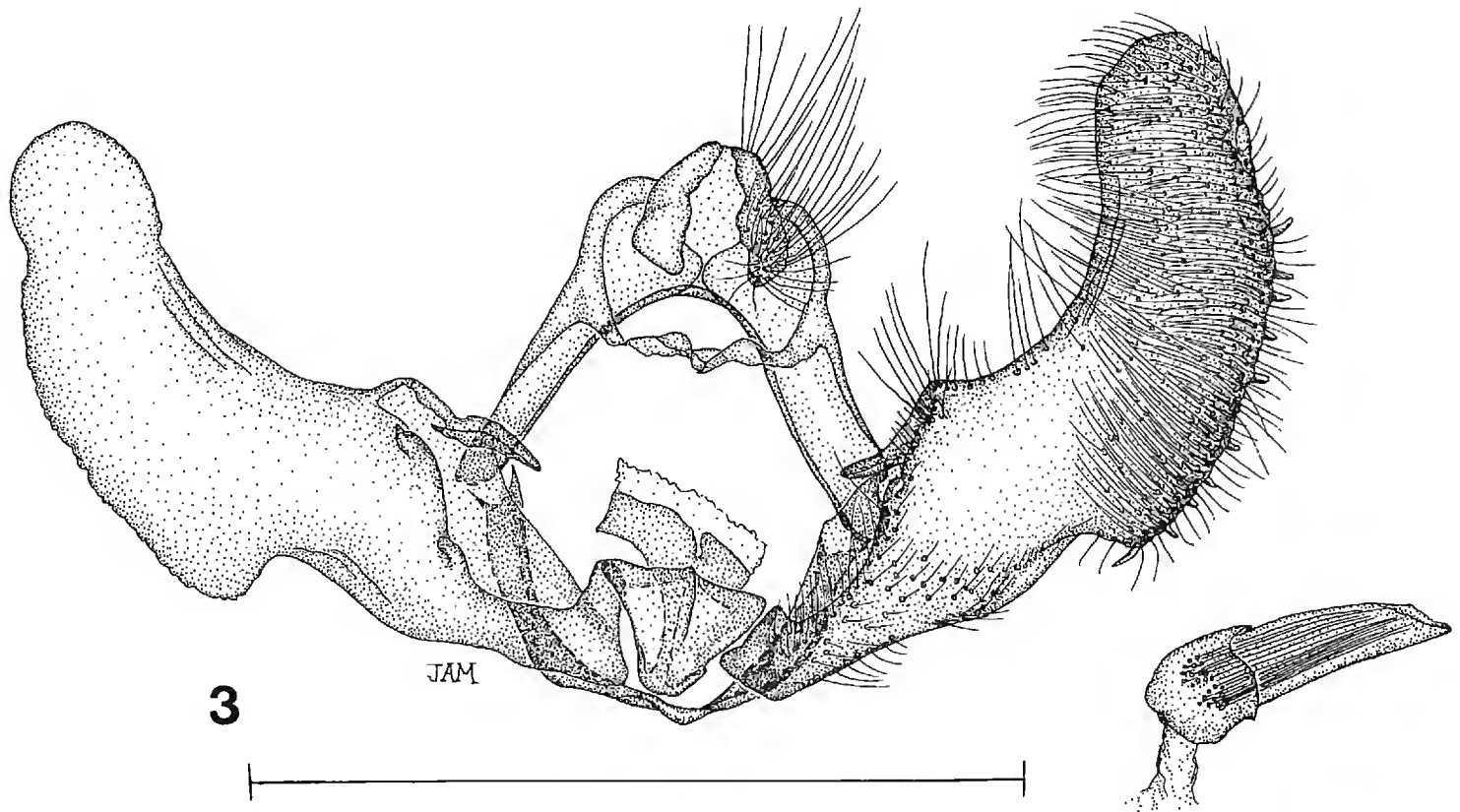


Figure 3. *Epiblema deverrae*, male genitalia with aedeagus detached. Scale line = 0.5 mm.

the head and labial palpi appear bushy due to long, erect, narrow scales, and the forewing lacks a large postmedian spot and a contrasting median fascia. The interfascial white spot is less well defined in *E. hirsutana*, and is not suffused with pale orange. The male genitalia of *E. hirsutana* has a valve with a broader cucullus and a single clasper. The female genitalia of *E. hirsutana* has a longer ductus bursae with a more lightly sclerotized colliculum. *Epiblema radicana* (Walsingham), also occurring in western North America, is a larger species with a forewing lacking an ocellus and having a paler interfascial area between the median fascia and postmedian fascia and with genitalia differing in several characters (Obraztsov 1965: Figs. 1–10). Allopatric species that are superficially similar to *E. deverrae* include *E. walsinghamsi* (Kearfott) and *E. infelix* (Heinrich), occurring in the eastern United States, *E. arctica* Miller, occurring in Alaska, and *E. graphana* Treitschke, *E. farfarae* Fletcher, *E. simploniana*, and some forms of *E. scutulana* (Denis & Schiffermüller), occurring in the Palearctic region. None of these latter species has a forewing with a large postmedian spot combined with orange scales in the apical area, and all differ in characters of the male genitalia, as figured by Miller (1985, 1987) and Kuznetsov (1978).

Comments. — The new species was discovered in Big Creek Reserve at two sites, about 2 km apart, in 1982: on the upper Brunette Creek trail at about 180 m elevation in the Big Creek drainage, and along the road above Devil's Creek Flat at 120–130 m. Additional individuals were collected in later years, subsequent to an extensive fire that burned both sites in July, 1985. Adults seem to be univoltine and diurnal; all were flying during afternoons and none have appeared at blacklights deployed in various areas of the reserve. They seem to be associated with *Madia madiodes* (Nuttall) (Asteraceae) growing in loose rocky talus in open areas in forests dominated by redwood (*Sequoia sempervirens* (D. Don.)). No gall formations were found on this herbaceous perennial, and we speculate that larvae of *E. deverrae* feed on underground rootstocks.

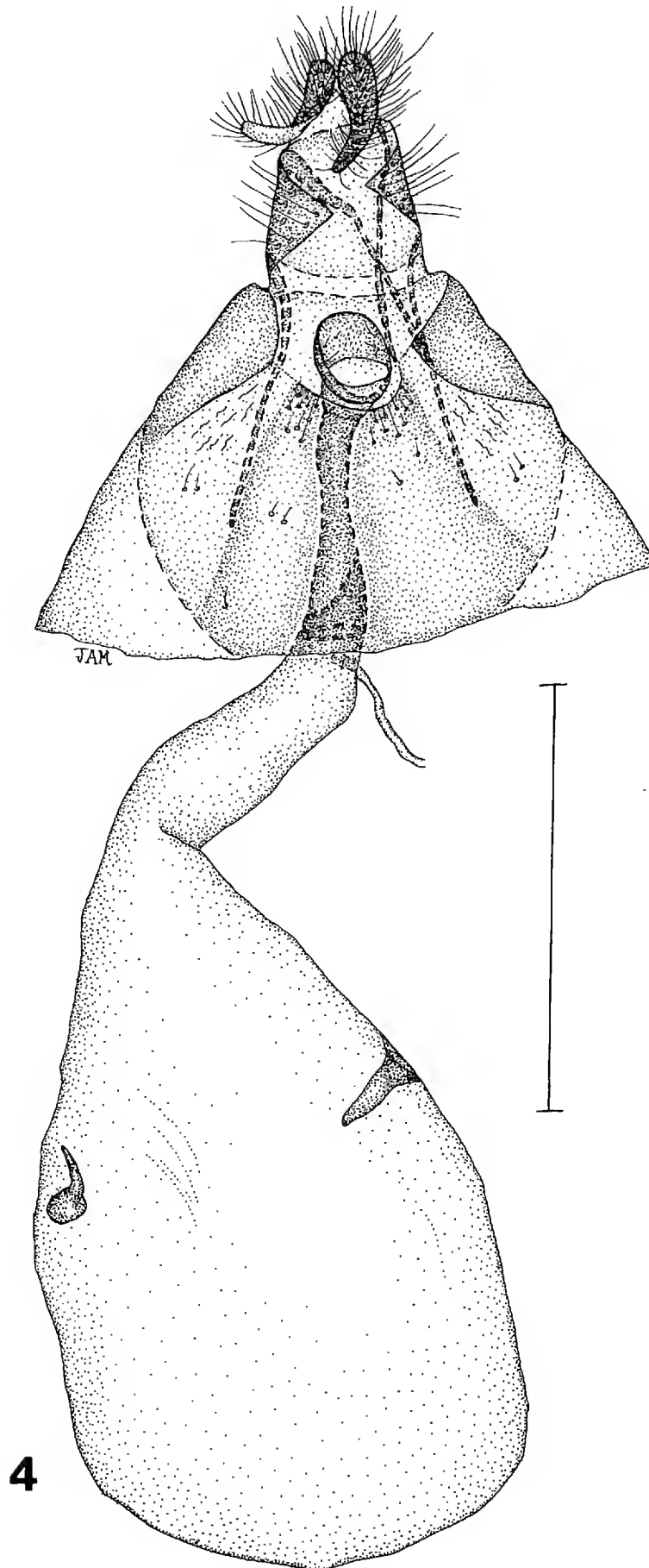


Figure 4. *Epiblema deverrae*, female genitalia. Scale line = 0.5 mm.

Madia madioides ranges from Monterey County, northward, along the Pacific coast, in mixed evergreen and coastal coniferous forests, to Vancouver Island (Munz 1959).

Etymology.—The specific name *deverrae* is formed from Deverra, the Roman goddess of brooms and sweeping.

Material Examined.—See types.

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A REVIEW OF THE GENUS *MICROTHURGE* (HYMENOPTERA: MEGACHILIDAE)

TERRY L. GRISWOLD

USDA–ARS Bee Biology and Systematics Laboratory, Utah State University,
Logan, Utah 84322-5310

Abstract.—A new South American *Microthurge*, *M. furcatus* NEW SPECIES, is described. *Microthurge boharti* NEW SYNONYM is synonymized with *M. corumbae*. The male of *M. pharcidontus* is described. New records and keys to the species for males and females are presented.

Key Words.—Insecta, taxonomy, bees, floral records

In a recent revision of the megachilid subfamily Lithurginae (Michener 1983), a new genus *Microthurge* Michener was described to accommodate a small group of heriadiform bees from southern South America. Four species were included: *Microthurge pygmaeus* (Friese), *M. pharcidontus* (Moure), *M. boharti* Michener and *M. corumbae* (Cockerell), the last based only on the description, because Michener was unable to locate the type. Here, I report on the identity of *M. corumbae*, the discovery of a new species, describe the male of *M. pharcidontus* and give new records for the genus. Depositories for specimens (cited by cities) are: University of California (Davis), University of Kansas (Lawrence), American Museum of Natural History (New York), Philadelphia Academy of Sciences (Philadelphia), Carnegie Museum of Natural History (Pittsburgh), USDA Bee Biology and Systematics Laboratory (Logan).

KEYS TO SPECIES

Males

1. Scutal surface roughened medially by transverse rugulae; scutellum rounded in profile; mesopleural surface granular *pharcidontus* (Moure)
Scutal surface not roughened by transverse rugulae; scutellum flat in profile; mesopleural surface shiny 2
- 2(1). Hind basitarsus with ventral hairs black in part; punctures on medial area of mesopleuron nearly contiguous; basal depression of mandible wide *pygmaeus* (Friese)
Hind basitarsus with ventral hairs light; punctures on medial area of mesopleuron well separated; basal depression of mandible linear . . . 3
- 3(2). Punctures on upper part of clypeus foveolate, larger than those on frons; frons with punctures contiguous; eyes slightly diverging above (ratio of upper interorbital distance at level of lateral ocelli/minimal lower interorbital distance < 1.35) *furcatus* NEW SPECIES
Punctures on upper part of clypeus fine, not foveolate, not larger than those on frons; frons with punctures not contiguous; eyes strongly diverging above (ratio of upper interorbital distance at level of lateral ocelli/minimal lower interorbital distance > 1.4)
. *corumbae* (Cockerell)

Females

1. Upper margin of mandible with basal, dorsoventrally flattened projection; abdominal scopa largely black *pygmaeus* (Friese)
 Upper margin of mandible without projection; abdominal scopa white except sometimes on S5 2
- 2(1). Scutum with broad median zone covered with coarse transverse rugulae; mesopleural surface granular; scutellum rounded in profile; apical hair of T6 dark brown *pharcidontus* (Moure)
 Scutum without transverse rugulae; mesopleural surface shiny; scutellum flat in profile; apical hair of T6 black 3
- 3(2). Facial projection carinate, with deep V-shaped emargination in dorsal view; labrum with conical basomedial projection; clypeus in part with large shiny interspaces between punctures *furcatus* NEW SPECIES
 Facial projection not carinate, with shallow rounded emargination in dorsal view; labrum with low, notched basomedial projection; clypeus contiguously punctate or essentially so *corumbae* (Cockerell)

MICROTHURGE PYGMAEUS (FRIESE)

Material Examined.—(New Records) ARGENTINA. *SALTA*: Rosario de Lerma, 10–14 Nov 1983, malaise trap, M. Wasbauer, 5 males, 17 females (Logan); same except 4–8 Nov 1983, 6 females; Rosario de Lerma, Oct 1984, M. Fritz, 1 male (Logan); same except Oct 1985, 1 male, 4 females (Logan); same except Oct 1986, 2 males (Logan). *CÓRDOBA*: LaCumbre, 1140 m, 21 Nov 1975, R. M. Bohart, 12 males, 7 females (Davis, Logan). *JUJUY*: Perico, S of Jujuy, 21 Oct 1968, L. E. Peña, 1 female (New York). *CATAMARCA*: Alijilan, 3 Nov 1972, *Argemone* sp., G. E. Bohart, 1 female (Logan). *TUCUMÁN*: Tucumán, 19 Oct 1972, *Argemone subfusiformis* G. B. Ownbey, G. E. Bohart, 1 male, 2 females (Logan); Cadillal, 4 Dec 1975, R. M. Bohart, 1 male (Logan).

MICROTHURGE PHARCIDONTUS (MOURE)

Redescription.—Male. Length, 5–7 mm; forewing length, 4–5 mm. Basal depression of mandible linear; pair of tubercles on supraclypeal area small and close or absent; punctures on upper part of clypeus foveolate, larger than punctures on frons; scutum roughened medially by transverse rugulae; mesopleural surface granular.

Diagnosis.—The transversely rugulose scutum, granular mesopleuron, and rounded rather than flat scutellum are unique to *M. pharcidontus*. Males share these unique characteristics, though the rugulae of the scutum are less well-developed.

Discussion.—Additional material available for this study supports the tentative association by Michener (1983) of males from Guayaramerin, El Beni, Bolivia with *M. pharcidontus*.

Material Examined.—(New Records) ARGENTINA. *SALTA*: Dique Itiyuro, nr Pocitos, 14 Aug 1976, C. Porter, L. Stange (Lawrence). *TUCUMÁN*: Tucumán, 19 Oct 1972, *Argemone subfusiformis* G. B. Ownbey, G. E. Bohart, 1 male (Logan); San José, Rio Marija, 3 Nov 1972, *Opuntia sulphurea* G. Don, G. E. Bohart, 1 male (Logan); Horco Molle, 4 Jan 1976, R. M. Bohart, 1 male, 2 females (Davis, Logan).

MICROTHURGE CORUMBAE (COCKERELL)

Lithurgus corumbae Cockerell, 1901. Proc. Acad. Nat. Sci. Phil., 1901: 216. Type deposited in Pittsburgh.

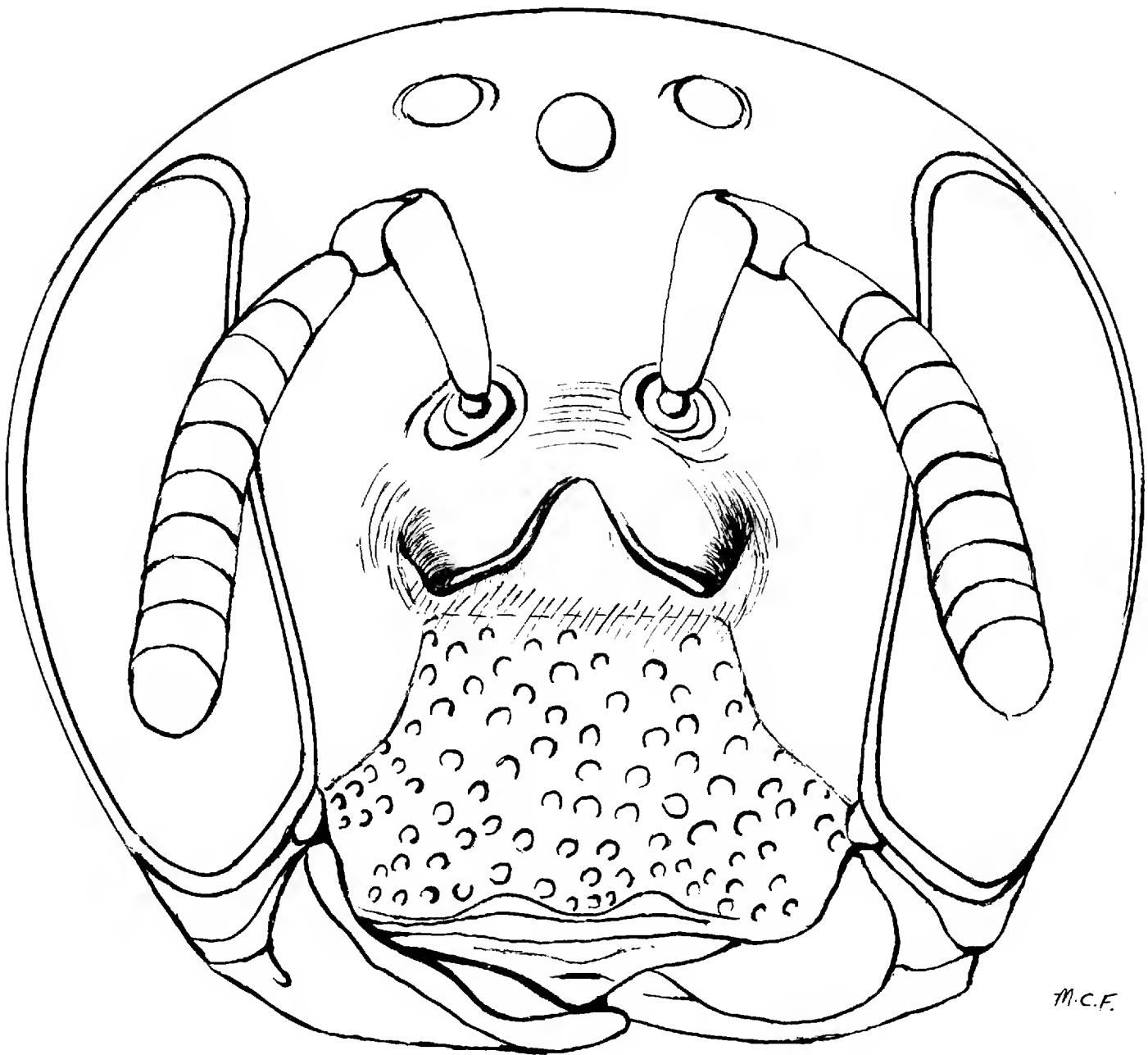


Figure 1. Head of *Microthurge furcatus*, female. Punctuation shown only for clypeus.

Microthurge boharti Michener, 1983. Pan-Pacif. Entomol., 59: 186. NEW SYNONYMY. Type deposited in Buenos Aires.

Diagnosis. — Males have eyes more strongly diverging above than in *M. furcatus* (ratio of upper interocular distance at level of lateral ocellus/minimal lower interocular distance 1.41–1.52; $n = 8$, $\bar{x} = 1.46$).

Discussion. — The holotype female of *Lithurgus corumbae* Cockerell from Corumba, Mato Grosso, Brazil, was recently located in the entomological collection of the Carnegie Museum of Natural History. It appears to be the same as *Microthurge boharti* from Córdoba Province, Argentina, despite the geographic separation and apparent ecological differences between the moist tropical region of Corumba and the more xeric environment of Córdoba. The only discernable difference is the slightly better developed frontal prominence in specimens from Argentina. This may be size related, because there appears to be size-dependent variation among the Corumba specimens.

Material Examined. — (New Records) BRAZIL. MATO GROSSO: Corumba, Apr, 4 males, 28 females (Philadelphia, Logan); same except Mar, 2 females (Philadelphia).

MICROTHURGE FURCATUS GRISWOLD, NEW SPECIES
(Fig. 1)

Types.—Holotype, female, data: BOLIVIA. *COCHABAMBA*: Peña Colorada, 1800 m, 21 Feb 1976, L. E. Peña. Paratypes; 7 males, data same as holotype; 3 males, 1 female, data: BOLIVIA. *COCHABAMBA*: (no local data), Nov 1976, L. E. Peña. Holotype deposited in American Museum of Natural History, New York; paratypes deposited in the American Museum of Natural History and USDA Bee Biology and Systematics Laboratory, Logan, Utah.

Female.—Length, 7.5–8 mm; forewing length 6 mm. Body black, apical tarsi red; wings heavily infuscated. Pubescence white; scopa off-white except for few dark hairs laterally and apically on S5. Mandible without projection basally on upper margin; labrum with basomedial cone-shaped projection; clypeus with punctures on disk scattered; facial projection carinate, in dorsal view with wide V-shaped notch; scutum without transverse rugulae; scutellum flat in profile; mesopleuron shiny, with punctures separated.

Male.—Length, 6–7 mm; forewing length, 4.5–5 mm. Basal depression of mandible linear; punctures on upper part of clypeus foveolate, larger than those on frons; punctures of frons contiguous; eyes slightly diverging above (ratio of upper interocular distance at level of lateral ocelli/minimal lower interocular distance 1.22–1.33; $n = 10$, $\bar{x} = 1.28$); ventral hairs on hind basitarsus all light.

Diagnosis.—*Microthurge furcatus* seems most closely related to *M. corumbae*. Males of the two species are very difficult to separate, differing as far as I can tell only by slight differences in punctation and by the less divergent inner eye margins. Females are more easily separated. In addition to the characters given in the key, the mandible is covered with a few large punctures, has a very strong dorsal carina, and is abruptly and strongly depressed basally. The mandible of *M. corumbae* has numerous small punctures, a weak dorsal carina, and is only slightly depressed basally.

Material Examined.—See types.

ACKNOWLEDGMENT

I thank John Rawlins and Robert Davidson (Carnegie Museum of Natural History, Pittsburgh) for assistance in locating and studying the type of *Lithurgus corumbae* and the following individuals and institutions for the loan of material: Manfredo Fritz (Instituto de Investigaciones Entomológicas Salta, Rosario de Lerma, Argentina), Jerome Rozen and Eric Quinter (American Museum of Natural History, New York); Robert Schuster (University of California, Davis); Donald Azuma (Academy of Natural Sciences, Philadelphia); Charles Michener (University of Kansas, Lawrence). Marianne Cha Filbert produced the illustration. This is a contribution from Utah Agricultural Experiment Station, Utah State University, Logan, Utah 84322-4810, Journal Paper Number 4074, and USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah 84322-5310.

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A NEW AND PRIMITIVE GENUS OF CRYPHOCRICINAE (HETEROPTERA: NAUCORIDAE)

JOHN T. POLHEMUS

University of Colorado Museum, Englewood, Colorado 80110

Abstract. — *Procryphocricos perplexus* NEW GENUS, NEW SPECIES is described and compared to *Cryphocricos* Breddin. The predominantly plesiomorphic character states of this new genus are discussed.

Key Words. — Insecta, Heteroptera, Naucoridae, Cryphocricinae

During an expedition to South America Dan A. Polhemus and I collected numerous naucorids among which is a remarkable new cryphocricine genus from Colombia that is superficially similar to *Cryphocricos* Breddin but possessing a number of plesiomorphic and some apomorphic characters that distinguish it.

The subfamily Cryphocricinae was proposed by Montandon (1897) to hold *Cryphocricos* Breddin and *Cataractocoris* Montandon. It was redefined by Usinger (1941) to exclude *Cataractocoris*, which was placed in his new subfamily Ambrysinae. Usinger proposed a family level classification of Naucoridae, based on a number of characters, that was a radical departure from that of Montandon (1897). Since then alternative arrangements the family-group classification of Naucoridae have been proposed by a number of authors (e.g., Popov 1970, De Carlo 1971, Lopez Ruf & Bachmann 1987, Stys & Jansson 1988; the latter overlooked the work by Lopez Ruf & Bachmann). In these proposals the rank and relationships of many family group taxa have been shifted, and a new taxon, Pelocoridae, was proposed by De Carlo (1971), supported by Lopez Ruf & Bachmann (1987), but rejected by others (e.g., Polhemus 1979, Stys & Jansson 1988). The various schemes have been discussed by the latter, who placed *Cryphocricos* in the monotypic tribe Cryphicricini. Both D. A. Polhemus and I consider all of these proposals to be poorly founded, based on too few characters, and none of them have been supported by a convincing phylogenetic analysis; this matter will be treated in detail later, and supported by a cladistic analysis. Although the suprageneric classification of the Naucoridae remains in my view an open question, I have used the classification of Stys & Jansson (1988) in order to establish a framework for this paper.

The addition of *Procryphocricos* NEW GENUS does not require redefinition of the family group taxon that holds *Cryphocricos*, the Cryphocricini, but instead supports Usinger's decision to separate it. In Table 1 these two genera are compared and the polarity of characters shown. Their prosterna, abdominal sense organs, brachyptery and apparent plastron are so similar, but so different from any other closely related naucorid genera (e.g., *Cataractocoris* Montandon) that I consider it unnecessary to include other genera in the comparison. The morphology used here follows Parsons (1966) and Parsons & Hewson (1974).

The CL number following locality data refers to codes used by the author to reference ecological data.

Table 1. Comparison of *Cryphocricos* and *Procryphocricos*. Apomorphic character states are marked with an asterisk.

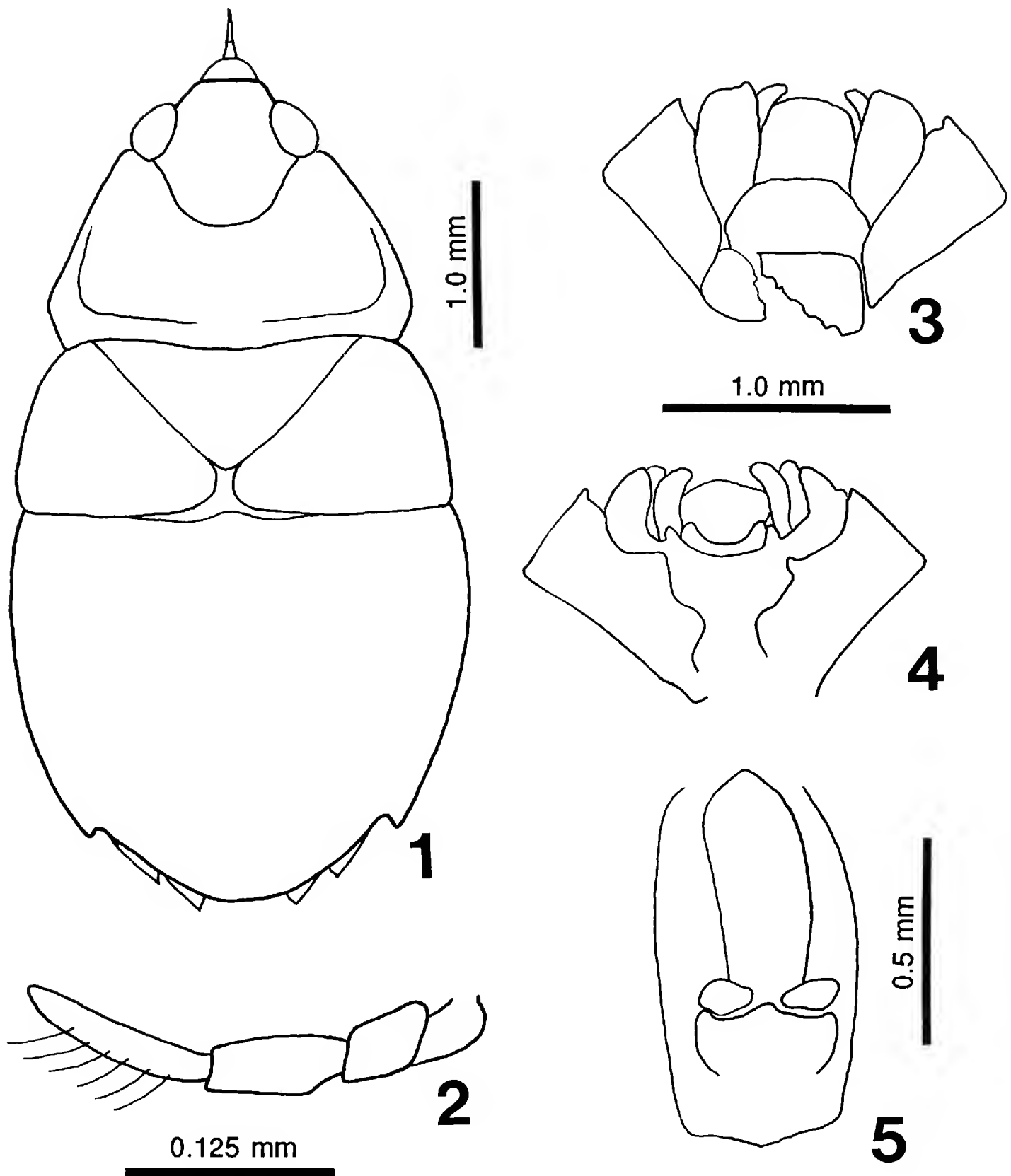
Character	<i>Cryphocricos</i>	<i>Procryphocricos</i>
Setae on ventral surface	very short; plastron only*	scattered long silky setae plus plastron
Mid and hind femora armed (knobs, spines)	present*	absent
Distal tibial spines	2 close packed rows*	1 short distal row, ragged sub-distal row
Lateral pronotal margins	crenulate, without obvious setae*	smooth, set with short stiff setae
Male abdominal tergite 7	asymmetrical; spur on right side*	symmetrical; no spur
Aedeagus	strongly asymmetrical flagellum very long*	weakly asymmetrical; short flagellum
Antennal segments, length	3 very short; 4 long*	3 and 4 long, subequal
Prosternum, proepimeron	separated by distinct suture	fused, junction faintly demarcated*
Male paratergite 8	large, size equal to 7, exposed; projecting	small, mostly covered by 7; angled medially*
Male abdominal sternite 7	fused with paratergites*	free from paratergites
Loral plates	produced anterad of eyes*	not produced anterad of eyes
Base of rostrum	ahead of eyes*	between and below eyes
Ocular setae	absent	2 kinds present*
Abdominal tergites	distinct	fused*

PROCRYPHOCRICOS J. T. POLHEMUS, NEW GENUS

Figs. 1–5

Type-species. — *Procryphocricos perplexus* J. T. Polhemus, NEW SPECIES.

Description. — Small, ovate, brachypterous. Length 5.1 mm, width 2.7 mm, widest across abdomen (Fig. 1). Entire dorsum rugose, set with short appressed scale-like setae. Head narrow, produced anteriorly $0.5 \times$ eye length, anteclypeal margin almost straight; vertex slightly domed medially, produced behind eyes $0.75 \times$ eye length, with two (1 + 1) trichobothria adjacent to middle of eyes. Eyes $1.5 \times$ as long as wide, with narrow posterior flange; raised, rounded, not forming smooth transition to head, but set off by shallow sulcus on head; ocular setae of two kinds, many short mushroom-shaped setae scattered among the ommatidia, and longer slender setae, two of medium length on inner eye margin, one long setae on lateral margin. Labrum small, arising at anterior margin of anteclypeus, rounded; maxillary plates projecting anteriorly, tips pointed, extending to middle of rostral segment three (second visible). Rostrum short, segment two (first visible) very short, recessed into head, segment three much longer and slightly shorter than four. Antennae of moderate length, segments one and two short, three and four subequal (Fig. 2). Pronotum convex, with broad shallow median depression, margins depressed and demarcated posteriorly and posterolaterally (Fig. 1); lateral margins not crenulate, set with short stiff setae. Scutellum triangular, slightly raised above level of adjacent wing pads, declivant anteriorly. Wing pads triangular, not touching medially, reaching posterior margin of abdominal tergite two; embolium poorly defined, set off mesad by a broad weak longitudinal carina not reaching posterior margin. Abdomen moderately convex dorsally, transversely rugose, connexiva evenly rounded, tergites three to five fused, intersegmental sutures weakly indicated only at lateral margins; connexival margin depressed; posterior margin of tergite five broadly rounded posteriorly, obscuring most of remaining tergites. Ventral surface sparsely set with long dark silky appressed setae absent only on head and prosternum; anterior one-third of prosternum carinate medially, anteromedial portions angled forward over base of carinate gula; prosternum completely exposed, very similar in shape to *Cryphocricos* (see Usinger 1941: fig. 1), fused with proepisternum, demarcated by weak



Figures 1–5. *Procryphocricos perplexus*. 1. Habitus. 2. Antennae. 3. Male abdominal terminalia, dorsal view. 4. Male abdominal terminalia, ventral view. 5. Aedeagus.

indication of suture. Mesosternal plate reflexed anteromedially forming tumescence, remainder medially carinate. Metasternal plate not carinate; metaxyphus triangular, posterior margins carinate. Abdominal venter narrowly glabrous laterally; sense organs similar to and in same position as *Cryphocricos* (see Usinger 1941: Fig. 1). Fore legs with femur broad, tibia narrow, tarsi single-segmented; single claw very short, triangular. Middle and hind femora slender, not modified, set with short stiff appressed setae; tibia set with spines except basally, distally with ventral row of closely set spines, subdistal ragged row of four spines, plus dorsal comb of many closely set stiff setae; tarsal segment one short, two long, three longer. Mid and hind pretarsi with long setiform parempodia; claws long, curved, each with large basal spur. Abdominal segments six to eight almost symmetrical (Figs. 3–4); genital capsule similar to *Cryphocricos*, elongate; aedeagus slightly asymmetrical; parameres small (Fig. 5).

Diagnosis.—*Procryphocricos* differs from *Potamocoris* by its smaller antennae, which are not visible in dorsal view, and by its brachyptery; only macropters of the latter are known. It differs from *Cryphocricos* by its vestiture of silky hairs on abdominal ventrites six through eight, and the characters given in Table 1.

Discussion.—As can be seen from Table 1, *Cryphocricos* possesses a number of apomorphies in comparison to *Procryphocricos*. Because both occur in the brachypterous form, both must possess a plastron, or there would be no way to obtain and hold an air store [see Usinger (1941), Parsons & Hewson (1974) and D. Polhemus (1986) for discussion]; this is an apomorphy for the Cryphocricini within the Cryphocricinae but is not unique within the Naucoridae; see Polhemus & Polhemus (1986) for discussion. In addition, all genera of the Cryphocricinae have a dorsal vestiture of silky hairs on abdominal segments six, seven and eight, but only in *Cryphocricos* these are absent ventrally.

To establish the polarity of characters in Table 1, the outgroup chosen for comparison is the genus *Potamocoris* Hungerford, which in my view is close to the ground plan for the Naucoridae [placed in a separate family by some authors; see Stys & Jansson (1988) for discussion]. *Procryphocricos* shares some primitive characters with *Potamocoris*, for instance similar antennal proportions, but in the latter genus the antenna are much longer and visible in dorsal view. In *Procryphocricos* one pair of facial trichobothria are present medially along the eyes, in the same position as in *Potamocoris*, but the latter has three pairs; also the lateral ocular setae are similar in the two genera, but the latter has no medial pair and lacks the mushroom-shaped ocular setae which constitute an autapomorphy for *Procryphocricos*.

Habitat.—The two known specimens of *Procryphocricos* were found among tangles of fine roots along a small section of steep bank bathed by the moderate current of the Rio Claro. A diligent search of other habitats of many kinds failed to yield additional specimens. Midstream riffles of the Rio Claro and a nearby tributary yielded *Ambrysus*, *Cryphocricos* and *Limnocoris*.

Material Examined.—See species types.

PROCRYPHOCRICOS PERPLEXUS J. T. POLHEMUS, NEW SPECIES

Figs. 1–5

Types.—Holotype, brachypterous male, data: COLOMBIA. *ANTIOQUIA*: Rio Claro, 13 km W of Doradal, 250 m, water temp 25° C, CL 2405, 21 Jul 1989, J. T. and D. A. Polhemus, in J. T. Polhemus Collection (JTPC). Paratype, 1 brachypterous male, same data as holotype (JTPC).

Description, Brachypterous Male.—(See generic description; only additional details given here.) Ground color yellow-brown; pronotum anteromedially and laterally, wing pads, fore legs distally tinged with brown; spines on mid and posterior legs orange-brown; eyes brown. Head deeply set into pronotum; length 0.90 mm, width through eyes 1.10 mm. Eyes with many ommatidia; embraced posteriorly by pronotum; length 0.38 mm, width 0.25 mm, interocular space 0.60 mm. Pronotum broad, maximum length 1.23 mm, length on midline 0.73 mm, width 2.13 mm. Scutellum triangular, roughly 2× as wide as long, length 0.70 mm, width 1.48 mm. Wing pad length 1.03 mm. Abdominal tergites three to seven each set laterally with two (1 + 1) long slender erect tufts of golden setae, on middle of connexival segment three, on posterior one-quarter of four to seven; combined length of fused abdominal tergites three to five, 2.13 mm. Antennal proportions as shown in Fig. 2; distal segment set with a row of stiff evenly spaced setae. Proportions of legs in mm (femur : tibia : tarsus 1:2:3):

anterior, 1.43:1.10:0.30:0:0; middle, 1.18:1.10:0.08:0.18:0.30; posterior, 1.43:1.53:0.10:0.20:0.33. Abdominal terminalia and genitalia as in Figs. 3–5.

Female and Macropterous Forms.—Unknown.

Diagnosis.—*Procryphocricos perplexus* is the only species of the genus.

Material Examined.—See types.

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THE MYDIDAE (DIPTERA) OF COSTA RICA

JUDITH L. WELCH AND BORIS C. KONDRATIEFF

Department of Entomology, Colorado State University,
Fort Collins, Colorado 80523

Abstract.—The species of Mydidae occurring in Costa Rica are reviewed. Four genera and seven species are reported, including *Nemomydas loreni*, NEW SPECIES. Additionally, *Mydas quadrilineatus* Williston, NEW SYNONYM, is synonymized under *M. rufiventris* Macquart.

Key Words.—Insecta, Diptera, Mydidae, Costa Rica, insect fauna

Costa Rica occupies part of the isthmus of Central America and is a complex ecological mosaic (Hall 1985). It has been estimated that upwards of 300,000 species of insects may occur in Costa Rica. This fauna is a complex mixture of Mesoamerican and South American species. One group of flies that attract the attention of even the most specialized collectors are mydas flies. Mydids are a small, but worldwide, family composed of medium to very large, usually sparsely pilose, flies that often resemble wasps (Fig. 1). Adults occupy a wide variety of habitats and can be locally common, especially in arid areas. Many species are restricted to hot, sandy habitats and can be found visiting blossoms or resting on bare ground.

The preparation of a section (JLW, unpublished data) on the Mydidae of Costa Rica for the “Guia para las familias de Insectos de Costa Rica,” stimulated this review. There is no single publication available treating all genera and species.

Morphology and terminology follows Wilcox (1981); genitalic structures are labeled in Figs. 4 and 12. Abbreviations for depositions that are used throughout the paper are: British Museum of Natural History, London (BMNH); University of California at Berkeley (UCB); Utah State University, Logan (USU); Museum National d’Histoire Naturelle, Paris (MNHN); Illinois Natural History Survey, Champaign (INHS); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); and Texas A&M University, Lubbock (TXA&M); collection of J. L. Welch (JLW).

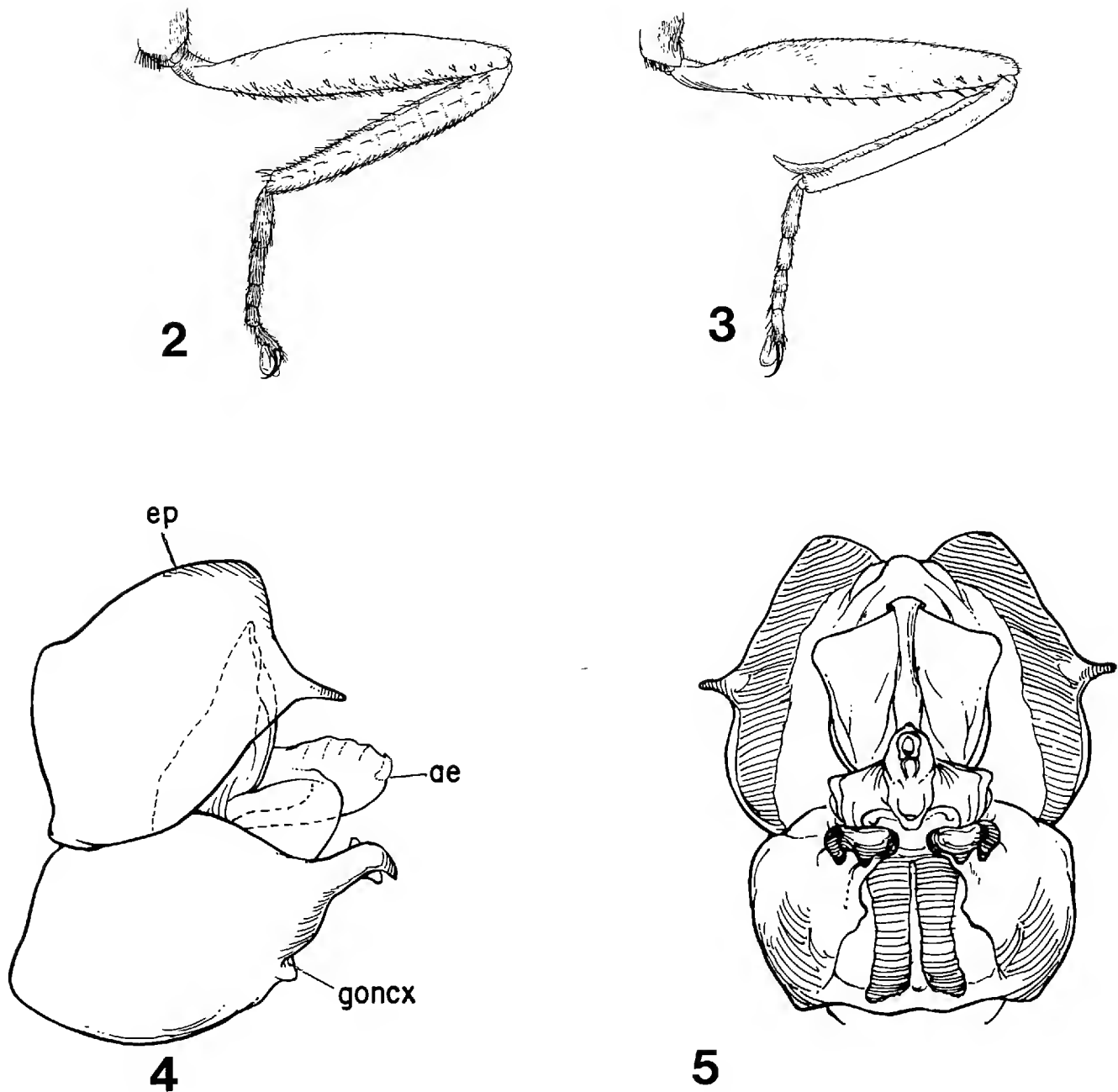
KEY TO THE GENERA OF MYDIDAE OF COSTA RICA (modified from Wilcox 1981)

1. Laterotergite completely bare; proboscis subequal in length to subcranial cavity; labella broad; apex of female abdomen with setae; length variable 2
- Laterotergite pilose; proboscis 1.0–2.0 × length of subcranial cavity; apex of female abdomen with circlet of spines; length 12–23 mm *Nemomydas* Curran
- 2(1). Prementum of proboscis 0.5 × length of subcranial cavity; labella attached to prementum near its midpoint, and subequal with subcranial cavity in length; anterior margin of subcranial cavity situated at about 0.4 × the distance from lower eye margin to base of antennae; length 15–29 mm *Messiasia* d’Andretta



Figure 1. *Mydas rufiventris*, general habitus.

- Prementum of proboscis and subcranial cavity subequal in length; labella attached to mentum near its apical one-half, and extending at about a 90° angle; anterior margin of subcranium level with lower margin of the eye 3
- 3(2). Carina on hind tibia partially developed (Fig. 2); apical spur of hind tibia reduced or absent (Fig. 2); epandrium strongly arched in lateral view (Fig. 4); process of gonocoxite digitiform (Figs. 4-5); gonostylus saddle-shaped in caudal view (Fig. 5); length 29-45 mm
 *Protomydas* Wilcox, Papavero & Pimentel
- Carina on hind tibia completely developed (Fig. 3); apical spur of hind tibia long and stout (Fig. 3); epandrium rounded in lateral view (Fig. 6); gonocoxite simple or falciform (Figs. 6-7); gonostylus bilobed in caudal view (Fig. 7); length 25-26 mm *Mydas* Fabr.



Figures 2–5. 2. *Protomydas rubidapex*, hind leg. 3. *Mydas clavatus*, hind leg. 4. *Protomydas rubidapex*, male terminalia, lateral view. 5. *Protomydas rubidapex*, male terminalia, caudal view.

MESSIASIA D'ANDRETTA

Messiasia d'Andretta 1951: 52.

Type Species. — *Messiasia carrerai* d'Andretta (by original designation).

Diagnosis. — See key to genera. Species included in this genus closely resemble, in general appearance those of *Mydas*, but they can be readily distinguished from Costa Rican *Mydas* species by their entirely black integument.

Discussion. — *Messiasia* is predominantly South American in distribution but five species are known to range from southwestern United States south to Panama (Wilcox & Papavero 1975).

Key to Costa Rican *Messiasia*

1. Wings pale amber; long white setae present above hind coxa; gonocoxite of male elongate, tapering to hook-like process; gonostylus serrate (Figs. 8–9) *decor* (Osten Sacken)
- Wings dull black; sparse black setae present above hind coxa; gonocoxite

of male truncate apically, upper process pointed; gonostylus broadly truncate (Figs. 10–11) *perpolita* (Johnson)

Messiasia decor (Osten Sacken)

Midas decor Osten Sacken 1886: 71.

Mydas decor; Williston 1898: 55.

Messiasia decor; d'Andretta 1951: 68.

Messiasia decor; Wilcox & Papavero 1975: 21 (includes specimens from La Suiza, Costa Rica).

Types.—Holotype, male; from: PANAMA. Bugaba; deposited in the British Museum (Natural History), London; examined.

Diagnosis.—The white setae above the hind coxae will usually separate both sexes of *M. decor* from *M. perpolita*.

Discussion.—This species is known from Costa Rica and Panama. Wilcox & Papavero (1975) indicate that this species occurs in forested areas. The illustration of the male terminalia of *M. decor* provided by Wilcox & Papavero (1975) is inaccurate.

Material Examined.—COSTA RICA. MONTEVERDE Prov.: 20–24 Jan 1986, W. Hanson and G. Bohart, 1 female (USU).

Messiasia perpolita (Johnson)

Mydas perpolita Johnson 1933: 72.

Messiasia polita; d'Andretta 1951: 64.

Messiasia perpolita; Wilcox & Papavero 1975: 31.

Types.—Holotype, male; from: MEXICO. YUCATAN: Chichen Itza; deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; examined.

Diagnosis.—The dull black wings and no white setae above the hind coxae will distinguish both sexes of this species from *M. decor*.

Discussion.—This species is relatively common in Mexico. Janzen (1986) described the unique tropical dry forest habitat in Costa Rica where this species was collected. Janzen's specimens collected by malaise traps represent the southernmost range extension for this species.

Material Examined.—COSTA RICA. GUANACASTE Prov.: Santa Rosa National Park, 14–17 Jun 1977, D. H. Janzen, 1 female (AMNH); same data except, 300 m, May 1983, D. H. Janzen and W. Hallwachs, 2 females (AMNH); same data except 1–15 Jun 1982, 300 m, D. H. Janzen and W. Hallwachs, 1 male (AMNH).

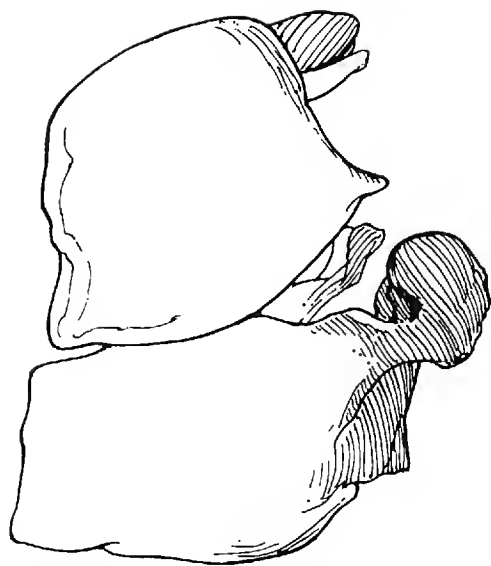
NEMOMYDAS CURRAN

Nemomydas Curran 1934: 165.

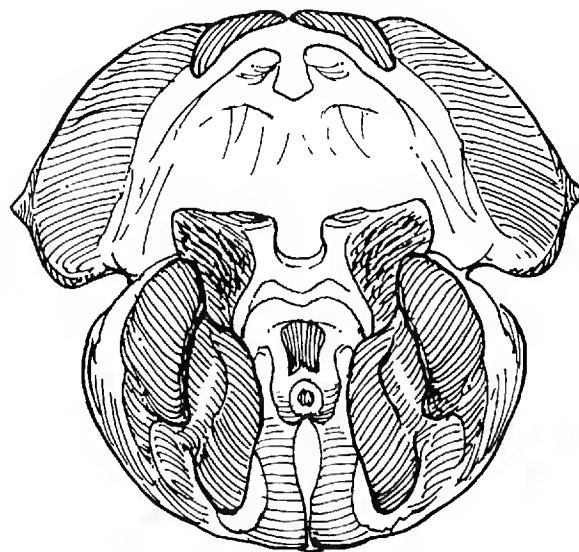
Type Species.—*Leptomydas pantherinus* Gerstaecker (by original designation).

Diagnosis.—See key to genera. Additionally, males are easily distinguished from all other mydids by the digitate processes of the gonocoxite.

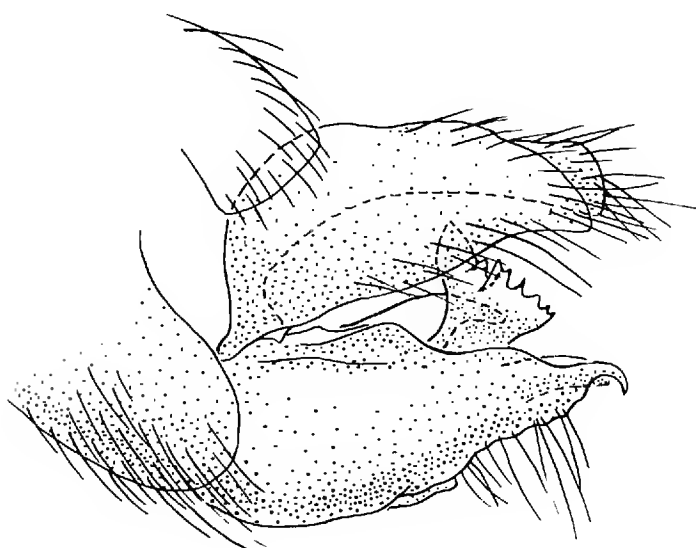
Discussion.—*Nemomydas* is restricted to North America and Central America and presently includes 19 species (Steyskal 1956, Kondratieff & Welch 1990,



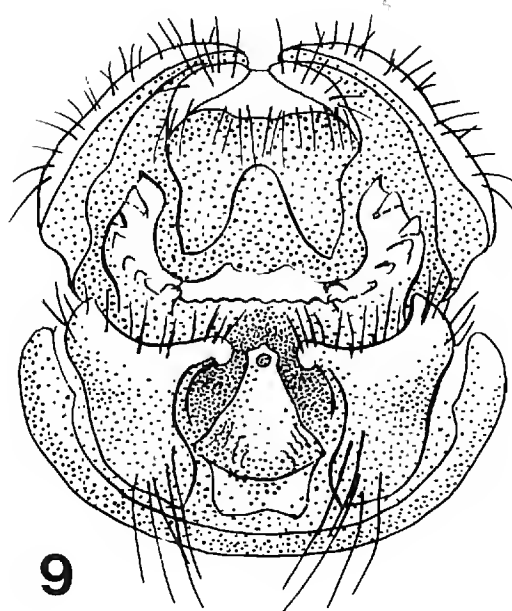
6



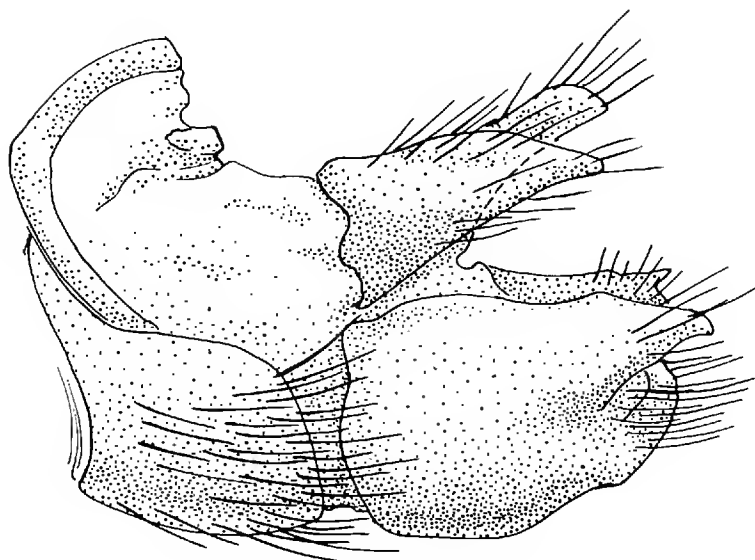
7



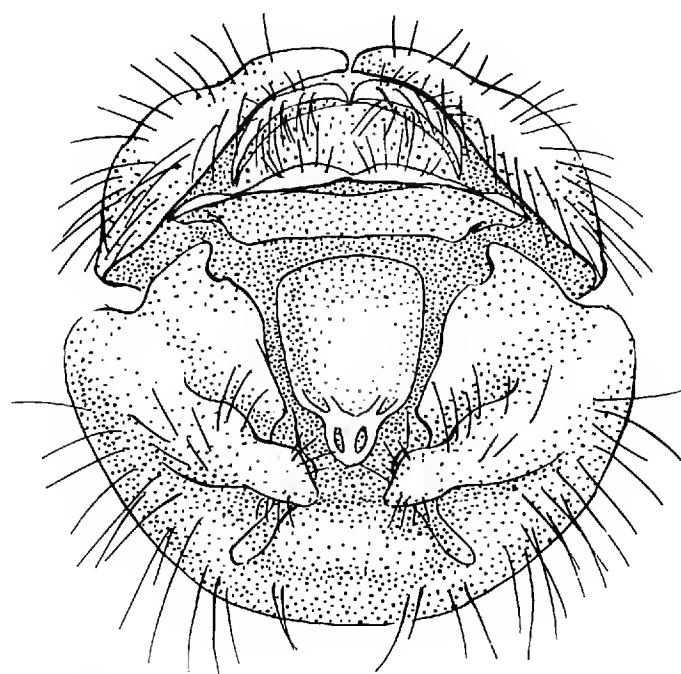
8



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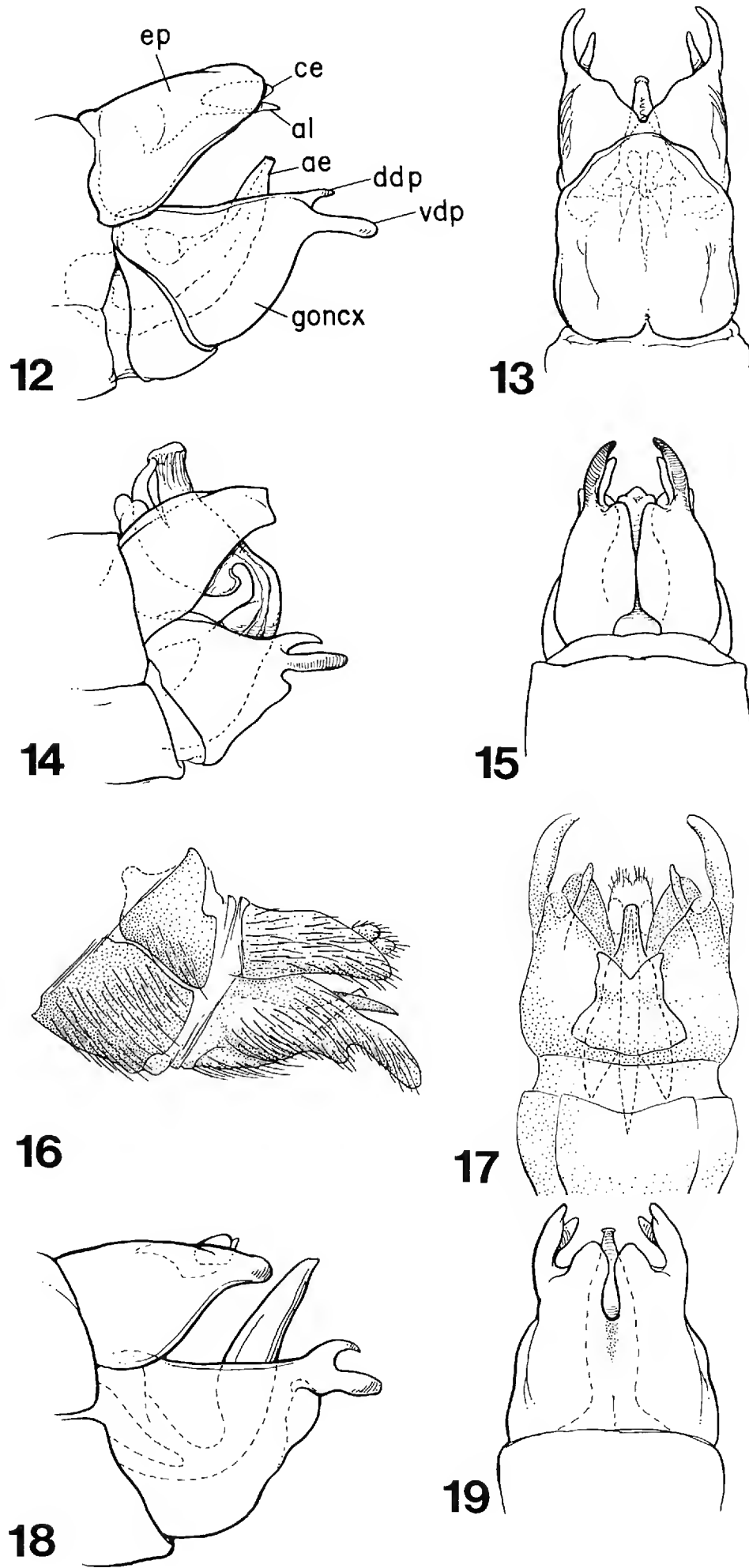


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11

Figures 6–11. Male terminalia. 6. *Mydas rufiventris*, lateral view. 7. *Mydas rufiventris*, caudal view. 8. *Messiasia decor*, lateral view. 9. *Messiasia decor*, caudal view. 10. *Messiasia perpolita*, lateral view. 11. *Messiasia perpolita*, caudal view. Abbrev.: ae, aedeagus; ep, epandrium; goncx, gonocoxite.



Figures 12–19. Male terminalia. 12. *Nemomydas bequaerti*, lateral view. 13. *Nemomydas bequaerti*, ventral view. 14. *Nemomydas sponsor*, lateral view. 15. *Nemomydas sponsor*, ventral view. 16. *Nemomydas loreni*, lateral view. 17. *Nemomydas loreni*, ventral view. 18. *Nemomydas lamia*, lateral view. 19. *Nemomydas lamis*, ventral view. Abbrev.: ae, aedeagus; al, anal lamellae; ce, cercus; ddp, dorsal digitate process; ep, epandrium; goncx, gonocoxite; vdp, ventral digitate process.

Welch & Kondratieff 1990). Three species occur in Costa Rica including a new species described here: *N. lamia* (Seguy), *N. sponsor* (Osten Sacken), and *N. loreni* NEW SPECIES. These three species are very similar in appearance; females are difficult to separate without associated males.

Key to *Nemomydas* males south of Mexico

1. Abdominal tergites black, posterior margins yellow 2
- Abdominal tergites yellow-brown with middorsal black-brown spots or dashes; terminalia as Figs. 12–13 (Honduras) *bequaerti* (Johnson)
- 2(1). Distal section of aedeagus in lateral view, abruptly expanded and re-curved medially (Figs. 14–15) (Guatemala, Costa Rica)
..... *sponsor* (Osten Sacken)
- Distal section of aedeagus in lateral view, tube-like (Figs. 16–17) or tongue-like (Figs. 18–19) 3
- 3(2). Distal section of aedeagus in lateral view, tube-like (Figs. 16–17)
..... *loreni* NEW SPECIES
- Distal section of aedeagus in lateral view, tongue-like (Figs. 18–19) ..
..... *lamia* (Séguy)

Nemomydas lamia (Séguy)

Nomoneura lamia Séguy 1928: 146.

Nemomydas lamia; Papavero & Wilcox 1968: 34.11.

Nemomydas lamia; Kondratieff & Welch 1990: 474.

Types. — Lectotype, male; from: COSTA RICA. La Caja; deposited in the Museum National d'Histoire, Paris; examined.

Diagnosis. — See key to *Nemomydas* species.

Discussion. — Kondratieff & Welch (1990) provided descriptions of both sexes of this uncommon species. The specimens examined are apparently the first additional material collected since its original description.

Material Examined. — COSTA RICA. GUANACASTE Prov.: S. Cañas, 26–31 Jan 1989, F. D. Parker, 1 male (CSU), 2 males (USU). La Caja, Paul Serre, 1920, 1 male, 6 females (MNHN).

Nemomydas sponsor (Osten Sacken)

Leptomydas sponsor Osten Sacken 1886: 68.

Nemomydas sponsor, Kondratieff & Welch 1990: 475.

Types. — Holotype, female; from: GUATEMALA. San Geronimo; deposited in the British Museum (Natural History), London; examined.

Diagnosis. — See key to *Nemomydas* species.

Discussion. — Kondratieff & Welch (1990) provided the first description of the male of this species.

Material Examined. — COSTA RICA. SAN JOSE Prov.: San Jose, 27–29 Dec 1987, F. D. Parker, 4 males, 2 females (USU); Escazu, 14–16 Jan 1989, F. D. Parker, 1 male (USU); 1 male (MNHN).

Nemomydas loreni Welch & Kondratieff, NEW SPECIES

Types. — Holotype male, data: COSTA RICA. GUANACASTE Prov.: S. Cañas, 1–3 Feb 1989, F. D. Parker; deposited: Utah State University, Logan. Paratypes deposited in Utah State University, Logan, except as indicated; data: 16 males,

1 female, same data as holotype (1 male deposited CSU), (1 male deposited JLW); same data except 1–5 Mar 1989, 1 male; same data except 21–25 Jan 1989, 4 males; same data except 26–31 Jan 1989, 3 females; same data except 9–14 Feb 1989, 1 male, 9 females (1 female deposited CSU); same data except 22–24 Feb 1989, 1 male (deposited CSU); Tamarindo, 6 Nov 1977, M. E. Irwin, ex. beach sand, 1 male (deposited INHS). *SAN JOSE Prov.*: Escazu, 14–16 Jan 1989, F. D. Parker, 2 females (1 female deposited JLW); Puntarenas, 19 Dec 1989, F. D. Parker, 2 males; Comelco Property, 30 Jan 1976, H. Reed, 1 male (deposited TXA&M).

Description.—*Male.* Length 12–16 mm. Head shiny black, with white, erect setae; orbital of eye yellow pollinose; antenna 3.6–3.8 mm long, black, flagellomere two white pollinose dorsally, brown pollinose ventrally; proboscis long, 2.6 times as long as subcranial cavity, black. Scutum black, with a pair of submedian yellow pollinose stripes that converge posteriorly, and a pair of lateral yellow pollinose stripes, setae yellow, long, erect, sparse; postpronotal lobe yellow pollinose; scutellum yellow pollinose, black posteriorly; metanotum black, yellow pollinose anteriorly. Wings brown, longitudinal veins brown, costa black with black setae; knob of halter black, stem brown. Foreleg and midleg brown black, setae white dorsally, black ventrally; hind femur white basally, black apically; hind tibia white dorsally, brown-black ventrally; with short, white setae, dorsally, black ventrally; tarsomeres brown-black. Abdominal tergites shiny black, posterior margins yellow to brown; bulla black; tergite one with setae white, long anteriorly, short, sparse posteriorly; tergite two with setae black, short, decumbent, medially; setae white, long, divergent, anteriorly and laterally; tergites three to five with setae black, short, decumbent; tergites six and seven with setae white, long, decumbent; sternites shiny black, sternites two to five with posterior margins yellow to brown; sternites two to four with setae white, long, decumbent; sternites five to seven with setae black, long, decumbent. Terminalia brown-black. Gonocoxite with dorsal digitate process distinctly claw-like, ventral digitate process oblong, rounded, slightly directed inwardly; a smaller rounded protrusion ventrally. Aedeagus tube-like distally, swollen basally (Figs. 16–17).

Female.—Length 12–16 mm. Color and structure similar to male, except setae on abdominal tergites short and sometimes tergites six and seven without yellow posterior margins.

Diagnosis.—The male of *N. loreni* can be distinguished from all other meso-american species by the combination of black abdominal tergites with yellow posterior margins and tube-like distal section of the aedeagus. The female cannot be satisfactorily separated from *N. lamia*.

Etymology.—This species is named in memory of JLW's father, who encouraged her to take an interest in Diptera because of their intriguing life histories.

Material Examined.—Type series.

PROTOMYDAS WILCOX, PAPAVERO & PIMENTEL

Protomydas Wilcox, Papavero & Pimentel 1989: 13.

Type Species.—*Mydas coerulescens* Olivier (by original designation).

Diagnosis.—See key to the genera.

Discussion.—Wilcox et al. (1989) recognized three species in this primarily Neotropical genus; only one is known from Costa Rica and listed here. D'Andretta (1951) provided illustrations of the male terminalia and other characters for these species.

Protomydas rubidapex (Wiedemann)

Mydas rubidapex Wiedemann 1830: 626.

Mydas dives Westwood 1841: 50. (Synonymized by Wilcox, Papavero & Pimentel 1989: 16.)

Protomydas rubidapex; Wilcox, Papavero & Pimentel 1989: 16.

Types. — The type of *P. rubidapex* is from MEXICO, and is deposited in Humboldt Universitat, Berlin; it was not examined. The type of *P. dives*, from an unknown locality, is deposited in Hope Museum, Oxford, England, and was not examined.

Diagnosis. — *Protomydas rubidapex* is easily separated from all *Mydas* species by the reduced or absent carina of the hind tibia, the arched epandrium, digitiform process of the gonocoxite, and the saddle-shaped gonostylus.

Redescription. — *Male.* Length 29–45 mm long. Head shiny black, with long, erect, black setae; mystax with long, decumbent, black and yellow setae; orbital margin of eye black; antenna 10–12 mm, orange or black with flagellomere 2 orange; proboscis black. Scutum dull black; setae sparse, decumbent, black; wing opaque orange to brown, wing margin broadly brown to black; veins orange, or sometimes brown apically, costa with black setae basally, and mixed black and orange setae apically; calypter with long dense fringe of black squamose setae; halter black; legs black, setae and bristles black; hind tibia with carina absent or reduced, apical spur weakly developed, shorter than width of first hind tarsal segment. Abdominal tergite one black, with long, decumbent, sparse, golden setae; tergite two black, with short, recumbent, golden setae; bulla black; tergites three to seven with short, recumbent, black, setae; sternites with short, sparse, recumbent setae. Terminalia with epandrium, in lateral view (Fig. 3) arched, concave above spur; gonocoxite with produced, “grasping” digitiform process that is incurved in caudal view; gonostylus saddle shaped; aedeagus tube-like, ribbed dorsally, with lateral rounded ridges (Fig. 4).

Female. — Length 35–40 mm. Antenna length 14.0–15.5 mm. Coloration and structure similar to male.

Discussion. — Wilcox et al. (1989) did not provide a thorough description of this species, and the redescription above is based on Costa Rican specimens. This species ranges from northern Mexico to Venezuela and Brazil.

Material Examined. — COSTA RICA. GUANACASTE Prov.: Santa Rosa National Park, 21–24 Dec 1979, D. H. Janzen, ex malaise trap, 1 male (AMNH); same data as above except, 1–15 Jan 1982, 300 m, D. H. Janzen and W. Hallwachs, 1 male (AMNH); Sotobosque, Cerro El Hacha, 12 Sep–2 Jan 1988, Tacotal, ex malaise trap, 1 female (AMNH).

MYDAS FABR.

Mydas Fabr. 1794: 252.

Type Species. — *Musca clavata* Drury (by subsequent designation).

Diagnosis. — See key to the genera.

Discussion. — This genus and its allies were recently revised by Wilcox et al. (1989); we do not agree with several of the taxonomic conclusions reached in that study and will publish our interpretations elsewhere. *Mydas rufiventris* is the only *Mydas* known from Costa Rica.

Mydas rufiventris Macquart

Mydas rufiventris Macquart 1850: 364.

Mydas vittatus Macquart 1850: 364.

Mydas militaris Gerstaecker 1868: 99. (New name for *Mydas vittatus*, preoccupied.)

Stratiomydas rufiventris; Wilcox et al. 1989: 127.

Mydas quadrilineatus Williston 1898: 56. NEW SYNONYM.

Stratiomydas quadrilineatus; Wilcox et al. 1989: 125.

Types. — The holotype male of *M. rufiventris* is labeled “BRAZIL” (in error); it is deposited in the Museum National d’Histoire Naturelle, Paris, and was ex-

amined. The holotype female of *M. vittatus* is labeled MEXICO; it is deposited in the Museum National d'Histoire, and was examined. The syntypes of *M. quadrilineatus* are labeled "MEXICO"; they are deposited in the British Museum (Natural History), London, and were examined.

Diagnosis.—The white to yellow mystax and the four pollinose stripes of the mesonotum will easily distinguish this species from all other possible *Mydas* species.

Discussion.—In a recent review of the Mydini by Wilcox et al. (1989), *M. rufiventris* was distinguished from *M. quadrilineatus* by the color of the abdominal tergites which are primarily black in *M. quadrilineatus* and red in *M. rufiventris*. Examination of specimens throughout the range of both species (Arizona, Mexico, El Salvador, and Costa Rica) indicated the presence of only one variable species. The male terminalia of both forms are alike. The key of Wilcox et al. (1989) to this group is unusable, however, especially with females. The series of both sexes, collected by Paul A. Opler near Cañas, contains all color morphs, ranging from specimens with all abdominal tergites completely black to some with tergites two through five or two through seven red. This often extreme polymorphism in abdominal color is common in other species groups of *Mydas* (e.g., *Mydas ventralis* Gerstaecker of the southwestern United States).

Material Examined.—COSTA RICA. GUANACASTE Prov.: Cañas, 6.4 km NW of La Pacifica, 14 May 1971, P. A. Opler, ex *Casearia* sp. ("nitida"), 1 male, 1 female (UCB); same data except 15 Nov 1971, 1 female; same data except 23–30 May 1972, ex *Forsteronia* sp. ("spicata"), 2 males, 2 females (UCB), 1 male (CSU); same data except 6 Jun 1973, ex *Asclepias* sp. ("liana"), 2 males (UCB); same data except 2–4 June 1973, *Asclepias* vine, 1 male, 2 females (UCB).

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**POST-EGESTIVE SURVIVAL OF
SPHENOPHORUS PHOENICIENSIS CHITTENDEN
(COLEOPTERA: CURCULIONIDAE) EGESTED BY
WESTERN TOADS**

CARL D. BARRENTINE

Department of Biology, California State University,
Bakersfield, California 93311

Abstract.—Billbugs (Coleoptera: Curculionidae) are eaten by toads and egested alive in fecal pellets. This study examines post-egestive weight loss and survivorship of *Sphenophorus phoeniciensis* Chittenden after passing through the digestive tract of the western toad, *Bufo boreas* Baird & Girard. Weight loss (mg/h) in egested billbugs exceeds that found for nonegested billbugs at both low and high RH. Egested billbugs do not live as long as nonegested billbugs at the same relative humidity.

Key Words.—*Bufo boreas*, *Sphenophorus phoeniciensis*, Curculionidae, weevils, billbugs, fecal pellets, toads, survival

Toads (Bufonidae) are known to ingest billbugs (Coleoptera: Curculionidae). Some billbugs (*Sphenophorus* spp.) resist digestion by toads (*Bufo boreas* Baird & Girard) and emerge alive from fecal pellets (Barrentine in press). Egested billbugs have reduced survival at low humidities (Fair 1969). This is putatively due to increased water loss resulting from epicuticular damage. This study compares weight loss and survivorship between egested and nonegested billbugs (*Sphenophorus phoeniciensis* Chittenden) at both low and high relative humidities.

MATERIALS AND METHODS

Billbugs, *S. phoeniciensis*, in treatment samples were collected from infested turfgrass (2200–2300 h) and immediately fed to captive adult toads (*B. boreas halophilus* Baird & Girard). After two to three days, billbugs were isolated from freshly egested toad fecal pellets, individually weighed (0.1 mg) and then placed in one of two Scheibler desiccators. Both desiccators were kept at room temperature at 23° C, but differed in < 5% versus > 95% RH. Humidity was controlled using Drierite® (anhydrous calcium sulfate) or distilled water. Weight loss and survivorship of individual weevils were recorded at 24 h intervals. Because curculionids are capable of feigning death (DuPorte 1916, Weiss 1940), mortality was confirmed by lack of antennal reflex (flexor response to mechanical stimulation). After death, billbugs were oven dried at 68° C to constant weight. Billbugs in control samples were collected and handled as described above, for treatment samples, except that these were not fed to toads. Billbugs in treatment and control samples were paired by weight (± 0.1 mg, wet) before comparison using Student's *t*-test.

RESULTS AND DISCUSSION

At low humidity, there was no difference in weights between paired treatment and control samples at the time of death (Table 1). Although death weights were

Table 1. Weights of *Sphenophorus phoeniciensis* (mg, $\bar{x} \pm SE$).

	<i>n</i>	Wet weight (mg) $\bar{x} \pm SE$	Death weight (mg) $\bar{x} \pm SE$	Dry weight (mg) $\bar{x} \pm SE$
<5% RH				
Control	50	18.62 \pm 0.48	10.90 \pm 0.36	7.93 \pm 0.19
Treatment	50	18.62 \pm 0.48	11.28 \pm 0.39	7.89 \pm 0.19
>95% RH				
Control	50	18.57 \pm 0.54	12.68 \pm 0.35	} ^a 6.97 \pm 0.18
Treatment	50	18.57 \pm 0.54	15.44 \pm 0.53	

^a $t = 4.29$, $P < 0.01$.

similar for both samples (40%), billbugs in the treatment sample did not, on the average, survive as long as those in the control sample (Table 2). Mean weight loss for egested billbugs was 0.153 mg/h (7.34 mg/48.0 h) at < 5% RH. Mean weight loss in nonegested (normal) billbugs was 0.134 mg/h (7.72 mg/57.6 h). Assuming that weight loss is proportional to water loss, the desiccation rate for egested billbugs is 15% higher than that for normal billbugs at low humidity.

At high humidity, death weights between paired treatment and control samples differed (Table 1). Death occurred at 17% and 32% weight loss in treatment and control groups, respectively. Billbugs in the treatment sample did not, on the average, survive as long as those in the control sample (Table 2). Mean weight loss for egested billbugs was 0.022 mg/h (3.13 mg/144.5 h) at > 95% RH. Mean weight loss in nonegested (normal) billbugs was 0.020 mg/h (5.89 mg/295.7 h). Again, assuming that weight loss is proportional to water loss, the desiccation rate for egested billbugs is 10% higher than that for normal billbugs at high humidity.

These results both corroborate and extend observations made by Fair (1969). Fair observed that lowered humidity (39–43%) induced death in egested billbugs and that reduced survival was probably the result of increased water loss caused by damage to the epicuticle. This study thus documents reduced survivorship for egested billbugs at both low and high humidities and quantifies weight (water) loss for both egested and nonegested billbugs.

Table 2. Time of death for *Sphenophorus phoeniciensis* (hours, $\bar{x} \pm SE$ and range).

	<i>n</i>	Hours $\bar{x} \pm SE$	Hours (Min–Max)
<5% RH			
Control	50	57.6 \pm 1.81	} ^a (48–96)
Treatment	50	48.0 \pm 1.94	
>95% RH			
Control	50	295.7 \pm 17.07	} ^b (72–528)
Treatment	50	144.5 \pm 20.29	

^a $t = 3.58$, $P < 0.01$.

^b $t = 5.65$, $P < 0.01$.

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SEASONAL PATTERNS IN A SAN FRANCISCO BAY, CALIFORNIA, SALT MARSH ARTHROPOD COMMUNITY

STEVEN S. BALLING AND VINCENT H. RESH

Department of Entomological Sciences, University of California,
Berkeley, California 94720

Abstract.—Biomass, abundance, and species richness patterns of detritivore, herbivore, and carnivore components of a San Francisco Bay, California, salt marsh arthropod community were examined over an annual cycle. Abundance and species richness patterns for herbivores and detritivores did not track the occurrence of their respective food resources, perhaps because of the influence of salinity levels, and the frequency and duration of tidal inundation. In contrast, abundance and species richness of carnivores corresponded well with occurrence of their herbivore and detritivore prey, perhaps because carnivores are less susceptible to salt marsh environmental extremes. Trophic biomass analysis showed a typical pyramid-shaped relationship among producer, herbivore and detritivore, and carnivore components in spring; during autumn, however, the biomass of carnivores exceeded that of herbivores and detritivores.

Key Words.—salt marsh, wetlands, seasonality, trophic, arthropods, insects, *Salicornia*

Over an annual cycle, salt marshes are subject to relatively large seasonal fluctuations in tidal inundation frequency and duration, and in soil, ground water, and tidal water salinity. Does the composition of the arthropod fauna show similar temporal fluctuations? If all species of salt marsh arthropods are well adapted to the full range of tidal inundation and salinity that occurs over a year, the occurrence of a trophic group and the availability of its food resources should correspond, as has been reported for more seasonally constant environments (e.g., Hurd & Wolf 1974, Brown & Southwood 1983). However, if physical conditions disrupt the ability of a trophic group to track its food resources, poor correspondence may result. In this paper, we describe the seasonal occurrence of arthropods (as measured by biomass, abundance, and number of species), and relate these findings to the above considerations.

MATERIALS AND METHODS

The study was conducted in Petaluma Marsh, Sonoma Co., California (for map of area, see Balling & Resh 1983: Fig. 1), which is the largest of the San Francisco Bay tidal marshes and one of the largest (1145 ha) estuarine marshes along the Pacific Coast of North America. The marsh is dominated by pickleweed (*Salicornia virginica* L.).

Arthropods were collected using a D-vac suction device with a 0.25 mm mesh collection bag, and were separated from plant matter using a Berlese-Tullgren funnel; a complete description of arthropod sampling methods is given in Balling & Resh (1982). Samples for the present analysis were chosen from a series that was taken approximately monthly from January to November 1978 (representing 12 sampling dates). Specimens were separated into three categories: detritivores, herbivores, and carnivores. Primary feeding habits of the species were obtained from taxonomic specialists in these groups and from existing literature (e.g., Cameron 1972). Although some species do not feed restrictively within a single trophic

group, we used the predominant feeding mode of a species to describe its trophic status.

Arthropod abundance and species richness (number of species per 0.09 m² sample) were based on data from six samples collected each month. Arthropod biomass was determined from two samples each month, which were individually oven dried at 100° C to a constant weight.

Detailed measurements of physical variables (salinity, tidal inundation, and air temperature) were not done in Petaluma Marsh until 1980; however, values during that year matched periodic observations made during 1977–1979. In 1980, salinity of tidal waters was measured weekly (during high tide) with a refractometer; periodic measurements of interstitial water salinity (Balling & Resh 1983) indicated similar seasonal trends observed to those for tidal water salinity. Tidal inundation frequency of the marsh surface was calculated using data from a tide gauge located on a nearby slough. Average air temperature was determined from constant temperature recordings.

RESULTS AND DISCUSSION

Biomass. — Arthropod biomass during the year was characterized by three narrow, well-defined peaks; each peak represented a different trophic level: detritivores peaked in March, herbivores in May and June, and carnivores in September and October (Fig. 1a). At least in part, these biomass patterns reflected the phenology of the large sized species in the arthropod community. For example, the peak in detritivores closely followed peak occurrences of the amphipod *Orchestia traskiana* Stimpson and the isopod *Littorophiloscia richardsonae* (Holmes & Gay). Herbivores were not dominated by any single species; instead the peak largely resulted from four species of brine flies [Ephydriidae: *Psilopa* (*Ceropsilopa*) *coquilletti* (Cresson), *Scatella* (*Scatella*) *stagnalis* Fallen, *Scatella* (*Neoscatella*) *setosa* Coquillett and *Scatophila* sp.] and two species of leafhoppers [Cicadellidae: *Strepitanus confinus* (Reuter) and *Macrosteles* sp. near *fascifrons* (Stål)]. The carnivore peak reflected the maturation of the population of the large wolfspider (Lycosidae) *Pardosa ramulosa* (McCook).

Abundance. — Of all trophic groups, more individuals of carnivores than herbivores or detritivores were collected throughout the year; however, the abundance peaks were less well defined than the biomass peaks (Fig. 1b). Abundance of all groups peaked in spring and then again in autumn. In contrast to the influence of large individuals on biomass, changes in abundance are often biased toward the smaller sized, more numerous species (e.g., Odum 1971). For example, the spring detritivore peak was dominated by the sminthurid collembolan *Sminthurides* (*Sminthurides*) *malmgreni* Tullberg and the autumn peak was dominated by the psocopteran *Lachesilla pacifica* Chapman. The spring peak in herbivores was dominated by the same species of brine flies and leafhoppers as the herbivore biomass peak. However, the earlier rise in abundance seen in March was caused by early instar leafhoppers, whose small size made them proportionately more important in abundance measures than in biomass measures. Carnivore abundance peaks in spring and autumn were dominated by the small predaceous phytosieid mite *Amblyseius scyphus* Schuster & Pritchard, and also included a broad array of other mites and spiders.

Species Richness. — Like abundance, the peaks in species richness were less well

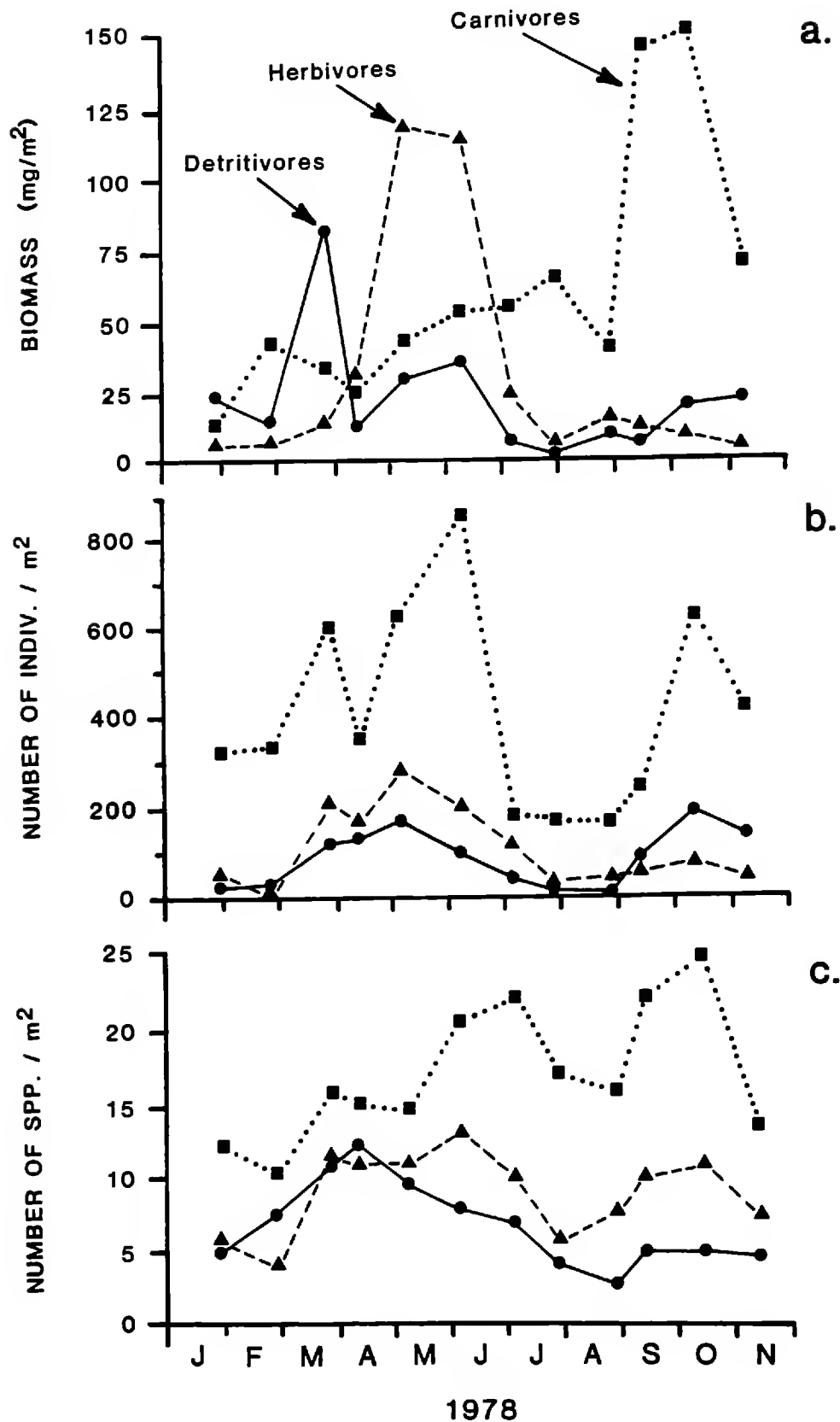


Figure 1. Mean (a) biomass, (b) abundance, and (c) species richness of terrestrial arthropods collected in Petaluma Marsh during 1979; squares represent carnivores, triangles represent herbivores, and circles represent detritivores.

defined than those for biomass. Detritivore species richness was highest in April, with only a small increase in autumn. Herbivore species richness was highest in June (although this was preceded by similarly high levels that began in March), decreased in July and August, and increased again in September and October. Carnivore species richness peaked in May, June and July, and October.

Trophic Pyramids.—Because biomass relationships among different trophic groups changed seasonally (Fig. 1a), the shape of ecological pyramids that are developed from biomass data vary depending on the time of year. For example,

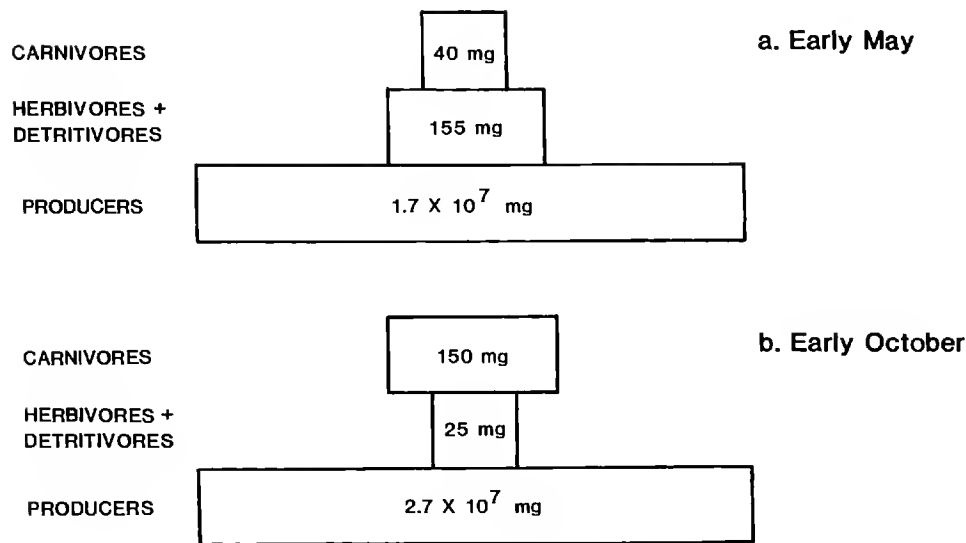


Figure 2. Trophic pyramids of pickleweed and arthropod biomass in (a) early May and (b) early October 1979. Plant biomass data are from Cameron (1972) and Balling & Resh (1983). Pyramid widths are given as the \log_{10} of the biomass (mg/m^2).

during early May the trophic relationships were pyramid shaped; biomass estimates of producers (pickleweed), herbivores/detritivores (combined to estimate potential carnivore prey), and carnivores decreased at successively higher trophic levels (Fig. 2a). In contrast, during early October the carnivore and herbivore/detritivore relationship was inverted (Fig. 2b).

Interaction of Trophic Groups and Abiotic Factors. — Although biomass patterns in this salt marsh arthropod community showed seasonal changes indicating trophic succession, the abundance and species richness patterns showed neither trophic succession nor the typical numerical domination of herbivores. Perhaps this is related to the seasonal patterns of physical features of the salt marsh environment.

In Petaluma Marsh, water salinities were lowest in February, March, and April; they steadily increased through the following summer, and then decreased with the onset of rain at the beginning of the wet season in October (Fig. 3a). Tidal inundation frequency (Fig. 3b) and air temperature (Fig. 3c) showed similar patterns.

Detritivores had their highest biomass, abundance, and species richness during spring, even though their primary food resource (which in a pickleweed monoculture is composed of litter from senescent stems) was most abundant in October and November (Cameron 1972). The early spring flushing of the marsh surface by rainfall and low salinity tides reduces the salt content of surface litter, which may make it more palatable to insect detritivores (Foster & Treherne 1976). In addition, microbial colonization may condition the litter by this time, which also provides bacterial and fungal food sources.

Abundance, richness, and biomass of detritivores declined gradually until August, even though abundant litter still occurred in the marsh; perhaps this decline resulted from high salinities of tidal water (over 20 ppt, Fig. 3a) and frequent tidal inundation of the marsh (Fig. 3b). During July and August, the marsh surface is inundated by tides approximately 10% of the time and for periods of up to 5.5 h. Such inundations are stressful to arthropods that remain under water, and also to those that remain on the water surface or migrate to the tops of emergent

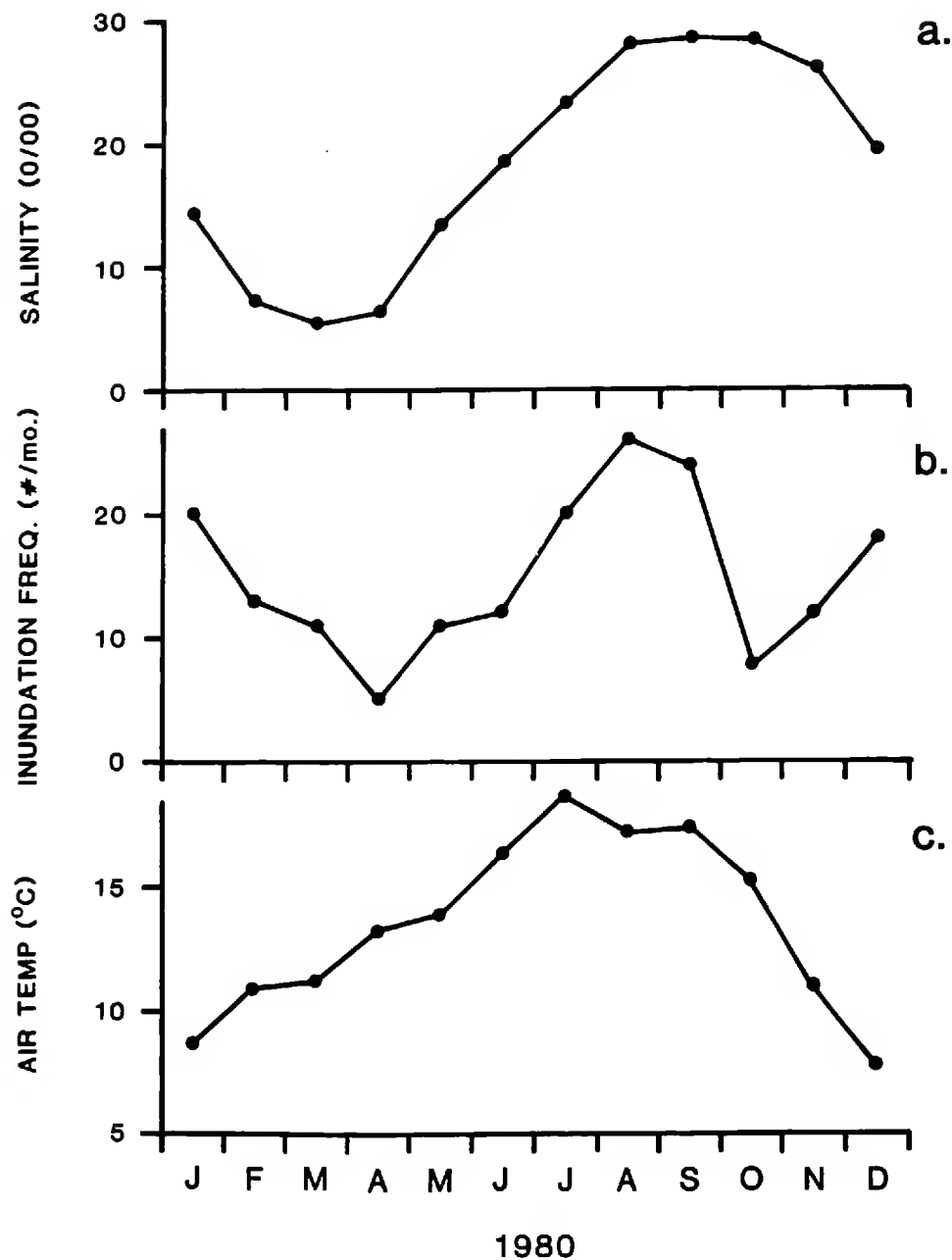


Figure 3. (a) Mean salinity of tidal water, (b) frequency of tidal inundation (per month), and (c) mean maximum air temperature in Petaluma Marsh during 1980.

vegetation because they will be more susceptible to predation or washout by receding tides (Foster & Treherne 1976).

In autumn, the psocid *L. pacifica* was the only detritivore to increase in abundance. The apparent salt tolerance of this species allows it to use this abundant food source at a time when few other detritivore species are present (e.g., Fig. 1c shows an average of only four detritivore species per sample during September and October).

Abundance and biomass of herbivores is highest in late spring even though their food, which consists mostly of surface algae and the annual succulent component of pickleweed, increases in quantity from March through October (Cameron 1972, Mahall & Park 1976, Zedler 1982, Josselyn 1983). The rise in herbivores coincides with the most rapid increase in succulent plant biomass, and with the seasonal increase in air temperature (Fig. 3c). The rather sudden decline coincides with the combination of peak tidal inundation (Fig. 3b) and peak salinities (Fig. 3a).

Tidal salinities, which correlate with groundwater salinities, indirectly affect sap-feeders such as leafhoppers through reductions in their food quality because

pickleweed sap salinity increases as groundwater salinity increases (Flowers et al. 1977). For example, Regge (1973) has shown that salt marsh aphids will seek plants with lower sap salinity, and Vince et al. (1981) have shown that a positive relationship between *Spartina* nutritional quality and herbivore abundance occurs in an Atlantic coast salt marsh.

The decline of herbivores at the end of spring also coincided with the rise in carnivore abundance; thus, predation may also be an important regulating factor. Again, as with the detritivores, high tides of mid-summer may drive some insects to the plant tops or water surface, and thus increase the chances of predation. Vince et al. (1981) also indicated that spider predation may limit herbivore abundance.

The seasonal patterns of carnivore abundance and species richness corresponded well with the occurrence of expected food sources (i.e., herbivores and detritivores). Carnivores, represented primarily by mites, reached their peak abundance in spring, which coincided with the herbivore and detritivore abundance peaks. Although carnivore abundance declined through the summer, biomass continued to rise. Most of the autumn predators are spiders that are well adapted to traversing water surfaces and capturing prey that are found there (Roth & Brown 1976). Because most of their prey regulate the salinity of their hemolymph (at least to some extent), predators may be less affected by the rise in salinities during summer and autumn.

In conclusion, salt marsh herbivores and detritivores apparently do not closely track changes in the quantity of their food. In fact, the inefficiency of the detritivores may help promote the rapid accumulation of peat that occurs in many salt marshes. The results of this study suggest that the phenologies of salt marsh herbivores and carnivores are determined less by the quantity of food than by tidal inundation and the quality of food, which in turn is affected by tidal and groundwater salinities (Collins et al. 1986, Collins & Resh 1989). Carnivores, in contrast, appear to respond to food availability rather than to the physical extremes of the salt marsh environment.

ACKNOWLEDGMENT

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Scientific Note

ATYPICAL SEX ROLE BEHAVIOR IN THE BALL-ROLLING DUNG BEETLE, *CANTHON PILULARIUS* L. (COLEOPTERA: SCARABAEIDAE)

During July, 1990, I observed unusual feeding and reproductive behavior in the ball-rolling dung beetle, *Canthon pilularius* L. On three occasions, females engaged in what have been described as exclusively male behaviors for this species. These observations suggest that the behavioral roles of the sexes of this species may not always be clear-cut.

The feeding and reproductive behavior of this species, and of the Scarabaeinae in general, are described elsewhere (Matthews, E. G. 1963. *Psyche*, 70: 75–93; Halffter, G. & E. G. Matthews. 1966. *Folia Entomol. Mex.*, 12–14: 1–312; Halffter, G. & W. D. Edmonds. 1982. *Publ. Inst. Ecol., Mex. D.F.* 10). In all of these accounts, the male is reported to be the active partner in reproducing pairs; only males engaged in combat over possession of dung balls, and only males initiated formation of brood balls. I report females engaging in both of these activities at the Central Plains Experimental Range near Nunn, Colorado.

Groups of four and 12 beetles were maintained in 0.84 m² outdoor screen cages. The cages were open to the ground to allow normal ball-rolling and digging behavior, and the beetles were provided with a continuous supply of fresh cow dung. The sides of the cages restricted the distances that beetles could roll their dung balls, but this did not appear to affect their behavior in any other way. All individuals were marked with dots of paint to facilitate field identification without disturbance. I observed the beetles on 31 days at 1–4 day intervals throughout the summer of 1990.

On 11 Jul 1990, I observed a female cut and roll a dung ball that later became a brood ball. The cutting process lasted about 20 min, after which the female beetle continued to shape the ball, with occasional attempts at rolling it. Some difficulty was encountered in rolling due to a small stick and a maggot that protruded from the ball. More than 3 h after initiating ball formation, the female began rolling the ball, and 17 min later she began burying it. Six min later, when the ball was already partially buried, she was joined by a male beetle; the two immediately began rolling the ball as a pair, with the male rolling and the female riding atop the ball. After 32 min of rolling, they began burying the ball together. It is not certain that the female initially intended this ball to be a brood ball rather than a food ball, although the extraordinarily long time taken to create the ball is suggestive.

On two other occasions I observed female beetles engage in combat; in at least one of these the combat was initiated by the female. On 7 Jul 1990, when a pair was in the process of burying a brood ball with the male digging beneath the ball to bury it, and the female on top of the ball, another female approached. The two females grappled together, producing clearly audible scraping, while the male continued digging and standing beside the ball. After approximately 1 min, the

intruding female departed and the original pair continued to bury the brood ball. At no time did the male enter the combat, although he emerged from beneath the ball while the combat was still occurring.

The second instance was on 26 Jul 1990. A male was cutting and shaping a dung ball at the dung source when he was approached by a female. A brief fight ensued. Normally this would end quickly with pair-bond formation when the male recognized the sex of the opposing beetle. In this case, however, the fight ended with the female rolling the ball away by herself, the male remaining behind atop the dung pat. The female buried the ball 15 min later, and the male burrowed under the dung pat.

These observations, although anecdotal, indicate that the behavior of *C. pilularius* may be even more complex than has been reported. Previous accounts have shown that males will make a brood ball in the absence of females, apparently choosing the riskier investment in reproduction rather than the more certain feeding opportunity. My observation of a female making a brood ball suggests that females may follow the same strategy. The observations of females engaged in combat suggest that females will fight to defend their reproductive investment if a male is not present, and that females may choose to feed rather than reproduce by stealing a dung ball from a male rather than mating with him.

The unusual behaviors that I observed may be partly due to a more arid environment with shorter summers than those in which previous observations were made (e.g., Miller, A. 1954. *Am. J. Trop. Med. Hyg.*, 3: 372–389; Matthews 1963). The Nunn, Colorado observation site is a semiarid shortgrass prairie near the edge of the geographical range of *C. pilularius*; winters are long and cold, summers are dry and hot, and annual precipitation averages about 325 mm. Different climatic conditions may impose different behavioral strategies upon the beetles. Future observations on these beetles may reveal if the behaviors I observed are repeatable or if they were chance aberrances.

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David S. Guertin, *Department of Biology, Colorado State University, Fort Collins, Colorado 80523.*

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PROCEEDINGS OF THE PACIFIC COAST ENTOMOLOGICAL SOCIETY

FOUR HUNDRED AND FIFTY EIGHTH MEETING

The 458th meeting of the Pacific Coast Entomological Society was held on Friday, 15 Jan 1988, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The minutes of the 457th meeting were read by the recording secretary and accepted. Mr. Daniel Gross, membership chairman, proposed three new regular members and two new student members, who were accepted as members. Several guests were introduced: Laurie Swiadon, who recently received her masters from Hebrew University of Jerusalem, Dr. John E. Lattke of the University of Maracay, Venezuela, Mr. Albert Hom, David Zuckermann of the East Bay Regional Parks and Margaret Kelley of the Tilden Nature Center. Darryl Ubick announced the spider workshop would be postponed until February. Several notes were given. Kirby Brown presented three slides of insect art and artifacts from Hong Kong, China, Singapore and Thailand. The slides depicted stamps, coins, carvings and etchings. Dr. Ferguson presented a note on recovering a tagged monarch butterfly at an overwintering site in Mexico, 80 miles from Mexico City. It is the longest migrant ever recovered. It was tagged on the eastern shore of Georgia Bay in Canada. Contact Dr. Ferguson for detailed direction to the overwintering site. Mr. Kaplan announced that Gail Grodhaus of the State Department of Public Health passed away Christmas eve, 1987. The Gail Grodhaus Memorial Fund will be set up for chironomid study. For tax deductible contributions to the fund in memory of Gail Grodhaus, checks can be sent to the Chironomis Grodhaus Memorial Fund, % Dr. James Sublette, Life Science Building, University of Southern Colorado, 2200 Bonfort Blvd., Pueblo, Colorado 81000.

President Kaplan introduced the speaker for the evening, John Lane, Education Director of the Santa Cruz Museum. Mr. Lane presented an interesting lecture titled "Overwintering Monarch Butterflies in California: Past and Present." The monarch butterfly is the only insect that has a long distance, annual, two way migration. A survey of California overwintering sites of the monarch butterfly was given. Historical documentation was presented along with a summary of the natural history of the monarch and a list of the trees used for overwintering. The Natural Bridges State Park has from 40,000-50,000 butterflies overwintering and sometimes up to 200,000.

President Kaplan announced that the next meeting would be held on 19 Feb 1988 and the speaker would be Leslie Saul. The title of the talk will be "Insect Zoos and their role in Public Education." The meeting was adjourned at 9:30 PM and a social hour was held in the entomology department of the California Academy of Sciences. The following 43 persons were present: (27 members) P. H. Arnaud Jr., A. Balmy, L. G. Bezark, D. S. Brennan, T. S. Briggs, K. W. Brown, H. K. Court, K. Dabney, L. Dong, S. S. Ferguson, W. E. Ferguson, D. F. Gross, A. I. Kaplan, B. Keh, C. Y. Kitayama, V. F. Lee, P. A. Luft, S. S. Mead, J. A. Powell, E. S. Ross, L. S. Saul, W. E. Savary, H. I. Scudder, C. Y. Takahashi, J. E. Tobler I, D. Ubick, and M. L. Utheim; (16 guests) M. M. Arnaud, L. M. Bravo I. Brown, J. E. Court, P. R. Craig, M. Davies, T. W. Davies, L. V. Dubay, D. Hayward, A. Hom, M. Kelley, J. E. Lattke, W. C. Rauscher, L. Swiadon, B. Tobler, and D. Zuckermann.

FOUR HUNDRED AND FIFTY NINTH MEETING

The 459th meeting of the Pacific Coast Entomological Society was held on Friday, 19 Feb 1988, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The minutes of the 458th meeting were read by the recording secretary and accepted. Mr. Daniel Gross, membership chairman, proposed one new student member, three new regular members, who were accepted as members. Tom Briggs and Darrell Ubick are working to get threatened status for a species of phalangid at Edgewood Park whose habitat is the site of a proposed golf course. Dr. Edward Smith presented a note on new thysanuran drawings by Dr. Kukalova-Peck. Leslie Saul presented a note on several insects that have been used as ornamental jewelry.

President Kaplan introduced the speaker for the evening, Leslie Saul, Director of the Insect Zoo at the San Francisco Zoological Gardens. Ms. Saul presented a slide lecture titled "Insect Zoos and their Role in Public Education." Ms. Saul gave an informative talk on the scope and mission of the Insect Zoo's public education program and detailed the criteria for choosing insects for public exhibit. Methods of collecting, maintaining and transporting live insects for public exhibit were also illustrated.

President Kaplan announced that the next meeting would be held on 18 Mar 1988 and the speaker will be Dr. William Olkowski of the Bio-Integral Resource Center. The title of the talk will be "Recent Developments in Urban Integrated Pest Management." The meeting was adjourned at 9:30 PM in memory of Dr. Donald Denning, a world renowned authority on caddisflies. Dr. Denning died on 7 Feb 1988. A social hour was held in the entomology department of the California Academy of Sciences. The following 50 persons were present: (35 members) P. H. Arnaud Jr., B. T. Berke, L. G. Bezark, F. E. Cave, J. S. Chinn, J. R. Clopton, H. K. Court, T. D. Cuneo, D. K. Dabney, J. G. Edwards, R. Fall, S. V. Fend, N. E. Gershenz, D. F. Gross, J. E. Hafernik Jr., A. Hom, A. I. Kaplan, B. Keh, R. L. Langston, V. F. Lee, J. Leong, P. A. Luft, S. S. Mead, D. P. Pline, R. G. Robertson, L. S. Saul, W. E. Savary, H. I. Scudder, E. L. Smith, G. S. Spicer, R. E. Stecker, C. Y. Takahashi, D. Ubick, M. A. Wolf, and R. L. Zuparko; (15 guests) M. M. Arnaud, L. W. Berke, J. E. Court, P. R. Craig, M. Davies, T. W. Davies, T. Eager, P. Guard da Silva, K. Hobson, S. Kauffman, P. K. Kleintjes, G. Peterson, S. Renkes, J. Robertson, and L. Swiadon.

FOUR HUNDRED AND SIXTIETH MEETING

The 460th meeting of the Pacific Coast Entomological Society was held on Friday, 18 Mar 1988, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The minutes of the 459th meeting were read by recording secretary Leslie Saul and accepted. Mr. Daniel Gross, membership chairman, proposed one new student member, Mr. John W. Brown and two new regular members: Mr. James C. Milstead and Mr. John D. McCarty, who were accepted as members. Several announcements were made. Ben Keh announced that Dr. Y. Z. Erzinclioglu of the Department of Zoology, University of Cambridge will be giving a U.C. Berkeley departmental seminar titled "Application of Entomology to Forensic Sciences" on 18 Apr, in 101 Moffitt Hall at 4:00 PM. Bill Olkowski will have a poster display with handouts after the meeting. A memorial service was held for Dr. Donald Denning. President Kaplan announced that he was still seeking speakers for April and May and called for any speaker suggestions from the members. It was suggested that one evening could be devoted to member notes and exhibits.

President Kaplan introduced the speaker for the evening, Dr. William Olkowski, Technical Director of the Bio-Integral Resource Center in Berkeley. Dr. Olkowski gave an interesting lecture on "Recent Developments in Urban Integrated Pest Management." The Bio-Integral Resource Center publishes two journals: one for professionals, "The IPM Practitioner," and one for non-professionals, "Common Sense Quarterly." Dr. Olkowski outlined the principles of integrated pest management and the various approaches which can be used on shade trees, home vegetable gardens, structural and medical pest problems. He discussed several programs that BIRC had designed and mentioned several new techniques for monitoring, detection and control.

President Kaplan announced that the next meeting would be held on 15 Apr 1988. The meeting was adjourned at 9:20 PM. A social hour was held in the entomology department of the California Academy of Sciences. The following 36 persons were present: (24 members) P. H. Arnaud Jr., A. M. Balmy, L. G. Bezark, T. S. Briggs, P. Buickerood, R. Buickerood, J. S. Chinn, J. R. Clopton, D. K. Dabney, L. Davis, N. E. Gershenz, A. Hom, A. I. Kaplan, B. Keh, L. P. Kite, V. F. Lee, L. B. Mak, W. W. Pitcher, L. S. Saul, W. E. Savary, H. I. Scudder, M. M. Tierney, D. Ubick, and R. L. Zuparko; (12 guests) M. Anstett, M. M. Arnaud, M. Brennan, N. Brownfield, S. Chinn, M. Furey, S. V. Garity, M. Haines, C. Harvey, D. Mello, W. Olkowski, and W. C. Rauscher.

FOUR HUNDRED AND SIXTY FIRST MEETING

The 461st meeting of the Pacific Coast Entomological Society was held on Friday, 15 Apr 1988, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The minutes of the 460th meeting were read by recording secretary Leslie Saul and accepted. Mr. Daniel Gross, membership chairman, proposed one new student member, Mr. John K. Jackson and two new regular members: Mr. Don C. Force and Mr. Tony Harris, who were accepted as members. Several announcements were made. Leslie Saul announced that the Insect Zoo's Annual open house would be held on 12 Jun 1988. Alan Kaplan thanked Albert Hom for making arrangements for the speaker for April. He also thanked Pat Kite, Nancy Brownfield and Dr. Harvey Scudder for their suggestions for future speakers for PCES.

President Kaplan introduced the speaker for the evening, Dr. Fernando Agudelo Silva, Senior Researcher at BIOSYS, a Palo Alto firm. Dr. Silva's talk was titled "The Worm's Turn: Developing Nematodes for Insect Pest Management." Dr. Silva gave a very interesting talk on the methods used for mass culturing nematodes for use in biological control programs. These nematodes can be used to control borers in oak and fig trees, in the greenhouse, in cranberry bogs and in apple and almond orchards. In the future it may be possible to control cockroaches, black fly and fire ants. In 1979, the use of nematodes for control took a big leap when an artificial media was developed by Australian researchers. Infective stages are reared. These enter the host through the mouth, spiracles, anus, or through the integument. Once inside, a bacteria is released which quickly kills the insect host. The nematodes are nonpathogenic for people and nontarget organisms.

President Kaplan announced that the next meeting would be held on 20 May 1988. The meeting was adjourned at 9:20 PM. A social hour was held in the entomology department of the California Academy of Sciences. The following 22 persons were present: (17 members) P. H. Arnaud Jr., T. S. Briggs, P. Buickerood, R. Buickerood, L. Davis, W. A. Doolin, J. G. Edwards, A. Hom, A. I. Kaplan, L. P. Kite, V. F. Lee, G. J. Mallick, S. W. Miller, L. S. Saul, C. Y. Takahashi, D. Ubick, and R. L. Zuparko; (5 guests) F. Agudelo Silva, M. M. Arnaud, P. R. Craig, S. Pollitt, and W. C. Rauscher.

FOUR HUNDRED AND SIXTY SECOND MEETING

The 462nd meeting of the Pacific Coast Entomological Society convened 20 May 1988, at 8:10 PM, in the Morrison Auditorium of the California Academy of Sciences. PCES president Alan Kaplan presided. The minutes of the 461st meeting were read by Mr. Warren Savary and accepted as read. Mr. Daniel Gross, PCES membership chairman, proposed four individuals for student membership: Mr. Gordon C. Snelling, Ms. Danielle Jahnke, Ms. Robin Jean Rathman and Mr. Martin Melia; three individuals for regular membership: Dr. V. R. Vickery, Mr. John Steiner, Mr. Patrick R. Craig; and one individual for sponsoring membership: Ms. Nancy T. Brownfield. The proposal was seconded and these individuals were granted membership. Mr. Warren Savary announced that he had been asked by the San Francisco Beekeepers Association to make available a petition that proposed making the honey bee (*Apis mellifera*) the national insect. Mr. Alan Kaplan introduced the guest speaker of the evening, Mr. Glenn Conner of the Alameda County Mosquito Abatement District, who presented an informative lecture entitled "*Aedes albopictus*: Asian Tiger Mosquito, a New Threat to California's Health." Mr. Conner detailed the spread of this potential disease vector which apparently entered the United States at Memphis, Tennessee in 1983. By 1987, it had been reported from 77 counties in 17 states, and had reached California. This tree-hole breeding mosquito, which feeds aggressively throughout the day, has been shown to serve as vector of dengue fever. Although a lack of summer rains may serve as a barrier to its establishment in California, its potential transport in used tires suggests our need for continued vigilance. The meeting adjourned for refreshments at 9:45 PM. The following 27 persons were present: (23 members) P. H. Arnaud Jr., L. G. Bezark, T. S. Briggs, P. Buickerood, R. Buickerood, R. Fall, D. F. Gross, A. Hom, A. I. Kaplan, B. Keh, W. A. Maffei, G. J. Mallick, S. M. McIlraith, S. S. Mead, M. Melia, W. E. Savary, G. A. Sayre, H. I. Scudder, S. S. Shanks, R. E. Stecker, C. Y. Takahashi, D. Ubick, and T. J. Zavortink; (4 guests) M. M. Arnaud, G. E. Conner, W. C. Rauscher, and S. Renkes.

FOUR HUNDRED AND SIXTY THIRD MEETING

The 463rd meeting of the Pacific Coast Entomological Society was held on 16 Sep 1988, at 8:10 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The acting recording secretary read the minutes of the 462nd meeting. The minutes were approved as read. Five persons were proposed by Daniel Gross and elected as new regular members: Dr. Elizabeth A. Bernays, Dr. Ryutaro Iwata, Dr. Penelope F. Kukuk, Ms. Patricia F. Neyman, and Dr. Richard S. Zack. The following guests were introduced: Dr. Janice Edgerly-Rook and her husband, Edward; Dr. C. Riley Nelson, Tilton Fellow in the Department of Entomology, California Academy of Sciences; and Mrs. Heidi E. M. Dobson.

Mr. Warren Savary showed some slides showing the orientation of first instar larvae in several genera of vaejovid scorpions. Mr. Kaplan announced that some members from Chico will host a collecting trip in their local area for the June, 1989, annual meeting of the American Association for the Advancement of Science, Pacific Division, in Chico.

Mr. Kaplan introduced the featured speaker, Dr. Gordon Frankie, who spoke on "Lomas Barbudal: A New Biological Reserve in Costa Rica." Dr. Frankie, president of Friends of Lomas Barbudal, discussed the formation, goals and future plans for the Lomas Barbudal Reserva Biologica, a lowland dry forest. He compared the preserve with the well known wet forests of La Selva and Monteverde and showed that a dry forest can also harbor unique and distinct fauna and flora. He talked about fire as a major problem in Costa Rica, where introduced vegetation gets established after a fire outcompetes the native flora which is not adapted to it. He stressed the importance of educating local people about their native fauna and flora. He also stressed that it is important for them to get involved in conservation projects and decision making regarding the use of their land.

The meeting was adjourned and a social hour was held in the entomology department of the California Academy of Sciences. A total of 52 persons attended the meeting: (30 members) P. H. Arnaud Jr., T. S. Briggs, K. W. Brown, J. S. Chinn, J. S. Cope, K. Dabney, L. H. Davis, H. E. M. Dobson, J. G. Edwards, S. V. Fend, S. S. Ferguson, E. M. Fisher, G. W. Frankie, D. F. Gross, J. E. Hafernik, Jr., A. I. Kaplan, B. Keh, L. P. Kite, R. L. Langston, V. F. Lee, L. B. Mak, G. J. Mallick, M. Melia, N. D. Penny, L. Saul, W. E. Savary, H. I. Scudder, S. S. Shanks, M. M. Tierney, and D. Ubick; (22 guests) M. M. Arnaud, B. Atkinson, D. De Raue, R. W. Douglas, C. W. Fox, J. Edgerly-Rooks, M. Flexer, J. Frankie, J. B. Fraser, M. H. Fraser, M. Furey, J. Hirabayashi, R. Nelson, T. K. Ohsumi, R. A. Raguso, S. Renkes, N. Robinson, E. Rooks, D. Schmidt, P. Sullivan, and A. Zoidis.

FOUR HUNDRED AND SIXTY FOURTH MEETING

The 464th meeting of the Pacific Coast Entomological Society was held on Friday, 21 Oct 1988, at 8:10 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The acting recording secretary read the minutes of the 463rd meeting and they were accepted as read. Two new members were proposed and accepted. Several announcements were made. President Kaplan announced the possibility of having a joint meeting with AAAS and that Vincent Lee has suggested presenting papers; the deadline for the decision on participation is 15 Mar 1988. Mr. Kaplan also announced that a field day will be held in Chico, which will coincide with the June AAAS meeting. Vincent Lee described the Academy's new exhibit "Wild California" and urged all members to make plans to see it. The following guests were introduced: Nora Welk and Derham Giuliani. Mr. Giuliani has been donating specimens to the entomology department at the California Academy for many years. Edward Smith showed a paper wasp nest that he collected near his home. He noted that moths were beginning to emerge in great numbers. Larry Bezark announced that he had brought along some arthropod specimens which had been collected in Papua New Guinea by Larry Orsak. The specimens were available for examination during the social hour. Mr. Kaplan announced that he was preparing to call on members to serve on various committees for the upcoming year.

President Kaplan introduced the speaker for the evening, Mr. Patrick Craig, of Antioch West College in San Francisco, who presented a slide lecture on "Amber and its Inclusions." Mr. Craig began by discussing the different types of amber collected in various parts of the world. His talk focused on the amber mined in the Dominican Republic where amber is an important commodity. Mr. Craig discussed the mining process, how the amber is fashioned and marketed. He pointed out that scientific collectors could not financially compete with merchants that were willing to pay more than twenty thousand dollars for single pieces with large inclusions. He showed photographs of animals preserved in amber which included a fossilized slug, an entire gecko and a variety of arachnids, insects and other arthropods. He noted that animals preserved in amber retained their genetic material which could still be analyzed. He also noted that even though the arthropods in amber are mostly pre-Oligocene, they are for the most part indistinguishable from the species living today in the same type of habitat, indicating the stability of tropical ecosystems over time.

President Kaplan announced that the next speaker would be Dr. Vincent Resh of U. C. Berkeley who would speak on "Geothermal Development and Endangered Species." The meeting was adjourned at 9:20 PM and a social hour was held in the entomology department of the California Academy of Sciences. The following 60 persons were present: (38 members) P. H. Arnaud Jr., L. G. Bezark, T. S. Briggs, K. W. Brown, J. S. Chinn, J. R. Clopton, Patrick R. Craig, T. D. Cuneo, L. Dong, J. T. Doyen, B. Ehreth, S. S. Ferguson, W. E. Ferguson, C. W. Fox, D. F. Gross, D. R. Herlocker, A. Hom, P. S. Johnson, A. I. Kaplan, L. P. Kite, R. L. Langston, V. F. Lee, W. E. Maffei, L. B. Mak, G. J. Mallick, M. Melia, N. D. Penny, D. P. Pline, K. J. Ribardo, R. G. Robertson, W. E. Savary, H. I. Scudder, S.

S. Shanks, E. L. Smith, G. S. Spicer, C. Y. Takahashi, D. Ubick, and T. J. Zavortink; (22 guests) M. M. Arnaud, F. Baker, I. Baker, Y. Black, T. L. Davis IV, E. A. Doyen, D. Giuliani, B. Hall, B. I. Hiler, T. F. Hlavac, D. Maffei, D. L. Mead, C. R. Nelson, B. Ohlanul, J. Ohlanul, W. C. Rauscher, J. Ribardo, J. Robertson, L. S. Saul, M. A. Tenorio, R. Teys, and B. A. Wilson.

FOUR HUNDRED AND SIXTY FIFTH MEETING

The 465th meeting of the Pacific Coast Entomological Society was held on Friday, 18 Nov 1988, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The minutes of the 464th meeting were read and accepted by Leslie Saul, recording secretary. Mr. Daniel Gross proposed two new members, Bernice Demarce and C. Riley Nelson, and they were accepted as members. Several notes were given. Larry Bezark presented a note on rain beetles in the genus *Pleocomma* stating that there were 25 species found throughout California. Another note was presented on insect avoidance behavior in found in caribou where biting flies occur. It was determined that 7–50% of caribou time was spent in insect avoidance behavior depending on biting fly population density. Leslie Saul presented two slides of a species of Amblypigida from the Jimba Caves, Kilifi district of Kenya, Africa collected by Dr. Robert Drewes in May 1988. The first slide was of an adult female with 25–30 young on her back that hatched on 14 Nov 1988. The second slide was a close-up of a one week old juvenile that was 6 mm in length. A third slide was of an artistically decorated cockroach from a nonentomological conference to demonstrate the increasing public interest in entomology. President Kaplan announced that PCES will have a contributed paper session at the AAAS meeting to be held in Chico in June. Detail will be included in the January newsletter and AAAS newsletter. The Society of Vector Ecologists and the American Ecological Society will also be participating. Committee members were announced. Vannoy Davis will be a member of the audit committee; Stanley C. Williams, Larry Bezark, and Curtis Takahashi will be members of the nominating committee. The nominating committee will make their recommendations next meeting. Mr. Kaplan announced that PCES dues are due.

President Kaplan introduced the speaker for the evening, Dr. Vincent Resh of U. C. Berkeley, whose talk was titled "Hot Springs, Geothermal Development, and Rare and Endangered Species: The Search for the Wilbur Spring Shore Bug." Dr. Resh gave a brief history of geothermal energy in the west. Dr. Resh detailed the natural history of the hot springs-inhabiting shore bug, *Saldula usingeri* which was proposed for listing as an endangered species. Dr. Resh studied 119 springs discovering a range for this saldid from Glenn to Contra Costa County. *Saldula usingeri* was discovered to be sluggish, a behavioral advantage in hot spring habitats. It does not drink in highly mineralized springs but instead gets its water by feeding on an ephydrid which is a good osmoregulator. It is thought that spider predation keeps the shore bug from some habitats that it could otherwise occupy. Because of its wide distribution, the Wilbur Springs Shore Bug was not listed as an endangered species.

President Kaplan announced that the next meeting would be held on 16 Dec 1988 and the speaker would be Alan Kaplan. The title of the talk will be "Insects in the News." The meeting was adjourned at 9:35 PM and a social hour was held in the entomology department of the California Academy of Sciences. A total of 46 persons attended the meeting: (35 members) P. H. Arnaud Jr., L. G. Bezark, T. S. Briggs, J. Burberry, J. R. Clopton, S. V. Fend, W. E. Ferguson, S. S. Ferguson, C. W. Fox, N. E. Gershenz, D. F. Gross, D. A. Jensen, P. S. Johnson, A. I. Kaplan, L. P. Kite, R. L. Langston, V. F. Lee, G. J. Mallick, S. S. Mead, M. Melia, C. R. Nelson, N. D. Penny, D. P. Pline, V. H. Resh, K. J. Ribardo, L. S. Saul, W. E. Savary, S. S. Shanks, W. D. Shepard, R. E. Stecker, C. Takahashi, M. M. Tierney, D. Ubick, T. J. Zavortink, R. L. Zuparko, and one unreadable; (11 guests) M. Arnaud, W. Cole, G. T. Coppe, B. I. Hiller, D. Mead, A. M. L. Penny, S. Renkes, J. M. Ribardo, L. Saul, S. M. Villegas, and A. Zoidis.

FOUR HUNDRED AND SIXTY SIXTH MEETING

The 466th meeting of the Pacific Coast Entomological Society was held on Friday, 16 Dec 1988, at 8:20 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Alan I. Kaplan presiding. The minutes of the 465th meeting were read by recording secretary Leslie Saul and accepted. Membership chairman Mr. Daniel Gross proposed two new student members, Mr. Erik Johanson and Noel Caroline, and two new regular members, Mr. Scott Beckman and Ms.

Irene Terry, who were accepted as members. Several announcements were made. Daniel Gross announced that old schmidt boxes were available in the entomology department for a nominal donation. A request was made for increased support of the refreshment committee. Larry Bezark announced that Cornell press was offering a 20% book discount for a limited time. Two notes were given. Wesley Maffei showed SEM slides of *Morpho* butterfly scales and discussed the possibility of their use taxonomically. Slides of *Morpho cypris*, *M. aega*, *M. deidamia*, *M. achilles*, *M. godarti*, *M. menelaus*, *M. didius* and *M. amathonte* were shown. Larry Bezark made two literary presentations: one covering a robbery by men armed with a cicada; and another about a mouse-eating locust from 1915. President Kaplan called for the annual committee reports. Membership chairman Daniel Gross reported that in 1988, 40 new members were admitted: 25 regular, 14 student and 1 sponsoring, bringing the total number of members to 467. Dr. Paul Arnaud gave the Treasurer's report for Dr. W. Pulawski. He reported that the Society's income was \$28,880, expenses were \$22,968, resulting in a balance of \$5,912. A thank you was extended to H. Vannoy Davis for his services on the auditing committee. The Auditing Committee reported that all was in order and that a statement will be published in the Annual Report. Dr. Paul Arnaud reported for the Historical Committee that the reorganization of the archives has been completed with 161 archive boxes. A special thanks was extended to Madeline Arnaud for her help with the archival material. Vincent Lee announced that the Society receives 63 serials from 51 institutions as exchanges. There have been six new exchanges this year. The Publications Committee reported that the Society will be returning to Allen Press after the 3rd issue which should be ready this week. Dr. Stanley Williams reported nominations for next year for the Nominating Committee: President 1989, Dr. Thomas Zavortink; President-elect 1990, Dr. Robert Dowell; Treasurer, Dr. W. Pulawski; Managing Secretary, Vincent Lee; and Recording Secretary, Leslie Saul.

Dr. Thomas Zavortink took charge of the meeting and introduced the speaker for the evening, current President of the Society Alan Kaplan. Mr. Kaplan, who received his Masters from U. C. Berkeley, is Naturalist at the Tilden Nature Center of the East Bay Regional Parks. President Kaplan gave an entertaining and informative talk titled "Insects and Entomologists in the media." Mr. Kaplan presented a synthesis of entomology through the ages which was well researched. He also summarized public attitude changes through time giving a survey of insect images in films.

The meeting was adjourned at 9:25 PM. A social hour was held in the entomology department of the California Academy of Sciences. The following 42 persons were present: (29 members) P. H. Arnaud Jr., L. G. Bezark, T. S. Briggs, K. W. Brown, P. Buickerood, J. S. Chinn, H. K. Court, J. G. Edwards, S. V. Fend, N. E. Gershenz, D. F. Gross, K. S. Hagen, P. S. Johnson, A. I. Kaplan, B. Keh, V. F. Lee, W. A. Maffei, L. B. Mak, C. R. Nelson, N. D. Penny, K. J. Ribardo, R. G. Robertson, L. S. Saul, W. E. Savary, S. S. Shanks, C. Y. Takahashi, D. Ubick, S. C. Williams, and T. J. Zavortink; (13 guests) M. M. Arnaud, K. Blakwell, R. Buickerood, J. E. Court, D. W. Fletcher, M. Furey, M. Hagen, A. M. L. Penny, W. C. Rauscher, S. Renkes, J. M. Ribardo, J. Robertson, and S. M. Villegas.

FOUR HUNDRED AND SIXTY SEVENTH MEETING

The 467th meeting of the Pacific Coast Entomological Society was held on 20 Jan 1989, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, president Thomas Zavortink presiding. The minutes of the 466th meeting were read by Leslie Saul, recording secretary, and accepted. Membership chairman Daniel Gross proposed four new members which were accepted: Mr. Donald Barwell, Mr. Randall Ridley, Dr. Richard Mason and Mr. Bruce Tilden. Several announcements were made. PCES will participate in a contributed paper session at the AAAS Pacific Division meeting being held in Chico, 11-15 Jun 1989. Rewards for student papers are being offered. A Program Committee was formed. Dr. John Hafernik was appointed as chairman and Dr. Jerry Powell will serve on the committee. Vincent Lee announced that money can be donated and designated specifically to the entomology department of the California Academy of Sciences. Daniel Gross will be retiring from the refreshment committee. Dr. J. W. Tilden passed away 30 Dec 1988, at the age of 83. His specialty was nymphalid butterflies. He was the author of the books "A Field Guide to Western Butterflies" and "California Butterflies." Ben Keh showed slides of the Penang Butterfly House and described its operation.

President Zavortink introduced the speaker for the evening, Dr. Robbin Thorp, professor of Entomology at U. C. Davis. Dr. Thorpe gave an interesting slide lecture titled "Australian Bees and Scenes," on his research trips to Australia covering several visits there to study the impact of the introduced honey bee on native bees and flora there.

Dr. Zavortink announced that the next meeting would be held on 17 Feb 1989 and the speaker would be Dr. C. Riley Nelson speaking on "Winter Stoneflies in California." The meeting was adjourned at 9:45 PM and a social hour was held in the entomology department of the California Academy of Sciences. The following 44 persons were present: (31 members) P. H. Arnaud Jr., F. L. Blanc, T. S. Briggs, K. W. Brown, J. S. Chinn, K. Dabney, J. G. Edwards, E. M. Fisher, D. F. Gross, A. Hom, B. Keh, R. L. Langston, V. F. Lee, M. Melia, N. D. Penny, D. P. Pline, K. J. Ribardo, R. G. Robertson, E. S. Ross, L. S. Saul, W. E. Savary, H. I. Scudder, S. S. Shanks, J. A. Skinner, J. T. Sorensen, R. E. Stecker, C. Y. Takahashi, R. W. Thorp, D. Ubick, S. P. Welles Jr., and T. J. Zavortink; (13 guests) M. M. Arnaud, F. Blanc, L. M. Bravo, L. V. Dubay, A. M. L. Penny, W. C. Rauscher, J. M. Ribardo, J. Robertson, C. Thorp, J. Thorp, P. Thorp, S. M. Villegas, D. Welles, and P. Welles.

FOUR HUNDRED AND SIXTY EIGHTH MEETING

The 468th meeting of the Pacific Coast Entomological Society was held on 17 Feb 1989, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Thomas Zavortink presiding. The minutes of the 467th meeting were read by Leslie Saul, recording secretary, and accepted. Membership chairman Daniel Gross proposed one student member, Mr. Lee H. Simons, and one sponsoring member, Mr. Pat Sullivan, which were accepted. Several announcements were made. Daniel Gross will be retiring from the refreshment committee. A worthy replacement is still being sought. All members are encouraged to volunteer. Dr. Ross introduced guests Gene Hall and Dr. George Ball. Leslie Saul announced that the Insect Zoo's tenth anniversary celebration would be coming up in June. All PCES members are invited to contribute any ideas for this event.

President Zavortink introduced the speaker for the evening, Dr. C. Riley Nelson, current Tilden Fellow in the Department of Entomology at the California Academy of Sciences. Dr. Nelson gave an informative talk titled "Winter Stoneflies in California." Dr. Nelson began with an introduction and overview of early work on Plecoptera with an emphasis on the genus *Capnia*. He noted that there were 55 species found in North America exhibiting a high degree of endemism. Several habitats were discussed including the Feather River, Navarro River, Alder Creek, Long Valley Creek, Lake Tahoe, Dolores River and Lone Pine Creek. *Capnia licustra* from Lake Tahoe was noted to be aquatic in the adult stage and found at depths of 300 ft.

Dr. Zavortink announced that the next meeting would be held on 17 Mar 1989 and the speaker would be Dr. Edward Ross. The meeting was adjourned at 9:30 PM and a social hour was held in the entomology department of the California Academy of Sciences. A total of 47 persons attended the meeting: (26 members) L. G. Bezark, R. L. Bottoroff, P. Buickerood, J. S. Chinn, H. K. Court, T. D. Cuneo, J. G. Edwards, S. V. Fend, W. E. Ferguson, S. S. Ferguson, D. F. Gross, P. Johnson, D. H. Kavanaugh, B. Keh, G. Mallick, C. R. Nelson, N. D. Penny, W. W. Pitcher, K. J. Ribardo, R. G. Robertson, L. S. Saul, S. S. Shanks, W. D. Shepard, G. C. Snelling, C. Takahashi, and T. J. Zavortink; (21 guests) G. E. Ball, R. Buickerood, J. E. Court, M. Duffy, M. Gardner, T. Glenn, C. Greene, W. E. Hall, B. A. Knight, A. W. Knight, M. Monsees, A. M. L. Penny, P. Pitcher, S. Renkes, J. M. Ribardo, J. Robertson, D. Sipes, L. Snelling, J. Snelling, V. Snelling, and S. Wright.

FOUR HUNDRED AND SIXTY NINTH MEETING

The 469th meeting of the Pacific Coast Entomological Society was held on 17 Mar 1989, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Thomas Zavortink presiding. The minutes of the 468th meeting were read by Leslie Saul, recording secretary, and accepted. Membership chairman Daniel Gross proposed one student member, Mr. Alvin Glot, and two regular members, Dr. Susan B. Halbert and Dr. Robert S. Martin, which were accepted. Several announcements were made. PCES is still seeking a refreshment committee. Contributing papers for the AAAS meeting in Chico must be received by 31 Mar 1989. Student awards will be presented. Journal Volume 64 number is at A-R Editions and number 1 and 2 of volume 65 have been approved for publication. Daniel Gross gave a short slide presentation on insects of prehistoric nature and their extinction and survival, based upon a new exhibit at the Academy.

President Zavortink introduced the speaker for the evening, Dr. Edward Ross, who gave a slide lecture titled "Recent Entomological Experiences in Mexico." Dr. Ross gave a well illustrated lecture which focused on the embiids and various trips to Baja California spanning from 1931 to a recent

adventure along the same route. He also discussed witnessing the monarch butterfly overwintering sites in Mexico and mentioned Dr. Lincoln Brower's conservation efforts there. Unique arthropods, trees and angiosperms encountered were presented.

Dr. Zavortink announced that the next meeting would be held on 21 April and the speaker would be Dr. Robert Dowell. His talk will be titled "Evolution of the Host Range of the Citrus Blackfly." The meeting was adjourned at 10:00 PM and a social hour was held in the entomology department of the California Academy of Sciences. A total of 60 persons attended the meeting: (31 members) P. H. Arnaud Jr., B. T. Berke, F. L. Blanc, T. S. Briggs, K. W. Brown, D. J. Burdick, D. K. Dabney, L. H. Davis, J. Chinn, J. R. Clopton, J. G. Edwards, W. E. Ferguson, S. S. Ferguson, D. F. Gross, L. P. Kite, V. F. Lee, W. Maffei, J. D. McCarty, S. Mead, C. R. Nelson, W. W. Pitcher, K. J. Ribardo, R. G. Robertson, E. S. Ross, W. E. Savary, L. E. Serpa, W. D. Shepard, C. Takahashi, M. M. Tierney, J. E. Tobler I, D. Ubick, and T. J. Zavortink; (29 guests) M. Arnaud, K. Attipaid, F. Blanc, Y. Burgess, L. Disterheft, J. Edwards, T. Glenn, E. A. Goff, K. Haires, D. Holth, K. Hom, J. Johnnton, R. Kolesen, D. Maffei, D. Mead, M. Mistry, P. Pitcher, W. Rauscher, J. Ribardo, J. Robertson, N. Solberg, Ca. Tobler, Ch. Tobler, N. Tobler, A. Tung, S. Villegas, and three unreadable.

FOUR HUNDRED AND SEVENTIETH MEETING

The 470th meeting of the Pacific Coast Entomological Society was held on 21 Apr 1989, at 8:10 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Thomas Zavortink presiding. The minutes of the 469th meeting were read, corrected and accepted. One new member was proposed, David C. Taylor, and accepted. Several announcements were made. Five abstracts were submitted for presentation at the AAAS meeting to be held on 11 Jun 1989. A refreshment chairman is needed to provide refreshments for the social hour after the meetings. The program committee would welcome suggestions for speakers for upcoming meetings. Howell Daly would like to step down as publication chairman of *The Pan-Pacific Entomologist*. Leslie Saul announced that the zoo keeper association will be sponsoring a Bowl-A-Thon on 13 May 1989 at Rock and Bowl and the proceeds will go to benefit habitat protection in Guanacaste National Park in Costa Rica.

President Zavortink introduced the speaker for the evening, Dr. Robert Dowell of the California Department of Food and Agriculture and president-elect of PCES, who gave an interesting talk titled "Evolution and Host Range of the Citrus Black Fly." The citrus black fly is a whitefly in the Aleyrodidae family, that is now found in Africa, the Caribbean, Mexico and Florida. It originated in Malaya where citrus was the only host. This whitefly was first found in on Key West, Florida, in 1934 was eradicated using fish oil spray. It reappeared in 1976 in Broward County Florida and eradication with sprays failed. Two parasitic wasps were released reducing populations by over 95%. The pest is polyphagous, feeding on 48 genera of plants and 35 different families. Dr. Dowell presented a detailed description of the citrus black fly's life history, morphology, oviposition behavior, dispersal behavior and foodplant preference. Oviposition preference was studied and it was found that kumquat, mango and pink trumpet were as attractive as citrus. Dr. Dowell also discussed the spread of this insect and its correlation with the spread of different horticultural plants.

The meeting was adjourned at 9:35 PM and a social hour was held in the entomology department of the California Academy of Sciences. The following 22 persons were present: (19 members) P. H. Arnaud Jr., T. S. Briggs, W. A. Doolin, R. V. Dowell, J. G. Edwards, A. Hom, P. S. Johnson, R. L. Langston, V. F. Lee, W. A. Maffei, G. J. Mallick, C. R. Nelson, K. J. Ribardo, L. S. Saul, W. E. Savary, S. S. Shanks, C. Y. Takahashi, S. P. Welles, and T. J. Zavortink; (3 guests) D. Maffei, W. C. Rauscher, and J. M. Ribardo.

FOUR HUNDRED AND SEVENTY FIRST MEETING

The 471st meeting of the Pacific Coast Entomological Society was held on 19 May 1989, at 8:00 PM, in Morrison Auditorium of the California Academy of Sciences, San Francisco, with president Thomas Zavortink presiding. The minutes of the 470th meeting were read by recording secretary Leslie Saul, and accepted. Seven new regular members and one new student member were proposed by Daniel Gross and elected: Russell C. Bingham, Dr. Lloyd M. Dossdall, Dr. Boris C. Kondratieff, Dr. Robert E. Page Jr., Dr. Michael Pitcairn, James E. Wappes, Ms. Carrie J. S. Wong, as regular members, and Mr. Dean F. Messer, as a student member.

Several announcements were made. Mr. Warren Savary announced that seven papers were to be presented at the upcoming AAAS meeting. The Western Apiculturist Society will be meeting on the week of 10 Jun 1989 at San Francisco State University and a short course on starting an apiary will be given. Leslie Saul announced that the Insect Zoo's tenth annual open house will be held on 10–11 June 1989. James Toburn of Santa Rosa has back issues of the journal which will be sold individually or as a set for \$85.00. There is a new printing of *A Glossary of Entomology* by J. R. de La Torre-Bueno, which will be available at pre-publication price of \$35.00; the publication date is 1 Jun 1989; it will include an entomological spelling checker. Copies of the order forms will be available in the entomology department of the Academy. Dr. Thomas Zavortink announced that Volume 65, issue 1 should be arriving soon. Dr. Edward Ross introduced two guests, Dr. P. Jolivet, a chrysomelid expert, and J. Segress. Dr. Zavortink introduced the speaker for the evening, Dr. Kirby Brown of the San Joaquin County Department of Food and Agriculture. His talk was titled "Gold Bugs and other Numismatic Insects." Dr. Brown gave an informative talk on the field of insect coins. There are over 2500–3000 different types of coins that depict insects or bee hives. The first coins date back to 650 BC. Dr. Brown showed a series of slides of various coins depicting insects from his collection and studies from such places as Italy, Papua New Guinea, Panama, Tonga and Utah. Bees were the insect most often represented.

The meeting was adjourned at 9:40 PM and a social hour was held in the entomology department of the California Academy of Sciences. The following 35 persons were present: (23 members) P. H. Arnaud Jr., K. W. Brown, J. S. Chinn, H. K. Court, J. G. Edwards, A. Hom, A. S. Hunter, B. Keh, R. L. Langston, V. F. Lee, W. A. Maffei, G. J. Mallick, M. Melia, N. D. Penny, K. J. Ribardo, R. G. Robertson, L. S. Saul, W. E. Savary, R. E. Stecker, C. Y. Takahashi, J. E. Tobler, C. J. S. Wong, and T. J. Zavortink; (12 guests) M. M. Arnaud, J. E. Court, E. A. Goff, P. Jolivet, D. Maffei, D. S. Mayuoba, A. M. Penny, J. M. Ribardo, J. Robertson, J. Segress, S. Villegas, and one illegible signature.

FOUR HUNDRED AND SEVENTY SECOND MEETING

The 472nd Meeting of the Pacific Coast Entomological Society was held 17 Nov 1989, in the Goethe Room of the California Academy of Sciences with president Dr. Thomas Zavortink presiding. The meeting was called to order at 8:00 PM. Minutes of the 471st meeting were read, corrected and accepted. Four new regular members and one new student member were proposed and accepted.

The October 1989 meeting of the Pacific Coast Entomological Society meeting was cancelled due to the October 17th earthquake in San Francisco.

President Zavortink made several announcements. Dr. Zavortink read a letter from Howell Daly stating that Dr. John Sorensen will assume the duties of Editor of *The Pan-Pacific Entomologist*. A special thanks was extended to Dr. Chemsak for his effort to bring the journal, *The Pan-Pacific Entomologist*, up to date. The publication is now back with Allen Press because of their ability to produce a higher quality product. Thanks were also extended to Ken Cooper, Paul Arnaud and Wojciech Pulawski. The auditing committee members now include Helen Court, Vannoy Davis, chairman of the committee and Dr. Paul Arnaud. The publication committee needs one additional member. The nominating committee includes Ron Stecker. Patty Pratt announced that five of her sculptural works dealing with insects will be on display at the Insect Zoo through 15 Dec 1989. Leslie Saul announced that Dr. Robert Pyle, compiler of the IUCN Invertebrate Red Data Book, will give a lecture on "The Conservation of Monarch Butterflies" on 25 Jan 1990, in Morrison Auditorium at the California Academy of Sciences. Dr. Edward Smith described the exciting development of the new "Life through Time" exhibit at the California Academy of Sciences. The exhibit is scheduled to open in April. Dr. Scudder announced that 50% of the insect paleontology group in the U.S. is retired, but still going strong. Two volumes of "Genera of Fossil Insects" by Frank M. Carpenter from Harvard are being published. Dr. Edward Smith announced that Dr. Alex Rasnitsen, foremost specialist on fossil insects in the world, will be at the Academy in January. Wes Maffei and his wife have generously offered to serve on the refreshments committee for one year. There will be a meeting of the executive board of PCES on 15 Dec 1989. A notice will be sent. A special dedication for the R. L. Usinger Rare Book Collection in the Entomology Library will be held on 15 Dec 1989, at 7:00 PM in the Department of Entomology of the California Academy of Sciences. An invitation will appear in Bits & PCES. Debra Meed, a graduate student at San Francisco State University working on *Hygrotis*, was introduced. Charles Franklin, a graduate student at San Jose State University, was introduced.

Dr. Edward Smith gave a note describing the unusual life history of the primitive sawfly, *Cimbex americana*. It squirts fluid from pores above its spiracles. A large infestation was found on *Zorea americana* (Caprifoliacea). Slides picturing oviposition were shown. Eggs are laid in the leaf margin. After the first feeding, the larvae turn green and retain that color. The first instar have a waxy bloom; late instar larvae do not.

Dr. Zavortink introduced the speaker for the evening, Dr. Philip Ward from the Department of Entomology at U.C. Davis. His talk was titled "Ants in Plants." Dr. Ward discussed the debate about the origin and evolution of the interactions between ants and plants. Different associations between ants and plants were outlined: casual visitation to plants, detrimental to plant, beneficial to plant, and co-evolved mutualism. Plants with domatiums and their ant associates were discussed in detail. Fifty representative taxa were subjected to phylogenetic analysis and a consensus tree was drawn which suggested that these associations evolved a number of different times, perhaps 12 times. The ecology of various relationships was described.

The meeting was adjourned at 9:35 PM. Refreshment were served in the entomology department. A total of 45 persons attended: (32 members) P. H. Arnaud Jr., T. S. Briggs, R. Buickerood, P. Buickerood, J. S. Chinn, D. K. Dabney, S. S. Ferguson, W. E. Ferguson, C. W. Fox, D. F. Gross, P. S. Johnson, D. Kavanaugh, V. F. Lee, W. E. Maffei, L. B. Mak, G. J. Mallick, D. L. Mead, N. D. Penny, W. W. Pitcher, R. G. Robertson, L. S. Saul, W. E. Savary, H. I. Scudder, S. S. Shanks, E. L. Smith, G. S. Spreer, R. E. Stecker, C. Y. Takahashi, P. Welles, S. C. Williams, and T. J. Zavortink; (13 guests) M. M. Arnaud, V. M. Barlow, C. D. Franklin, C. Greene, S. Haughes, L. Hiugich, D. Maffei, M. Marcus, J. Osman, P. Pratt, W. Rauscher, A. A. Roberts, and P. Ward.

FOUR HUNDRED AND SEVENTY THIRD MEETING

The 473rd meeting of the Pacific Coast Entomological Society was held 15 Dec 1989 in the Goethe Room of the California Academy of Sciences at 8:10 PM with president Dr. Thomas Zavortink presiding. The minutes of the 472nd meeting were read, corrected and accepted. Two new candidates were proposed by Daniel Gross, chairman of the membership committee, and elected as new members: Mr. Charles Franklin, graduate student at San Jose State University, was elected as a new student member, and Mr. Gregory S. Sautter of Mishawaka, Indiana, was elected as a new regular member.

Several announcements were made. Vincent Lee turned in his letter of resignation as managing secretary of the Society to be effective 1 Jan 1991. Robin Thorpe will assume the position of chairman of the publications committee effective in January, 1990. Dr. Stanley Williams will join that committee. There were 1400 oral presentations made at the San Antonio meetings of the Entomological Society of America. The 1990 meetings of the ESA will be held in New Orleans, and the 1991 meetings will be held in Reno. Dr. Zavortink extended his thanks to everyone for their support during the year of his presidency. He announced that a PCES Board meeting was held on 15 Dec 1989 at 3:00 and summarized the meeting as follows. There was a discussion of the Society's financial situation. Data will be collected from other organizations on their dues and subscription rates. Dues were raised to \$20.00 for regular members, \$30.00 for subscribing members, \$40.00 for sponsoring members, \$21.00 for family members, \$10.00 for student members, and \$10.00 for retired members. The expenditure of money to defray speakers travel costs to AAAS meeting symposium was discussed. The production and mailing costs of Bits & PCES were also discussed.

Dr. Zavortink called for annual reports from the various committees. Daniel Gross, chair of the membership committee reported that in 1989 the membership remained fairly stable. Twenty-five new members were added (19 regular, 5 student and 1 sponsoring). In the past five years this was the lowest number to apply. There were a total of 448 members in 1989: 352 regular members, 55 student members, and 41 sponsoring members. Under the chairmanship of H. Vannoy Davis, Helen Court reported that the audit committee reports that everything is in order. The full report will be published in the proceedings. Lester Ehler and Ron Stecker asked Zavortink to report that the nominating committee proposed the following slate of candidates for office in 1990: Robert Dowell as president, Leslie Saul as president-elect, Sandra Shanks as treasurer, Leslie Saul as recording secretary, and Vincent Lee as managing secretary.

The gavel was passed to president-elect Dr. Dowell. Dr. Dowell introduced Dr. Tom Zavortink, of the University of San Francisco, who presented the presidential address. Dr. Zavortink presented an excellent and informative talk on "The Biology of Mosquitos." He related that there are 3146 species in the world, 167 species in North America and 47 species in California representing 38 genera.

The classification is conservative. The majority of the species fall into three genera: 379 in *Anopheles*, 946 in *Aedes* and 767 in *Culex*. The morphological differences between the three main genera were described. The largest mosquito in the world is in the genus *Toxerinchides*. This beautiful mosquito is incapable of penetrating the skin and only sucks nectar. The biology of several groups was discussed in detail focusing on oviposition behavior. Dr. Zavortink closed his lecture with a discussion of the difficulties with drawing phylogenetic trees for mosquitos considering all stages. Dr. Dowell announced the upcoming lecture in January "Grape Phylloxera in California: No Sex in the Vineyard" by Dr. Jeffrey Granett. The meeting was adjourned at 9:45 PM. The following 42 persons were present: (35 members) P. H. Arnaud Jr., L. G. Bezark, T. S. Briggs, P. Buickerood, R. Buickerood, J. S. Chinn, H. K. Court, L. Dong, R. V. Dowell, J. G. Edwards, R. Fall, D. W. Gray, D. F. Gross, J. E. Hafernik Jr., A. Hom, B. Keh, R. L. Langston, V. F. Lee, P. A. Luft, W. A. Maffei, L. B. Mak, D. L. Mead, S. S. Mead, N. D. Penny, K. J. Ribardo, R. G. Robertson, L. S. Saul, W. E. Savary, J. T. Sorensen, P. H. Sullivan, C. Y. Takahashi, D. Ubick, S. C. Williams, B. A. Wilson, and T. J. Zavortink; (7 guests) M. M. Arnaud, J. E. Court, C. D. Franklin, D. Maffei, A. M. L. Penny, W. C. Rauscher, and J. M. Ribardo.

ANNOUNCEMENT

Beginning with the July, 1990, issue of the Pan-Pacific Entomologist, the Pacific Coast Entomological Society began sending membership/subscription renewal notices for the following year with its July (number 3) issue. Please check the July issue of the journal for these renewal notices before discarding its shipping wrapper. Only a final subscription notice will be sent, if PCES does not receive a response to the July issue's enclosure.

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PAN-PACIFIC ENTOMOLOGIST
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See volume 66 (1): 1–8, January 1990, for detailed format information and the issues thereafter for examples. Manuscripts must be in English, but foreign language summaries are permitted. Manuscripts not meeting the format guidelines may be returned. Please maintain a copy of the article on a word-processor because revisions are usually necessary before acceptance, pending review and copy-editing.

Format. — Type manuscripts in a legible serif font IN DOUBLE OR TRIPLE SPACE with 1.5 in margins on one side of 8.5 × 11 in, nonerasable, high quality paper. THREE (3) COPIES of each manuscript must be submitted, EACH INCLUDING REDUCTIONS OF ANY FIGURES TO THE 8.5 × 11 IN PAGE. Number pages as: title page (page 1), abstract and key words page (page 2), text pages (pages 3+), acknowledgment page, literature cited pages, footnote page, tables, figure caption page; place original figures last. List the corresponding author's name, address including ZIP code, and phone number on the title page in the upper right corner. The title must include the taxon's designation, where appropriate, as: (Order: Family). The ABSTRACT must not exceed 250 words; use five to seven words or concise phrases as KEY WORDS. Number FOOTNOTES sequentially and list on a separate page.

Text. — Demarcate MAJOR HEADINGS as centered headings and MINOR HEADINGS as left indented paragraphs with lead phrases underlined and followed by a period and two hypens. CITATION FORMATS are: Coswell (1986), (Asher 1987a, Franks & Ebbett 1988, Dorly et al. 1989), (Burton in press) and (R. F. Tray, personal communication). For multiple papers by the same author use: (Weber 1932, 1936, 1941; Sebb 1950, 1952). For more detailed reference use: (Smith 1983: 149–153, Price 1985: fig. 7a, Nothwith 1987: table 3).

Taxonomy. — Systematics manuscripts have special requirements outlined in volume 66 (1): 1–8, including SEPARATE PARAGRAPHS FOR DIAGNOSES, TYPES AND MATERIAL EXAMINED (INCLUDING A SPECIFIC FORMAT), and a specific order for paragraphs in descriptions. See: Johnson, K. (1990. Pan-Pacif. Entomol., 66[2]: 97–125) for an example of format style and order for taxonomic descriptions, or contact the editor. List the unabbreviated taxonomic author of each species after its first mention.

Literature Cited. — Format examples are:

- Anderson, T. W. 1984. An introduction to multivariate statistical analysis (2nd ed). John Wiley & Sons, New York.
- Blackman, R. L., P. A. Brown & V. F. Eastop. 1987. Problems in pest aphid taxonomy: can chromosomes plus morphometrics provide some answers? pp. 233–238. In Holman, J., J. Pelikan, A. G. F. Dixon & L. Weismann (eds.). Population structure, genetics and taxonomy of aphids and Thysanoptera. Proc. international symposium held at Smolenice Czechoslovakia, Sept. 9–14, 1985. SPB Academic Publishing, The Hague, The Netherlands.
- 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 67

April 1991

Number 2

Contents

CHAPCO, W. & P. W. RIEGERT—Maternal effects and egg hatchability in <i>Melanoplus</i> (Orthoptera: Acrididae)	81
GOEDEN, R. D. & D. H. HEADRICK—Life history and descriptions of immature stages of <i>Tephritis baccharis</i> (Coquillett) on <i>Baccharis salicifolia</i> (Ruis & Pavon) Persoon in southern California (Diptera: Tephritidae)	86
DAANE, K. M., M. S. BARZMAN, C. E. KENNETT & L. E. CALTAGIRONE—Parasitoids of black scale in California: establishment of <i>Prococophagus probus</i> Annecke & Mynhardt and <i>Coccophagus rusti</i> Compere (Hymenoptera: Aphelinidae) in olive orchards ..	99
BROWN, R. L. & J. A. POWELL—Description of a new species of <i>Epiblema</i> (Lepidoptera: Tortricidae: Olethreutinae) from coastal redwood forests in California with an analysis of the forewing pattern	107
GRISWOLD, T. E.—A review of the genus <i>Microthurge</i> (Hymenoptera: Megachilidae)	115
POLHEMUS, J. T.—A new and primitive genus of Cryphocricinae (Heteroptera: Naucoridae)	119
WELCH, J. L. & B. C. KONDRATIEFF—The Mydidae (Diptera) of Costa Rica	124
BARRENTINE, C. D.—Post-egestive survival of <i>Sphenophorus phoeniciensis</i> Chittenden (Coleoptera: Curculionidae) egested by western toads	135
BALLING, S. S. & V. H. RESH—Seasonal patterns in a San Francisco bay, California, salt marsh arthropod community	138
SCIENTIFIC NOTE	
GUERTIN, D. S.—Atypical sex role behavior in the ball-rolling dung beetle, <i>Canthon pilularius</i> L. (Coleoptera: Scarabaeidae)	145
Pacific Coast Entomological Society, Proceeding for 1988	147
Announcement—notification of subscription renewals	157
Announcement—publications of the Pacific Coast Entomological Society	158

The
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THE ACANTHOSOMATIDAE (HETEROPTERA) OF NORTH AMERICA

DONALD B. THOMAS

U.S. Department of Agriculture, Agricultural Research Service,
Screwworm Research Laboratory,
Apartado Postal 544, Tuxtla Gutierrez, Chiapas, Mexico¹

Abstract.—The heteropteran family Acanthosomatidae (Pentatomoidea) is represented in North America by six species, one new, in two genera. The species are diagnosed and figures of the male and female genitalia and notes on the biology and distribution are given. Keys for the identification of genera and species are also provided.

Key Words.—Insecta, Heteroptera, Acanthosomatidae, taxonomy, stinkbugs

Acanthosomatids are stinkbugs (Pentatomoidea) that have two-segmented tarsi and a large, exposed, eighth abdominal segment in males. In other pentatomoids the eighth segment is reduced to a narrow ring at the base of the male genital cup (Schaeffer 1977) and is not visible externally. In most, but not all, genera of acanthosomatids, the female possesses a pair of abdominal structures known as Pendergrast's organs. These organs function during oviposition when the female transfers a secretion from the gland to the newly laid egg mass using her hind legs (Pendergrast 1953). Interestingly, in *Elasmucha*, one of the few genera lacking Pendergrast's organs, maternal brooding of the egg clutch and early instar nymphs is a characteristic behavior (Frost & Haber 1944, Kudo et al. 1989). Although Pendergrast's organs are unique to the acanthosomatids, paired external organs of unknown homology occur on the abdomens of scutellerids (Carayon 1984), asopine pentatomids (Aldrich 1988), cyrtocorids, plataspids and lestoniids (Miller 1971), although usually on males, not females. In male acanthosomatids inconspicuous pheromone secreting dermal glands are found in patches mainly on abdominal sternites V and VI (Staddon 1990).

Kirkaldy (1909) considered the Acanthosomini to be a tribe within the nominate subfamily of Pentatomidae. American workers Van Duzee (1916) and Torre-Bueno (1939a) placed them at the level of subfamily within the Pentatomidae. Subsequently, Kumar (1974) accorded the group family status, and most American workers since then (e.g., Rolston & McDonald 1979, Froeschner 1988) have treated the group as a full family. Kumar (1974) divided the acanthosomatids into three subfamilies and provided diagnoses for the world genera. Rolston & Kumar (1974) provided a key to the genera of the Western Hemisphere.

Acanthosomatids are most abundant in boreal or high latitude temperate regions or in subtropical regions at high elevation. In North America, the family is represented by six species in two genera. Until early in this century, North American species were placed in the genus *Acanthosoma* Curtis. Bergroth (1907) transferred the North American species to the genera *Elasmostethus* Fieber and *Elasmucha* Stål. *Elasmostethus* was revised by Torre-Bueno (1939b) who resolved the dispute

¹ Current Address: USDA-AG/SEA (TUXTLA), P.O. Box 3149, Laredo, Texas 78041.

over synonymies between Barber (1932) and Van Duzee (1935). Torre-Bueno (1939b) recognized three species and provided a key for their separation, but did not describe the genitalic structures on which definitive diagnoses depend. In his initial report of *Elasmotherus interstinctus* (L.) in North America, Barber (1932) included a figure of the male genitalia. Subsequently, McDonald (1966) described and figured the genitalia of males and females of *Elasmotherus cruciatus* and *Elasmucha lateralis*. Kumar (1974) described the male genitalia of *Elasmotherus dentatus* (DeGeer), a synonym of the Holarctic *E. interstinctus* (L.). Kumar also examined the female type of the Mexican *Acanthosoma flammatum* Distant, 1893, and removed it to *Elasmucha* Stål. Until recently, *Elasmucha flammatum* was known only from this single female type. However, I have been able to collect this species in Chiapas, Mexico, and subsequently numerous specimens have been located. In addition, a closely related but separate species was discovered in the Sierra Madres of Mexico with specimens occurring as far north as New Mexico in the United States. I have compared these specimens to Distant's type of *Acanthosoma flammatum* in the British Museum (Natural History). I have also been able to obtain specimens of *Elasmotherus interstinctus* (L.) from Alaska and have compared these to European specimens determined as either *interstinctus* or its synonym *dentatus*. I, therefore, have been able to study the genitalic structures of all five previously described species reported from North America and confirm their correct identity. In the present article I provide a description and comparison of the external morphology, including the male and female genitalia, for all six North American species.

KEY TO THE NORTH AMERICAN GENERA OF ACANTHOSOMATIDAE

1. Scent gland ruga auriculate, short, extending only half-way to metapleural margin; females lack glandular structures on abdominal segments VI and VII *Elasmucha*
- Scent gland ruga elongate, extending three-quarters of the distance to metapleural margin; females with glandular structures, visible as darkened, ovoid depressions on abdominal segments VI and VII *Elasmotherus*

ELASMUCHA STÅL

Clinocoris Hahn 1834:70 [not Fällén 1829]. (Type-species: *Cimex ferrugatus* Fabr.)
Elasmucha Stål 1864:54.

Meadorus Mulsant & Rey 1866:238, synonymized by Kumar (1974). Type-species: *Cimex griseus* L., designated by Kirkaldy (1909).

Pseudostollia Breddin 1901:65. (Type-species: *Acanthosoma delicatula* Walker, by monotypy), synonymized by Kumar (1974).

Galasastra Breddin 1903:205. (Type-species: *Galasastra salebrosa* Breddin, by monotypy), synonymized by Kumar (1974).

Type-species. — *Cimex ferrugatus* Fabr. designated by Kirkaldy (1909).

Diagnosis. — *Elasmucha* can be separated from other North American genera of Acanthosomatidae by the following character combinations: the anteclypeus is slightly longer than paraclypei; the first antennal segment reaches and slightly surpasses the apex of the paraclypeus; the mesosternal carina are elevated, projecting over the prosternum, with the carina received by a groove in the proster-

num; the margins of the prosternal groove are elevated and carinate; the scent gland ruga is auriculate and broad, reaching half-way to the metapleural margin; the base of the abdomen has an anteriorly projecting spine that reaches to the mesocoxae. Females lack Pendergrast's organs on abdomen.

Key to North American Species of *Elasmucha*

1. Anterolateral pronotal margin carinate, weakly reflexed; abdominal sternites with dark spot on each side (mainly Mexico) 2
- Anterolateral pronotal margin obtuse; abdominal sternites without dark spot laterally (USA & Canada) *lateralis*
- 2(1). Rostrum of moderate length, in repose attaining spine-bearing abdominal segment (second visible); male paramere with an angular tooth laterally (Fig. 3) *cordillera*
- Rostrum long, in repose attaining at least third visible abdominal segment; male paramere subcapitate and bent (Fig. 1) *flammatum*

Elasmucha lateralis (Say)

(Figs. 2, 7)

Edessa lateralis Say 1831:3.

Edessa nebulosa Kirby 1837:277, synonymized by Uhler (1878).

Acanthosoma affinis Westwood 1837:30, synonymized by Distant (1900).

Acanthosoma nebulosum: Dallas 1851:307.

Acanthosoma laterale: Distant 1881:101.

Meadorus lateralis: Van Duzee 1904:73.

Elasmucha lateralis: Bergroth 1907:49.

Clinocoris lateralis: Van Duzee 1908:109.

Types.—Not examined. Say collection largely destroyed (Beidleman 1986).

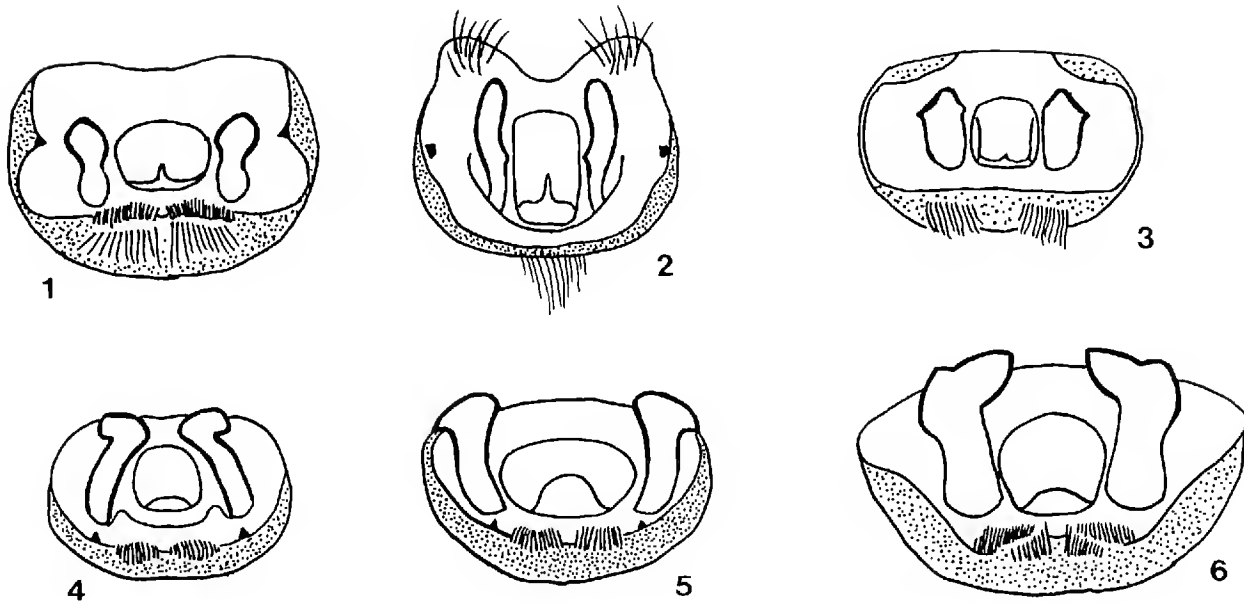
Redescription.—*Male*. Dorsal color yellow with tan or brown mottling; connexivum alternately yellow medially and red-brown near sutures; legs immaculate. Head, pronotum and scutellum with coarse dark brown punctures; punctures on hemelytral corium smaller. Pleura densely brown punctate; abdominal venter with few punctures. Length 6–9 mm. Antennal segment I thickest and longest, segment II almost as long as I, V shortest, III and IV subequal. Rostrum attains second or third visible abdominal sternite in repose. Mesosternum with elevated carina projecting over prosternum. Base of abdomen with anteriorly projecting spine which projects over metasternum reaching mesocoxae, its apex acute and lying aside mesosternal carina. Pendergrast's organs absent. Dorsoposterior margin of proctiger with reflexed carina bearing erect spine mesially. Pygophore with fringe of setae on ventro-posterior margin (Fig. 2); on each side, lateral margin at middle with sclerotized cusp; dorsoposterior margin deeply emarginate, emargination flanked on each side by setose lobes. Parameres elongate, undulate.

Female.—Basal gonocoxites longer than wide (Fig. 7). Eighth paratergite with deep, U-shaped mesial emargination; spiracles present.

Diagnosis.—See the key to species of *Elasmucha*.

Biology.—The primary hosts are birch and beech trees (Jones & McPherson 1980). A good account of the biology is given by McPherson (1982). The brooding behavior was studied by Frost & Haber (1944). I have collected *E. lateralis* in numbers on beech on the margins of lakes in Ontario and Manitoba.

Distribution.—Maine to British Columbia, south to Tennessee in the east, to Nevada in the west. Froeschner & Halpin (1981) report it from Alaska. I have seen one specimen from Dallas, Texas, which I consider probably mislabeled.



Figures 1–6. Male genital capsule, caudal view. Figure 1. *Elasmucha flammatum*. Figure 2. *Elasmucha lateralis*. Figure 3. *Elasmucha cordillera*. Figure 4. *Elasmotethus interstinctus*. Figure 5. *Elasmotethus cruciatus*. Figure 6. *Elasmotethus atricornis*.

Material Examined.—USA. CALIFORNIA. *MARIPOSA Co.*: Yosemite Natl Park, 4 Sep 1974, A.J. Gilbert, ex *Soldidago*, 1 female. MICHIGAN. *IRON Co.*: 29 Jul 1975, C. Buskirk, 1 female. *MARQUETTE Co.*: Champion, 14 Jun 1977, D. Flynn & J. Mahar, 1 male. MINNESOTA. *BECKER Co.*: Itasca St Park, 28 Jun 1984, N. Downie & J. Wappes, 1 male. *CROW WING Co.*: 4 Jul 1983, D.L. Caldwell, 1 female. *ITASCA Co.*: Deer Lake, 15–21 Jun 1986, D.A. Rider, 5 males, 3 females. NEW JERSEY. *MONMOUTH Co.*: Lincroft, 30 Jul 1979, A. Hook, 1 female. NEW YORK. *ESSEX Co.*: Whiteface Mtn, 16 Jul 1990, J. Huether, 2 males, 3 females. OREGON. *LINCOLN Co.*: Agate Beach, 15 Jun 1976, R.L. Westcott, in beach wash, 1 female. PENNSYLVANIA. *ALLEGHENY Co.*: Pittsburgh, 14 Jun 1982, D. Colterrah, on birch, 2 males, 1 female. TEXAS. *DALLAS Co.*: Dallas, 5 Apr 1981, J. Wellso, 1 male. VIRGINIA. *WASHINGTON Co.*: Clinch Mtn, Hidden Valley, 24 May 1990, B. Kondratieff, J.L. Welch, R.F. Kirchner, 1 male. WASHINGTON. *KING Co.*: Hwy I-90 & S Fork of Snoqualmie River, 15 May 1988, M.E. Rice, 1 female. CANADA. *BRITISH COLUMBIA*: Lions Bay, 7 Jul 1988, D.B. Thomas, 3 males, 6 females; Spahats Creek Prov Park, Spahats Creek, 17 Aug 1986, P.H. Arnaud, 2 males, 2 females. *ONTARIO*: Quetoco Prov Park, 8–9 Aug 1978, D. Legg, 2 males, 1 female.

Elasmucha flammatum (Distant)
(Figs. 1, 8)

Acanthosoma flammatum Distant 1893:458.

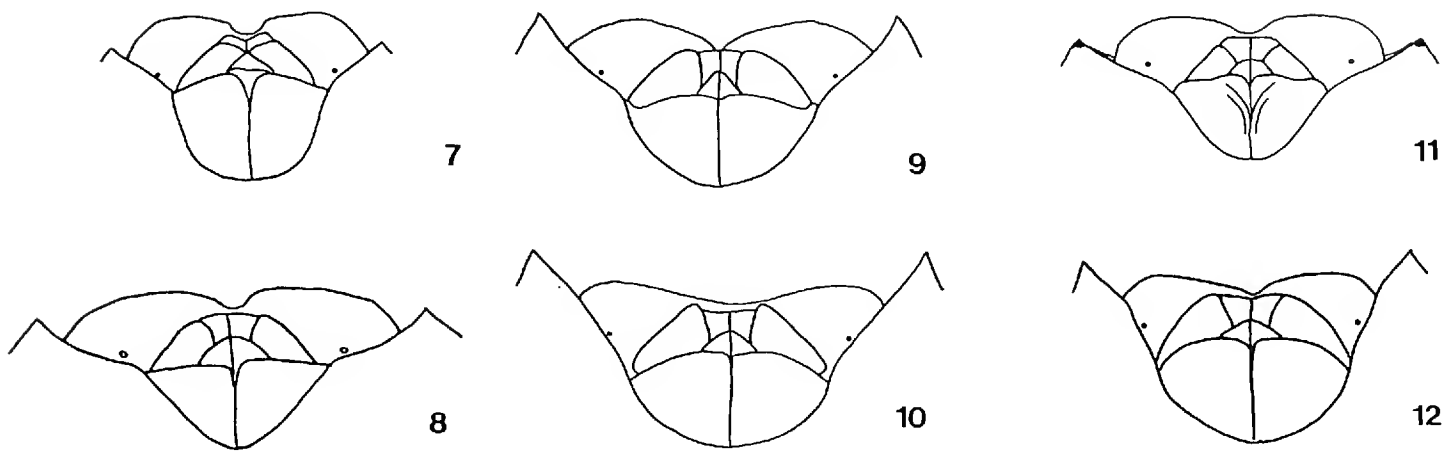
Elasmucha flammatum: Kumar 1974:49.

Types.—*Holotype*, female, data: MEXICO. *GUERRERO*: Omilteme, July, H.H. Smith; deposited in the British Museum (Natural History), London.

Redescription.—*Male*. Dorsal color yellow-tan with dense red-brown punctation. Connexivum alternately yellow mesially, dark brown near sutures. Pleura punctate; legs immaculate. Length 7–11 mm. Antennal segment II longest, I shortest, III, IV and V subequal. Rostrum long, attaining third or fourth visible abdominal sternite in repose. Anterolateral pronotal margin weakly reflexed, carinate. Abdominal sternites with shagreened, dark spot on each side just mesad of trichobothria. Pendergrast's organs absent. Proctiger with low, carinate fold mesially on dorsal surface. Ventroposterior lip of pygophore bearded with double row of setae: ental row short and dense, ectal row long, paler, both rows interrupted mesially (Fig. 1). Lateral margin of pygophore with sclerotized cusp on each side at middle. Dorsoposterior margin of pygophore not deeply emarginate. Parameres asymmetrically clavate.

Female. Similar to male except distinctly larger and paler. Basal gonocoxites about equally long as wide (Fig. 8). Eighth paratergite with deep U-shaped emargination mesially; spiracles present.

Diagnosis.—See the key to the species of *Elasmucha*.



Figures 7–12. Female genital plates, ventral view. Figure 7. *Elasmucha lateralis*. Figure 8. *Elasmucha flammatum*. Figure 9. *Elasmostethus atricornis*. Figure 10. *Elasmostethus cruciatus*. Figure 11. *Elasmucha cordillera*. Figure 12. *Elasmostethus interstinctus*.

Biology.—I collected two specimens at light at two different localities in Chiapas. One of these locations, El Chorreadero, is a tropical deciduous forest; the other, near Cuxtepeques, is a pine-oak forest. Both collection localities were montane riparian habitats.

Distribution.—Mexico and Guatemala.

Material Examined.—GUATEMALA. Bananera, Apr 1930, J.J. White, 1 male. MEXICO. CHIA-PAS: Cuxtepeques, 15 Jun 1987, D.B. Thomas & A.M. Mendoza, 1 male; Chorreadero Cyn, 9 km E of Chiapa de Corzo, 18 Sep 1985, D.B. Thomas, B.C. Ratcliffe & C. Messenger, 1 female; Chorreadero, 26 May 1987, D.A. Rider, D.B. Thomas, E.G. & T.J. Riley, 1 female; Municipio Pantepec, road from Rayon between Pantepec and Tapalapa, 1707 m, 22 Sep 1981, D.E. Breedlove, 1 female. NUEVO LEON: 29 km W of Linares, 23 Jul 1976, Peigler, Gruetzmacher, Murray & Schaffner, 3 males, 4 females; Monterrey, 4 Nov 1978, L.M. Koenig, 1 male. VERACRUZ: Fortin de las Flores, Planta de la Cerveceria Moctezuma, 17–18 May 1965, D. Rabago, 1 male, 1 female.

Elasmucha cordillera Thomas, NEW SPECIES
(Figs. 3, 11, 13)

Types.—*Holotype*, male, data: NEW MEXICO. CATRON Co.: Whitewater Forest Camp, 9 km (5 mi) NE of Glenwood, 21 Aug 52, H.B. Leech & J.W. Green; deposited, California Academy of Sciences, San Francisco. Paratypes: 6 males and 6 females. One male, data: NEW MEXICO. SANTA FE Co.: 10 Jul 1940, D.J. & J.N. Knull; deposited in the personal collection of D.B. Thomas. One male, data: MEXICO. OAXACA: 10 km N of Oaxaca, 1900 m, 13 Sep 1986, R. Baranowski, sifting litter at small stream, trop. mont. forest; deposited, private collection of D.A. Rider. Two males, 5 females, data: MEXICO. “2390,” C.F. Baker; deposited, United States National Museum of Natural History. One male, data: MEXICO. San Antonio, “No. 114,” 1 May 1945, with leaf mold; deposited, United States National Museum of Natural History. One female, data: MEXICO. MEXICO D.F.: L. Conradt; deposited, United States National Museum of Natural History. One male, data: GUATEMALA. Bananera, Apr 1930, J.J. White; deposited, United States National Museum of Natural History.

Description.—*Male*. Elongate-oval (Fig. 13), depressed dorsally, convex ventrally. Color yellow with dense, irregularly dispersed, red-brown punctations. Length from tip of tylus to apex of abdomen: 6.5 mm. **Head:** elongate; tylus gradually widened apically and slightly surpassing juga. Antennal segments variably black or darkened; segment I shortest, II longest, III, IV and V subequal. Rostrum in repose attaining base of abdominal sternite III (second visible). **Thorax:** anterolateral pronotal margin with obtuse reflexure; weakly concave in dorsal view. Humeri obtuse, not produced. Corium with lateral

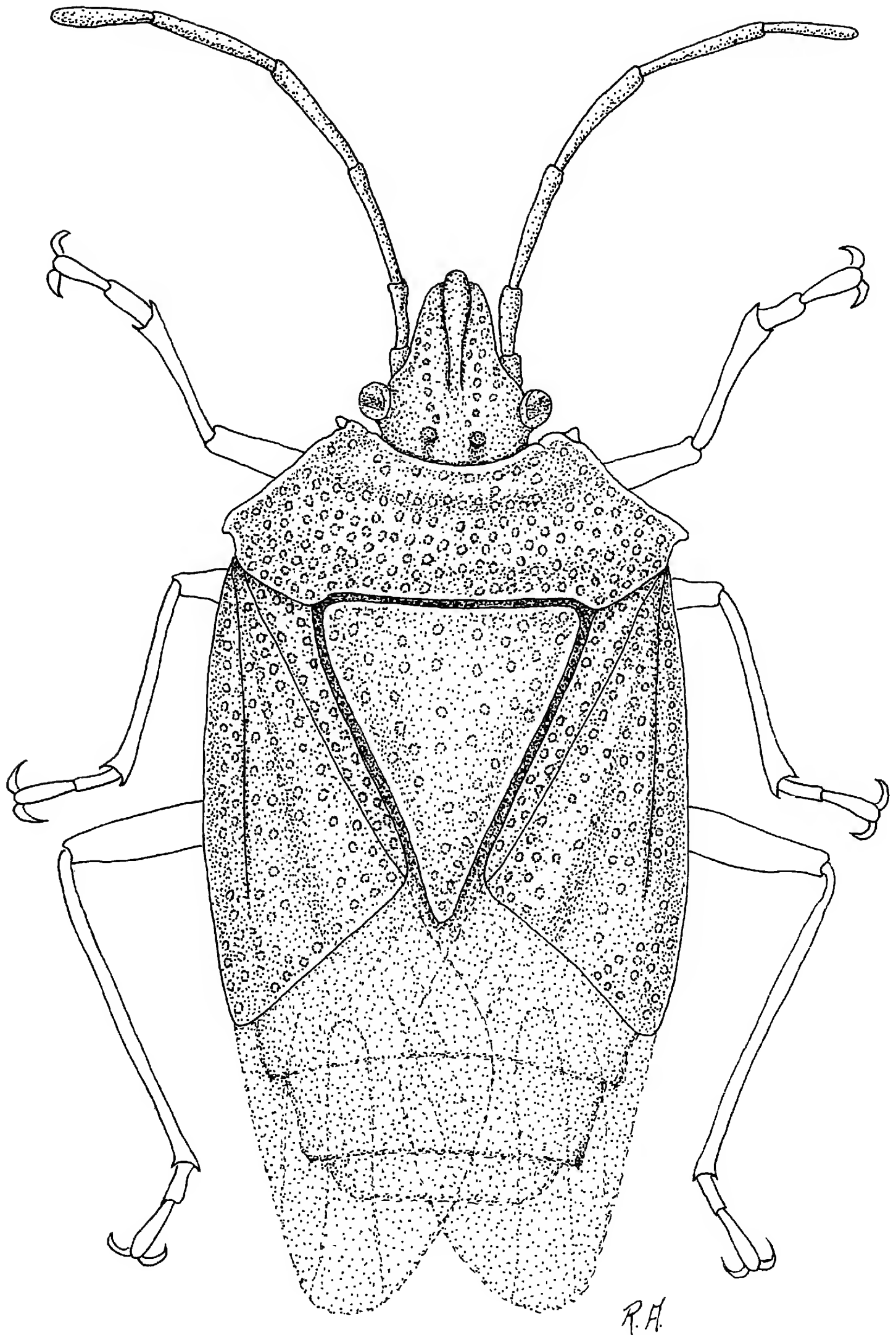


Figure 13. *Elasmucha cordillera*, dorsal habitus.

punctures larger and denser. Scent gland auricle reaching almost one-half distance to metapleural margin. Pleura strongly punctate. Legs yellow, tibia terete, except protibiae prismatic distally. *Abdomen*: venter yellow, impunctate; each sternite with round dark spot on each side just mesad of spiracle. Connexivum appearing alternate with apex of each segment having a broad nearly square dark spot. *Genitalia*: ventral margin of pygophore bearded with thick fringe of setae each side of middle; lateral margin without tooth or spinous process (Fig. 3). Proctiger with small triangular tooth at middle on posterior margin. Parameres thick, compressed; ectal margin with small acute angular tooth-like projection (Fig. 3).

Female.—Length 8.0 mm. Basal gonocoxites with strong longitudinal wrinkles near and parallel to mesial margin. Posterior margin of ninth tergite with U-shaped mesial emargination; spiracles present (Fig. 11).

Diagnosis.—Definitive separation of this species from the others in the genus requires examination of the male genitalia. The male paramere has an angular tooth on the lateral margin that is lacking in the others.

Remarks.—The last mentioned paratype, from Bananera, Guatemala, may be mislabeled because it bears a collection label that is identical with a specimen of *flammatum*. Because both specimens are males, they are easily differentiated. Many of the paratypes bear no other locality information than "Mex." The range of this species is, therefore, open to question. Reliably labeled males are from New Mexico, in the United States, and Oaxaca, in Mexico.

Material Examined.—see types.

ELASMOSTETHUS FIEBER

Elasmostethus Fieber 1860:78.

Cypostethus Fieber 1860:78. (Type-species, *Cimex tristriatus* Fabr. by monotypy), synonymized by Kumar (1974).

Oxydalus Mulsant & Rey 1866:247. (Type-species: *Cimex dentatus* DeGeer, by monotypy), synonymized by Stål (1868).

Elasmatostethus Marshall 1868:281. [invalid emendation].

Stictocarenum Stål 1871:638. (Type-species: *Rhynchoris ligatus* Erichson, by monotypy), synonymized by Kumar (1974).

Dichobothrium Breddin 1903:207. (Type-species, *Dichobothrium sastragaloides* Breddin), designated by Kirkaldy (1909), synonymized by Kumar (1974).

Ditaenius Bergroth 1912:361. (Type-species, *Cimex emeritus* Bergroth, by monotypy), synonymized by Kumar (1974).

Type-species.—*Cimex dentatus* DeGeer [= *Cimex interstinctus* L.], by monotypy.

Diagnosis.—The following characters and states separate *Elasmostethus* from other New World genera of Acanthosomatidae: The anteclypeus is longer than paraclypei; the apex of antennal segment I clearly surpasses the anteclypeus; the mesosternum has an elevated carina projecting over the prosternum which is received by a groove in prosternum; the margins of the prosternal groove are elevated and subcarinate; the base of abdomen is produced forward as an elongate spine lying along side of the mesosternal carina and projects over the metasternum to the mesocoxae; the scent gland ruga are straight and elongate, about five times longer than wide, and reaching three-quarters of the distance to metapleural margin. Pendergrast's organs are present on the abdomen of females. These are glandular structures appearing as small, darkened, ovoid depressions on each side of

the abdomen, near the posterior border of sternite VI and the anterior border of sternite VII.

Key to North American Species of *Elasmotethus*

1. Pronotal disc and head with many dark punctures; first antennal segment pale 2
- Pronotal disc and head without dark punctures; first antennal segment dark *atricornis*
- 2(1). Abdominal venter with row of dark spots on each side *interstinctus*
- Abdominal venter immaculate *cruciatus*

Elasmotethus interstinctus (L.)
(Figs. 4, 12)

Cimex interstinctus L. 1758:445.

Cimex dentatus DeGeer 1773:260. Synonymized by Kirkaldy (1909).

Cimex haemagaster Schranck 1781:270. Synonymized by Kirkaldy (1909).

Cimex bidens Gmelin 1789:2149 [not Linnaeus 1758]. Synonymized by Kirkaldy (1909).

Cimex arboreus Gmelin 1789:2160. Synonymized by Kirkaldy (1909).

Cimex collaris Fabricius 1803:170 [homonym]. Synonymized by Stål (1868).

Pentatoma liturata Latreille 1804:192. Synonymized by Kirkaldy (1909).

Pentatoma stollii Le Pelletier & Serville 1825:53. Synonymized by Kirkaldy (1909).

Acanthosoma haematogaster (sic): Burmeister 1835:360.

Meadorus interstinctus Mulsant & Rey 1866:238.

Acanthosoma dentatum: Saunders 1892:39. Synonymized by Horvath (1899).

Elasmotethus interstinctus: Horvath 1899:366.

Types.—*Cimex dentatus* DeGeer [= *Cimex interstinctus* L.] designated by Stål (1864). Not examined.

Redescription.—*Male*. Dorsal color green-yellow with variable red tinge. Connexivum uniformly yellow. Dense black punctations on head, pronotum, scutellum and corium. Venter yellow, impunctate. Legs immaculate. Abdominal sternites with shagreened, dark, oval spot on each side just mesad of trichobothria. Length 8–10 mm. Antennal segment IV longest, I and III shortest, II and V subequal, longer than I and III. Rostrum in repose attaining metacoxae. Anterolateral pronotal margin calloused. Mesosternal carina elevated, projecting over prosternum and received by prosternal groove, margins of groove elevated, subcarinate. Scent gland ruga elongate, attaining three-fourths distance to metapleural margin. Posterior margin of proctiger arcuate, reflexed. Ventro-posterior margin of pygophore bearded with fringe of setae, interrupted mesially; margin of pygophore either side of fringe bearing sharp, sclerotized tooth (Fig. 4). Paramere elongate, compressed, with asymmetrical quadrate head.

Female.—Basal gonocoxites slightly wider than long (Fig. 12). Eighth paratergite undulately emarginate in caudal view; spiracles present.

Diagnosis.—See the key to the species of *Elasmotethus*.

Biology.—This bug is known as the “birch bug” in England. Kirkaldy (1909) also lists alders, beech and aspen as hosts. Staddon (1990) has studied the distribution of pheromone glands and the chemistry of their secretions.

Distribution.—Holarctic: Alaska, Northwest Territories of Canada, northern Europe and Asia.

Material Examined.—USA. ALASKA. Delta Junction, Fourth judicial district, Aug 1981, C. Papp, 3 males, 2 females. GREAT BRITAIN. ENGLAND. *NORFOLK*: Thetford, 16 Sep 1977, A.J. & M.E. Gilbert, 1 male; Cambridge, Wicken Fen, 16 Sep 1977, A.J. & M.E. Gilbert, 1 female.

Elasmostethus cruciatus (Say)
(Figs. 5, 10)

Edessa cruciata Say 1831:2.

Acanthosoma borealis Westwood 1837:30. Synonymized by Distant (1900).

Acanthosoma cruciata: Uhler 1861:23.

Acanthosoma cruciata var. *cooleyi* Van Duzee 1904:74.

Elasmostethus cruciatus: Bergroth 1907:49.

Elasmostethus cooleyi: Bergroth 1907:49. Synonymized by Torre-Bueno (1939b).

Types.—Not examined. Say collection reportedly destroyed (Beidleman 1986).

Redescription.—*Male.* Dorsal color yellow-tan with red band on ental margin of hemelytral corium. Red-brown punctures dense on pronotum, scutellum and most of corium, sparse on head and large spot on endocorium. Connexivum uniformly yellow. Venter yellow impunctate, immaculate; apices of last abdominal sternite red. Legs immaculate. Length 8–11 mm. Antennal segment III shortest, II, IV and V subequal, longer than I. Rostrum attains metacoxae in repose. Anterolateral pronotal margin calloused. Posterior margin of proctiger bluntly acuminate, broadly reflexed. Ventroposterior margin of pygophore bearded with dense fringe of setae, interrupted mesially; margin either side of fringe with a sharp, sclerotized tooth (Fig. 5). Paramere elongate, compressed, with ovoid head which has outer, apical margin deflexed.

Female.—Basal gonocoxites about as long as wide, posterior margin arcuate (Fig. 10). Posterior margin of eighth paratergite broadly V-shaped in ventral view with weak mesial emargination; spiracles present.

Diagnosis.—See the key to the species of *Elasmostethus*.

Biology.—Jones & McPherson (1980) report that this species feeds and reproduces on alders. McPherson (1982) provides notes on collection records, distribution and parasites. I have collected this species in numbers on alders in Nevada and in British Columbia.

Distribution.—Labrador to British Columbia in Canada, south to California, Texas and South Carolina.

Material Examined.—USA. CALIFORNIA. *SHASTA Co.*: Burney, 20 Aug 1969, R.P. Allen, 3 males, 3 females. COLORADO. *LARIMER Co.*: Cameron Pass, 19 Aug 1948, D.G. Denning, 1 female. NEVADA, *DOUGLAS Co.*: Carson City, Spooner Ridge, 6 Jul 1978, on *Alnus tenuifolia*, 3 males, 2 females. NEW YORK. *ESSEX Co.*: Whiteface Mt, 11 Jul 1990, J. Heuther, 2 males, 3 females. WASHINGTON. *THURSTON Co.*: Millersylvania St Park, nr Maystown, 53 m, 11 Jul 1988, E.L. Sleeper, 1 male. WYOMING. *ALBANY Co.*: Laramie, Pole Mtn, 7 Jul 1948, D.G. Denning, 1 male, 1 female. CANADA. *BRITISH COLUMBIA*: Lions Bay, 7 Jul 1988, D.B. Thomas, 1 male, 1 female; Vancouver, UBC campus, S.E. Woods, 2 Jul 1988, E.L. Sleeper, 1 male, 1 female. MANITOBA. Whiteshell Prov Park, South Cross Lake, 13 Aug 1983, D.B. Thomas & J.E. Pasek, 1 female.

Elasmostethus atricornis (Van Duzee)
(Figs. 6, 9)

Acanthosoma atricornis Van Duzee 1904:75.

Elasmostethus atricornis: Kirkaldy 1909:177.

Types.—Not examined.

Redescription.—*Male.*—Dorsal color yellow with humeral angles of pronotum and antennae black; scutellum basally and broad ental margin of hemelytral corium infuscated. Venter yellow with apices

of last abdominal segment orange. Anterior pronotum and head with colorless punctures; base of pronotum, corium and scutellum with scattered brown punctures. Venter and legs immaculate. Length 8–10 mm. Antennal segments II and IV longest, subequal, III and V shortest, subequal; rostrum attaining mesocoxae in repose. Anterolateral pronotal margins obtuse. Ventroposterior border of pygophore bearded with double row of setae, ental row short dense, ectal row longer, interrupted mesially; margin of pygophore lacking teeth or cusps (Fig. 6). Proctiger broad, obtusely acuminate distally, apex broadly reflexed. Head of paramere angulate, capitate, feebly bilobate.

Female.—Basal gonocoxites about as long as broad; posterior margin of eighth paratergite symmetrically biarcuate in ventral view; spiracles present (Fig. 9).

Diagnosis.—See the key to the species of *Elasmotherus*.

Biology.—This species breeds on *Aralia racemosa* L. (Blatchley 1926, Jones & McPherson 1980).

Distribution.—Quebec to Montana, south to South Carolina (McPherson 1982).

Material Examined.—USA. NEW YORK. *TOMPKINS Co.*: Ithaca, 13 Sep 1952, W.D. Stockton, 1 male, 2 females. CANADA. *QUEBEC*: 20 km SE of Kazabazua, 29 Jul 1989, B.D. Gill, 3 males, 3 females.

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NEST PROVISION AND POLLEN FORAGING IN THREE MEXICAN SPECIES OF SOLITARY BEES (HYMENOPTERA: APOIDEA)

STEPHEN H. BULLOCK,¹ RICARDO AYALA,¹
GREGORIO RODRÍGUEZ-GONZÁLEZ,¹ RODOLFO PALACIOS-CHÁVEZ,²
DELFINA RAMOS-ZAMORA,² D. LEONOR QUIROZ-GARCÍA² AND
MARÍA DE LA LUZ ARREGUÍN-SÁNCHEZ²

¹Estación de Biología Chamela, Universidad Nacional Autónoma de México,
Apartado Postal 21, 48980 San Patricio, Jalisco, México;

²Laboratorio de Palinología, Departamento de Botánica,
Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional,
Prol. Carpio y Plan de Ayala, 11340 México, D.F., México

Abstract.—Pollen selection was determined by two methods for three ground-nesting bees: analysis of nest cell contents (provisions or feces), and of female pollen foraging records. *Ancylloscelis wheeleri* Cockerell and *Melitoma marginella* Cresson (Anthophoridae) were oligolectic on different genera of Convolvulaceae. The two methods differed in emphasis of particular hosts. *Mesoxaea nigerrima* Friese (Oxaeidae) had unrelated hosts in different months. As many as nine pollen species were found in a single cell, but the dominant pollen comprised at least 95% in most cells for all three bee species. Not all minor pollen species were clearly contaminants.

Resumen.—La selección de polen fue determinada por dos métodos para abejas que anidan en el suelo: el análisis del contenido de las celdas de los nidos (provisión o excremento), y la observación de hembras en pecoreo de polen. *Ancylloscelis wheeleri* Cockerell y *Melitoma marginella* Cresson (Anthophoridae), fueron oligolécticos sobre diferentes géneros de Convolvulaceae. Los dos métodos enfatizaron diferentes hospederos. *Mesoxaea nigerrima* Friese (Oxaeidae) tenía plantas hospederas no emparentadas en los diferentes meses. Se encontraron hasta nueve especies de polen por celda, pero el polen dominante comprendió al menos un 95% en la mayoría de las celdas para las tres especies de abejas. No todas las minoritarias parecieron ser contaminantes.

Key Words.—Insecta, feeding specialization, tropical deciduous forest, Convolvulaceae, Leguminosae, Tiliaceae

Pollen is a major nutritional source for most larval bees. The eusocial Apidae in general are highly polylectic (Kleinert-Giovannini & Imperatriz-Fonseca 1987, Lobreau-Callen et al. 1986) and their selection of pollen may be greatly affected by its abundance (Roubik et al. 1986). However, pollen from various plant species may vary demonstrably in nutritional value, as shown for *Apis mellifera* L. (Herbert et al. 1970) and for the solitary bee *Osmia lignaria* Say (Levin & Haydack 1957). The vast majority of bee species are solitary (Linsley 1958), and their host selection evolves quite distinctly from that of eusocial bees (Lobreau-Callen & Coutin 1987). In solitary species the repetition of particular host relations across isolated generations may represent a physiological link. For example, *Colletes fulgidus longiplumosus* Stephen females show a preference for the surface oils of the pollen on which they were reared (Dobson 1987).

The diversity of hosts varies greatly between species of solitary bees (Linsley 1958), and to a lesser extent among their populations (Linsley et al. 1963, Tasei

1976), among individuals (Michener & Rettermeyer 1956), and during or between seasons (Rust 1990). These variations are particularly difficult to quantify in habitats with low visibility of nesting areas, flight patterns and hosts. Hosts for pollen are usually described from observation of foraging females, and not from direct quantitative assessments of pollen types in the nest cells; the latter is an important tool for studying feeding specialization (Cripps & Rust 1989). In this paper, we apply both of these approaches to evaluate the pollen selectivity of populations of three solitary species from a single locality in neotropical deciduous forest.

MATERIALS AND METHODS

The site of this study was the Estación de Biología Chamela (19°30' N, 105°03' W) in the Pacific lowlands (10–150 m) of Mexico, where the rainy season is typically four months long (Bullock 1986) and the mean annual rainfall is 714 mm (1977–1990). The vegetation at this site is principally tropical deciduous forest, with a floristically distinct semideciduous forest along the larger seasonal watercourses (Lott et al. 1987). General collection of bees on flowers has been made sporadically since 1980 by resident and visiting scientists (principally SHB and RA). Tree phenology was reported by Bullock & Solis (1990); other plants were observed while collecting the flora and fauna.

The bees studied were *Ancyloscelis wheeleri* Cockerell and *Melitoma marginella* Cresson (Anthophoridae), and *Mesoxaea nigerrima* Friese (Oxaeidae). Closed nest cells of each species were collected in November 1986. *Ancyloscelis* and *Melitoma* were nesting in dense aggregations, so the individual cells collected may have been from various nests. The *Mesoxaea* nests were solitary. *Ancyloscelis* and *Mesoxaea* nests were active but *Melitoma* nests were already closed; the respective samples were 17 cells, five cells from two nests, and 11 cells. In October 1988, 15 cells were collected from closed nests of *Melitoma* and one from a closed nest of *Mesoxaea*.

The pollen samples were prepared by standard acetolysis methods. Percentage composition was determined from counts of 1000 grains from three mounts (Ramalho & Kleinert-Giovannini 1986). Volumetric measurements are not a clear solution to the related problem of nutritional values.

RESULTS

Ancyloscelis wheeleri. — Pollen of five plant species was found in nest provisions, including three species of Convolvulaceae. *Merremia quinquefolia* (L.) Hallier f. contributed 99.67%, and there were small amounts of an *Ipomoea* sp. (0.28%) and of *Jacquemontia nodiflora* (Desrousseaux) G. Don (0.05%). The other two pollen types were *Heliocarpus pallidus* Rose (Tiliaceae), 0.09%, and an unidentified Compositae, 0.02%. The latter two may have come from exploratory or nectar foraging, or may have been introduced as contaminants by the bees because these forms are commonly airborne (RPC & SHB, unpublished data).

The nesting and principal flight period is October and November, but we have found occasional individuals as late as April. Pollen-foraging females were collected on only three plant species: *M. quinquefolia*, *J. nodiflora* and *Ipomoea crinicalyx* Moore. Nectar-foraging individuals of one or both sexes were collected on five Convolvulaceae, one Acanthaceae and one Boraginaceae species.

Melitoma marginella.—The 1986 nest samples all showed only one form of pollen, most closely resembling reference material of *Ipomoea pedicellaris* Benth.

In the 1988 sample, three species of *Ipomoea* were predominant: *I. pedicellaris*, *I. clavata* (G. Don) Oostroom and *I. wolcottiana* Rose. The most abundant species comprised 99% to 100% in eight cells (monospecific in *Ipomoea*), 87% to 97% in four cells, and 53.6% to 70.5% in three cells. As many as three *Ipomoea* species were present in only three cells. *Ipomoea nil* (L.) occurred only once (2.1%). Non-*Ipomoea* constituents in four cells were probably all contaminants introduced by the bees, including *Poëppigia procera* Presl (Leguminosae), an unidentified Poaceae, and two species not present in the area of the Chamela station, *Alnus* sp. (Betulaceae) and *Pteris* sp. (Adiantaceae), which are distributed by wind. In all the samples of fecal material, the pollen grains were broken into many pieces.

The flight season was September and October, and again February and March; the life cycle remains problematic (GRG, unpublished data). Pollen-foraging females were collected on *Ipomoea muricata* Cavanillas, *I. nil* and *I. pedicellaris*. Nectar-foraging males were collected on *I. muricata*, *I. trifida* (HBK) G. Don, and on *I. wolcottiana* (Bullock et al. 1987).

Mesoxaea nigerrima.—A single pollen type dominated the November 1986 nest samples: *Heliocarpus pallidus* comprised 99.9%, although trace amounts of *Phaseolus* sp. and *Apoplanesia paniculata* Presl (both Leguminosae) appeared also. The 1988 sample was collected before *Heliocarpus* began to flower: the contents were dominated by *Schrankia diffusa* Rose (Leguminosae, 95.6%), which is a common vine and the most frequently observed host of foraging *Mesoxaea* females. Eight other species were present in this single cell provision: *Poëppigia procera* (1%), *Cassia* sp. (0.8%), and *Senna* sp. (0.8%) (all Leguminosae), *Doyerea emetocathartica* Grosourdy (Cucurbitaceae, 0.7%), *Serjania brachycarpa* A. Gray (Sapindaceae, 0.6%) and trace amounts of *Psidium sartorianum* (Berg) Niedenzu (Myrtaceae, 0.2%), *Cleome* sp. (Capparidaceae, 0.1%), and *Pedilanthus calcaratus* Schlechtendal (Euphorbiaceae, 0.1%).

The flight season extended from July through November. *Mesoxaea* was collected foraging on 11 species from four families (Leguminosae, Malpighiaceae, Sapindaceae and Tiliaceae). Females were observed collecting pollen from four mimosoid and one caesalpinoid legume species (*Mimosa brandegei* B. L. Robinson, *M. leptocarpa* Rose, *Piptadenia obliqua* (Persoon) MacBride, *Schrankia diffusa*, and *Apoplanesia paniculata*) and from *Heliocarpus pallidus*.

DISCUSSION

Hurd (1979: 2118, 2123) stated that all species of *Ancyloscelis* and *Melitoma* visit flowers of *Ipomoea* for pollen and nectar, but also visit a variety of other flowers for nectar. Our results confirm the *Melitoma*–*Ipomoea* association and extend its generality in terms of species, habitat and geography. *Ancyloscelis wheeleri*, however, is a specialist on Convolvulaceae but not on *Ipomoea* at Chamela, as far as our samples are representative. Both fit the restricted definition of oligolecty—“species that confine their pollen foraging to species within a genus”—suggested by detailed comparative study of provisions in seven *Osmia* species of a montane meadow (Cripps & Rust 1989: 136).

Intermingled nests of *M. marginella* and *A. wheeleri* (Hurd 1979) have not been

observed at Chamela, although large aggregations of each are known. Our finding that virtually all grains in the feces of *M. marginella* are highly fragmented is apparently unique.

Both these anthophorids have relatively brief flight seasons which may not exceed the flowering seasons of single host species. Yet their host specificity is rather remarkable because of the range of closely related plants available simultaneously. October and November are the months of peak flowering of Convolvulaceae at Chamela, typically including six genera and 23 species, with 16 species of *Ipomoea* (as currently revised).

Pollen hosts of oxaeids are reported from Solanaceae, Zygophyllaceae and Leguminosae, especially *Cassia* (Hurd & Linsley 1976, Camargo et al. 1984). Flowers in the former two families are common at Chamela during the flight period of *Mesoxaea nigerrima*, but there are no foraging or provision records. Foraging has not been observed on *Cassia* or *Senna* but these were minor species in one cell provision. The rarity of visits to buzz-pollinated plants at Chamela is conspicuous; the common pollen hosts were mimosoid legumes. Typical of Oxaeidae, *M. nigerrima* is a polylectic species, and several plant families may be present in any cell; however, one species is heavily dominant.

Mesoxaea change principal host within an individual female's (?) flight season. *Schrankia* flowers for several months starting about the same time as the flight season of *Mesoxaea*, but *Heliocarpus* has only a brief abundant flowering in October or November. The flower visitation records and our observations on other plant species clearly show that *Mesoxaea nigerrima* discriminates and is not simply dependent on flower-frequency in its host selection.

Little is known about the means of pollen host recognition in newly emerged solitary bees. Experiments with *Colletes fulgidus* showed that bees can recognize their host plant by the odor of its pollen, suggesting that larvae may be conditioned to volatile oils of pollen in their provision (Dobson 1987). This hypothesis might be appropriate in *M. marginella* and *A. wheeleri*. However, our data suggest that some *M. nigerrima* individuals begin collecting pollen on plants that are unrelated to their larval host.

The actual host range in a bee population at any one time may be significantly greater than we could sample. Certainly the data indicate that generally only one host species is used over several to many foraging trips, over periods of days, and among neighboring females in *Ancyloscelis*. Any one larva of any of these species is unlikely to experience more than a one percent admixture of a second pollen type in its provision, and the combined percentage of secondary species exceeded five percent only in some cells of *M. marginella*.

Both flower visitation records and palynological analysis of nest contents have limitations in terms of optimum sampling—particularly in forests and for ground-nesting bees. In the present case the contribution of pollen analysis is in the quantification of the purity, or lack of it, in the provisions for individual bees. Observation of foraging females had not missed any major hosts. But in a forest habitat, following an individual bee throughout a single foraging trip, or during several trips or days, is virtually impossible.

The presence of pollen species other than the principal hosts may be attributable to several causes. Of considerable importance are the opportunities for contamination of the bee's pollen load. Foreign grains may be added to flowers of a given

species through the visits of more polylectic insects, somewhat analogous to intra-hive inter-bee transfer of pollen (DeGrandi-Hoffman et al. 1986). Also, airborne pollen is ubiquitous and remarkably diverse (Palacios 1985; RPC & SHB, unpublished data) which will also contact the bees via soil, leaves, etc. However, the most important causes are probably the admixture of pollen from plants visited for nectar, and from exploratory visits by bees to potential alternate resources (Heinrich 1979, Cripps & Rust 1989).

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FORAGING OF *STENOPOGON INQUINATUS* (LOEW) (DIPTERA: ASILIDAE) ON MONTANA RANGELAND SITES

KEVIN M. O'NEILL¹ AND WILLIAM P. KEMP^{1,2}

¹Entomology Research Laboratory, Montana State University,
Bozeman, Montana 59717

²USDA, Agricultural Research Service, Rangeland Insect Laboratory,
Bozeman, Montana 59717

Abstract.—The robber fly *Stenopogon inquinatus* Loew preyed upon a wide variety of insects at rangeland sites in Montana. As is typical of *Stenopogon*, prey use varied with local insect abundance. *Stenopogon inquinatus* tended to take alate male *Formica subpolita* Mayr near ant mating swarms, honey bees (*Apis mellifera* L.) near flowers, and dung beetles (Scarabaeidae) on open range. These three groups, and other robber flies, comprised 90% of the prey records for *S. inquinatus*.

Key Words.—Insecta, Diptera, Asilidae, *Stenopogon*, foraging, prey

Stenopogon is a wide-ranging genus of robber flies in western North America, where more than 50 species occur (Wilcox 1971). Several studies of the behavior and ecology of *Stenopogon* have been undertaken (Cole 1958, Powell & Stage 1962, Lavigne & Holland 1969, Dennis & Lavigne 1975, O'Neill & Kemp 1990, O'Neill in press). Foraging *Stenopogon* make short flights in pursuit of prey from perches on or near the ground and, as a group, prey on a variety of insects. Local populations tend to take a relatively narrow range of prey, but differences among species and populations of *Stenopogon* may be due to spatial and temporal variation in the abundance of potential prey, rather than to variation in prey preference (Powell & Stage 1962, Dennis & Lavigne 1975).

Stenopogon inquinatus Loew is a large species, 20 to 37 mm in length (Dennis & Lavigne 1975), that is widely distributed in North America (Wilcox 1971). Here, we report observations on prey use of *S. inquinatus* in Montana that supplement earlier studies from Wyoming (Dennis & Lavigne 1975) and provide evidence that prey use in this species reflects local insect abundance.

METHODS

Stenopogon inquinatus was studied at two sites, 14 km S of Three Forks and 5 km NE of Logan, Gallatin County, Montana, during the summers 1987–1990. The species was typically present from early June through early August and was easy to distinguish from other asilid species because of its large size. The sites are classified within the *Stipa comata* Trinius & Ruprecht/*Bouteloua gracilis* (Humboldt et al.) Lagasca y Segura ex. Steudel habitat type (Kemp et al. 1990). Prey and observations of predation events were sampled ad libitum. Body lengths of prey and head widths of robber flies were measured to the nearest 0.1 mm, using a micrometer accurate to 0.05 mm.

RESULTS

Foraging behavior for *S. inquinatus* followed the patterns observed by Dennis & Lavigne (1975) in Wyoming. Foraging flies perched on the soil surface or on plants up to 1 m in height and pursued insects flying within about 1 m of the perch. The 170 prey observed at our site included members of five orders, 16 families, and at least 21 species of insects.

The prey specimens that we collected were identified as (numbers of specimens are in parentheses): Hemiptera: Coreidae, *Chelinidea vittiger* Uhler (1); Pentatomidae, *Chlorochroa* sp. (2); Reduviidae, *Apiomerus* sp. (1); Coleoptera: Scarabaeidae, *Onthophagus nuchicornis* (L.) (1), *Aphodius fossor* L. (12), *Dichelonyx* sp. (1); Cicindellidae, *Cicindella punctata* Olivier (1), *Cicindella purpurea* Casey (1), Meloidae, *Epicauta* sp. (1); Lepidoptera: Noctuidae (2); Pyralidae (2); Diptera: Tipulidae (1), Calliphoridae (1); Stratiomyidae (1); Tabanidae (1); Asilidae, *Efferia staminea* (Williston) (13), *Megaphorus willistoni* (Williston) (1), *Machimus occidentalis* (Hine) (2), *Stenopogon inquinatus* (11); Hymenoptera: Formicidae, *Formica subpolita* Mayr (55 alates), *Formica* sp. (4 alates); Halictidae (2), Apidae, *Apis mellifera* (12). Forty-one other prey were identified in the field, but not collected: one *Efferia staminea*, one *Machimus occidentalis*, and 39 *Formica* alates.

The 129 prey collected had a mean length of 12.6 mm (SE = 0.50). Although the *S. inquinatus* collected at this site varied widely in body size (i.e., from 150 to 320 mg wet mass, O'Neill in press), there was no correlation between robber fly head width and prey body length for the 83 pairs for which both values were known ($r = 0.06$, $P = 0.59$). However, some constraints from predator size are evident. There was a significant correlation between predator head width and prey body length when only the largest prey for each predator size class (i.e., 0.1 mm increment) was used in the analysis ($r = 0.61$, $n = 11$, $P = 0.04$). Furthermore, all of the asilids taken as prey by *S. inquinatus* were smaller than the predator (O'Neill in press).

Although *S. inquinatus* had a relatively broad diet breadth, the type of prey used reflected local abundance of insects. For example, 93% of the prey ($n = 70$) collected on 10 days within 5 m of active mating swarms of the ant *Formica subpolita* were winged ants. On eight occasions, we observed *S. inquinatus* fly into swarms of *F. subpolita* on and above *Rhus trilobata* Nuttall and capture an ant. We also collected prey before and after *Formica* swarms on the same 10 days and on six other days when swarms did not appear (but during weeks when swarms appeared on other days). In combined records for these nonswarm periods, only 25% of the prey were winged *Formica* ($n = 28$, $\chi_1^2 = 40.2$, $P < 0.0001$).

By switching to winged *Formica subpolita* during swarms, *S. inquinatus* appeared to have a greater frequency of successful foraging flights. On 4 Jul 1990, 17 of the 20 *S. inquinatus* observed during ant swarms had prey, all but one of which were winged *Formica*. Four days later at the same location, when the ants were not swarming, only one of 55 *S. inquinatus* observed had prey ($\chi_1^2 = 31.71$, $P < 0.0001$). By taking *Formica*, they used smaller prey than at other times. The mean length of winged *Formica* prey was 9.1 mm (SE = 0.11, $n = 59$), although that of all other prey was 15.5 mm (SE = 0.76, $n = 70$; Mann-Whitney test, $P < 0.0001$). There was a limit to which *S. inquinatus* would switch to locally abundant insects. They did not prey upon winged *Leptothorax* sp. (Hymenoptera: Formic-

idae) that swarmed at the same location as the *F. subpolita* on several days in 1988. This ant, which ranged in length from 2.2 to 4.4 mm ($\bar{x} = 3.1$ mm, SE = 0.23, $n = 13$), was well below the size range (6.6 to 29.5 mm) of prey used by *S. inquinatus*.

Other examples of site-specific prey use are evident in the prey records. Most honey bee (*Apis mellifera*) prey were collected at patches of leafy spurge (*Euphorbia esula* L.) and Snowberry (*Symphoricarpos* spp.) on which the bees were foraging. There was an apiary about 1 km E of the study site. The presence of cattle in the area may account for dung beetles (Scarabaeidae) being commonly taken as prey on open range.

DISCUSSION

Stenopogon inquinatus, in the Montana population that we observed, used a great variety of insects as prey. However, we found site-specific prey use near ant swarms and flowers. Increased predation on alate ants near mating swarms was also observed in the robber flies *Heteropogon wilcoxi* (James) (Lavigne & Holland 1969) and *Efferia staminea* (Williston) (unpublished data). Site-specific predation by *Stenopogon* has also been observed in studies conducted near apiaries, where 68% of the prey of *S. inquinatus* (Dennis & Lavigne 1975: Riverton, Wyoming prey samples) and 89% prey of *S. rufibarbis* Bromley (Cole 1958) were honey bees. Bromley (1942, 1948) also documents that honey bees are common components of robber fly prey records near flowers and apiaries, but does not compare these to records in other locations. Powell & Stage (1962) noted a difference in prey types of *S. engelhardti* Bromley between dry and moist habitats, with prey records in the latter being dominated by *Tipula coloradensis* (Doane) (Diptera: Tipulidae).

Given such site specificity, it is perhaps surprising that our prey records and those from Wyoming (Dennis & Lavigne 1975) are similar. Honey bees, winged ants, scarab beetles, and robber flies comprised 82% of the prey in Wyoming and 90% in Montana, although our value may be somewhat inflated due to our frequent observations near ant swarms. The Wyoming prey records do not include Hemiptera, but do include insects from two orders, Homoptera and Orthoptera, not found in our samples. However, these orders comprised just a small proportion of all prey in both our samples and those of Dennis and Lavigne. The size range of prey from the Wyoming populations (Dennis & Lavigne 1975: range = 5.0 to 29.5 mm, $\bar{x} = 14.5$ mm, $n = 127$) was also generally similar to that at our site (range = 6.6 to 29.5 mm, $\bar{x} = 12.5$ mm). The correspondence of prey records between areas is probably a reflection of similar grassland insect communities at the two sites.

The prey records presented cannot be used to draw strong conclusions regarding prey preference in an opportunist such as *S. inquinatus*. Simple lists of prey, even from a relatively restricted array of habitats, are liable to reflect several unrelated correlates of prey use. The contents of prey records are not only a function of local insect abundance, but of variation in visibility and catchability among prey species, as well as evolved preferences of robber flies for nutritionally superior or non-toxic insects (Shelly 1984). Our observations and other published reports on *Stenopogon* suggest that both local abundance and catchability (as influenced by size and flight speed) influence prey use. Slow flying insects that are probably easy

to capture are common in *Stenopogon* prey records (e.g., the use of alate *Formica* by *S. inquinatus* and crane flies by *S. engelhardti*, Powell & Stage 1962). However, the flies also include several strong flying species in their diets, such as honey bees and robber flies. Although honey bees are strong fliers, their tendency to hover and approach flowers slowly probably makes them susceptible to robber flies while foraging. In all cases of *S. inquinatus* predation on robber flies, the predator was larger than its prey, suggesting that predator size constrains its ability to take relatively formidable and strong flying prey (O'Neill in press). Thus, the upper limit of *S. inquinatus* prey size (represented by conspecifics) is apparently determined by catchability. The lower limit may be defined by the lower visibility or perceived unprofitability of small insects, such as *Leptothorax* alates that may be locally abundant, but which do not appear in prey records.

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A NEW GENUS AND SPECIES OF TRICHIINI FROM MEXICO (COLEOPTERA: MELOLONTHIDAE)

LEONARDO DELGADO-CASTILLO AND MIGUEL ANGEL MORÓN

Instituto de Ecología, A.C., Apdo. Postal 63,
91000, Xalapa, Veracruz, México

Abstract.—The adult and larva of *Iridisoma acahuizotlensis* NEW GENUS, NEW SPECIES from the State of Guerrero, Mexico, are described and illustrated. Relationships with *Paragnorimus*, *Dialithus* and *Giesbertiolus* are discussed. A modification of Howden's key to the North and Central American genera of Trichiini is included.

Resumen.—Se describen e ilustran el adulto y la larva de *Iridisoma acahuizotlensis* nov. gen., nov. sp. colectados en el estado de Guerrero, México. El único ejemplar conocido se obtuvo a partir de la cría de una larva de tercer estadio encontrada dentro de un tronco podrido. Se discuten sus relaciones con *Paragnorimus*, *Dialithus* y *Giesbertiolus*, comentando su distribución geográfica-ecológica. También se incluye una modificación a la clave para los géneros Norte y Centroamericanos de Trichiini.

Key Words.—Insecta, Coleoptera, Melolonthidae, *Iridisoma acahuizotlensis*

The North and Central American Trichiini are represented by 37 species included in eight genera (Howden 1968, 1970, 1971, 1972, 1988). All these taxa are apparently related to Old World genera, and the distribution of most of their species is relictual. The relationships between the American genera are vague, and at present they appear as distant taxa (Howden 1968). Only the larva of eight species of American Trichiini are known; these are in *Trigonopeltastes*, *Gnorimella* and *Trichiotinus* (Ritcher 1966, Morón 1983).

During summer, 1986, one cetoniid-like larva was collected from a rotten log in a disturbed subdeciduous tropical forest near Acahuizotla, Guerrero, Mexico. The larva was reared in the laboratory for seven months, emerging as a perfect adult male that showed characters that permitted easy separation from all other known genera of American Trichiini. This paper describes the new genus and species, based on the adult male, and the third instar larva, based upon its cast skin.

IRIDISOMA DELGADO-CASTILLO & MORÓN, NEW GENUS

Type Species.—*Iridisoma acahuizotlensis* Delgado-Castillo & Morón, NEW SPECIES.

Description.—Body oval-elongate, with conspicuous dorsal and ventral setae, without scales or cretaceous marks. Pronotum, scutellum, pygidium and venter iridescent green; elytra dull orange. Clypeus nearly as long as wide, with short erect setae, anterior border thickened, moderately emarginated. Mandibles membranous, maxillae with long, apical setae, mentum weakly widened, deeply emarginated. Frons and vertex with dense erect setae. Anteocular nocht present. Antennae 10-segmented. Pronotum longer than wide, semi-hexagonal, posterolateral borders parallel to and longer than convergent anterolateral margins; posterior angles well marked; dorsal surface with iridescent, rugose striae and numerous short, erected setae; margins well defined. Scutellum iridescent setose. Elytra longer than wide, with nonelevated interstriae and striae nearly obsolete; surface setose; lateral elytral declivity separated from elytral disc by a strong carina running from humeral to apical callus. Ventral

region with long setae, especially on metasternum. Middle coxae contiguous; tarsi longer than tibiae, tarsal claws entire, equal in length.

Male.—Pygidium wider than long, strongly convex apically, with abundant setae; fore tibiae unidentate; middle tibiae short, recurved inward, with inner apex projected as a hook-like structure and with an articulated spur.

Diagnosis.—*Iridisoma* is related with *Paragnorimus*, *Dialithus* and *Giesbertiolus*, but can be distinguished by the following combination of characters: pronotum, scutellum, pygidium and venter completely iridescent, unique pronotal sculpture and elytral carina. The shape of the pronotum and elytra give a distinct appearance to this trichiine.

Distribution.—Known only from the type locality.

Etymology.—Greek: “*iridos*,” a rainbow, “*soma*,” the body, in relation with the iridescent color of all of the body.

Discussion.—Because this genus is described only with the male characters, it is possible that many of the female structures may be different, especially the shape of the clypeus, the pronotal convexity, the shape of pygidium and abdomen, the tarsal length, and the structure of the fore and middle tibiae.

Key to the North and Central American Genera of Trichiini
Modified from Howden (1968)

- | | | |
|--------|--|------------------------------------|
| 1. | Anterior border of clypeus rounded, truncate or slightly emarginated.
Color variable but not iridescent | 2 |
| 1'. | Anterior border of clypeus moderate or strongly emarginated. Color at least partially iridescent | 7 |
| 2(1). | Pronotal disc without complete “V”-shaped or triangular impressions, uniformly convex or with slight longitudinal or transverse depressions | 3 |
| 2'. | Pronotal disc with complete “V”-shaped or triangular impressions, these marks usually cretaceous | <i>Trigonopeltastes</i> Burmeister |
| 3(2). | Pronotal disc with at least some fine, erect setae; in some cases with transverse cretaceous stripes or spots. Body ovate | 4 |
| 3'. | Pronotal disc without setae or impressions, slightly and uniformly convex. Body elongate | <i>Apeltastes</i> Howden |
| 4(3) | Elytral disc pubescent | 5 |
| 4'. | Elytral disc without setae | <i>Gnorimella</i> Casey |
| 5(4). | Elytra dull, without shiny elevations | 6 |
| 5'. | Elytra shiny, sometimes with two shiny elevations | <i>Trichiotinus</i> Casey |
| 6(5). | Pronotal disc with an incomplete cretaceous “V”-shaped or middle transverse line | <i>Peltotrichius</i> Howden |
| 6'. | Pronotal disc without cretaceous lines or dots | <i>Paragnorimus</i> Becker |
| 7(1'). | Dorsal surface glabrous or with sparse setae. Pronotum, pygidium and venter partially iridescent; elytra with iridescent spots. Pronotum with simple punctures and lines or with longitudinal sulci. Elytra convex, with lateral declivity sparsely marked | 8 |
| 7' | Dorsal surface densely setose. Pronotum, pygidium and venter completely iridescent, elytra dull. Pronotum with dense, transversely, rugose striae. Elytra with a strong carinae between the calla | <i>Iridisoma</i> NEW GENUS |

- 8(7). Clypeus longer than wide, bilobed. Pronotum with three central, longitudinal sulci. Fore tibiae of male unidentated *Dialithus* Parry
 8'. Clypeus slightly wider than long and moderately emarginated. Pronotum with a single middle longitudinal sulcus. Fore tibiae of male bidentated. *Giesbertiolus* Howden

Iridisoma acahuizotlensis Delgado-Castillo & Morón, NEW SPECIES
 (Figs. 1–14)

Type.—Holotype male, deposited in M.A. Morón collection (Xalapa, Mexico), final deposition in Instituto de Ecología, A.C. (Mexico); data: “MEXICO: Guerrero, Mochitlán, Acahuizotla, Cañada de Río Escondido. Altitud 650 m. Bosque tropical mediano subperennifolio.” “Ex larva colectada 1-IX-86 en albura de *Cedrela* sp. C.Deloya y L.Delgado, cols. Prepupa 7-III-87. Pupa 14-III-87. Adulto 3-IV-87.”

Male.—Holotype (Fig. 1). Total length (from the apex of clypeus to the pygidium): 15.1 mm. Maximum elytral width: 6.4 mm. *Clypeus.* Nearly as long as wide (0.9:1.0), wide and strongly emarginated, but not bilobed; anterior border thickened, slightly elevated; lateral borders keeled from the antecular notch towards apical third; clypea dull orange, darkened in the emarginated area; regular or fine punctulate with short, sparse, semierect setae. *Frons.* Black, strongly rugose toward the apex, with long, erect, dense setae. *Antenna.* Club slightly shorter than the funicle. *Pronotum.* Slightly longer than wide (1.0:0.9), anterior angles scarcely marked, middle angles rounded, and posterior angles acute, directed ventrally. Margins black. Covered with dense, semierect setae. *Scutellum.* Semiovate, slightly concave, colored as pronotum, with some semierect setae. *Elytra.* Longer than wide (1.0:0.84); dull orange, lateral margins and sutura black; area contiguous to lateral margin darkened; elytral carina brilliant orange. Surface finely rugose (best seen with counterlight), with nearly obsolete striae, except sutural striae slightly elevated near posterior third; short, semierect setae best seen at base and center. *Venter.* Iridescent, more intense than on pronotum. Metasternum with long, dense, decumbent yellow setae and a central arrow-shaped mark on the flat semitriangular disc. *Abdomen.* Slightly concave. Sternites I–IV equal in length, sternite V as long as III+IV, with the posterior border broad, slightly emarginated. Anal plate as long as the sternite V, posterior border nearly straight. Setae on the sternites long and decumbent. *Pygidium.* Wider than long (1.0:0.72), same color as sternites, with only narrow mesial stripe and apex dark red; rugose, with long, abundant, semierect setae distributed evenly. *Legs.* Coxae iridescent; femora brilliant orange with iridescent green shine on the anterior face and near the coxae. Fore tibiae spur shorter than basal tarsomere. Fore tibiae orange ventrally and dorsally, dorsolateral face black. Fore tarsi black, almost one-third longer than fore tibiae; tarsomeres I–IV short tuft of ventral setae, denser towards the tibiae. Middle tibiae dark orange, bent at apical one-half; mesotibial spur shorter than basal tarsomere (Fig. 2). Middle tarsi 2.0× longer than middle tibiae. Hind tibiae black, long and fine, scarcely thickened towards the apex, with a short, dorsal, transverse carina and two elongated, apical spurs. Hind tarsi nearly twice as long as tibiae. Middle and hind tarsi with long, stout setae on the ventral and apical surfaces (except the last tarsomere). All the tarsal claws nearly as long as tarsus V. *Genitalia.* Basal piece and tectum strongly convex; paramera directed downward in the basal part, but abruptly bent distally, with two long and fine processes widened apically; the apices are rounded and mesially directed (Figs. 3–4).

Third Instar Larva.—(Figs. 5–14). *Head.* Maximum width of head capsule: 3.5 mm. Surface of cranium slightly rugose, light yellow. Frons laterally bearing one minute posterior seta, one minute exterior seta, and two minute anterior setae; remaining cranial surface glabrous, except one dorsal epicraneal seta and two paraocellar setae laterally. Clypeus laterally bearing two long anterior setae and one minute exterior seta. Labrum semiovate, with two central setae and two lateral setae. Ocelli present (Fig. 5). Epipharynx (Fig. 6), without clithra and zygum, with only nine erected setae on haptomera; right chaetoparia with 38–40 spine-like setae and few minute fine setae; left chaetoparia with 20–22 fine setae; dextiotorma, laeotorma and sense cone well developed, acanthoparia with four or five curved setae. Scissorial area of left mandible with three teeth, well separated by two notches; molar area with one lobe, rounded acia, very prominent, acute ventral process, dense brüstia (Fig. 7). Scissorial area of right mandible with two teeth; molar area with three acute lobes, ventral process

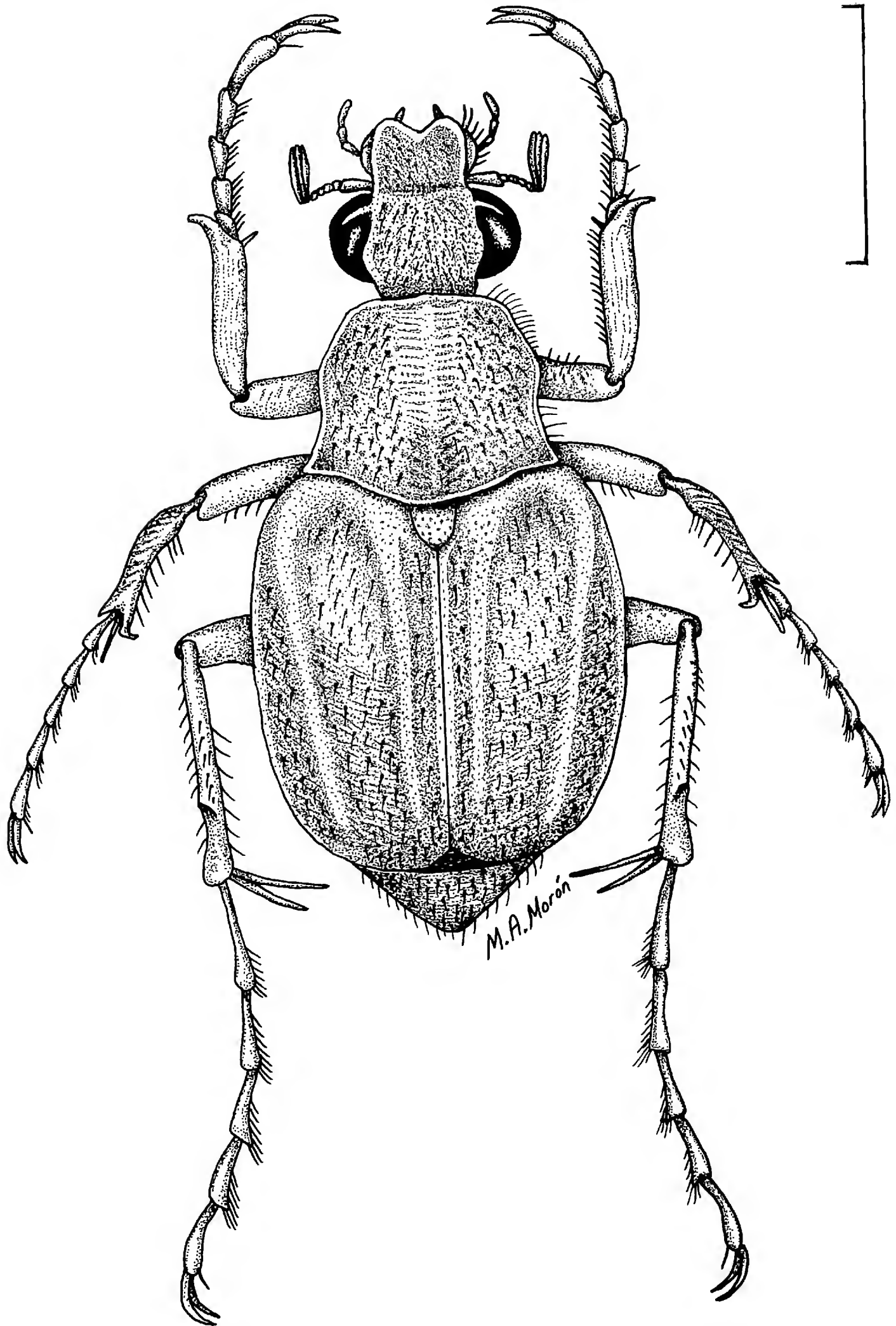
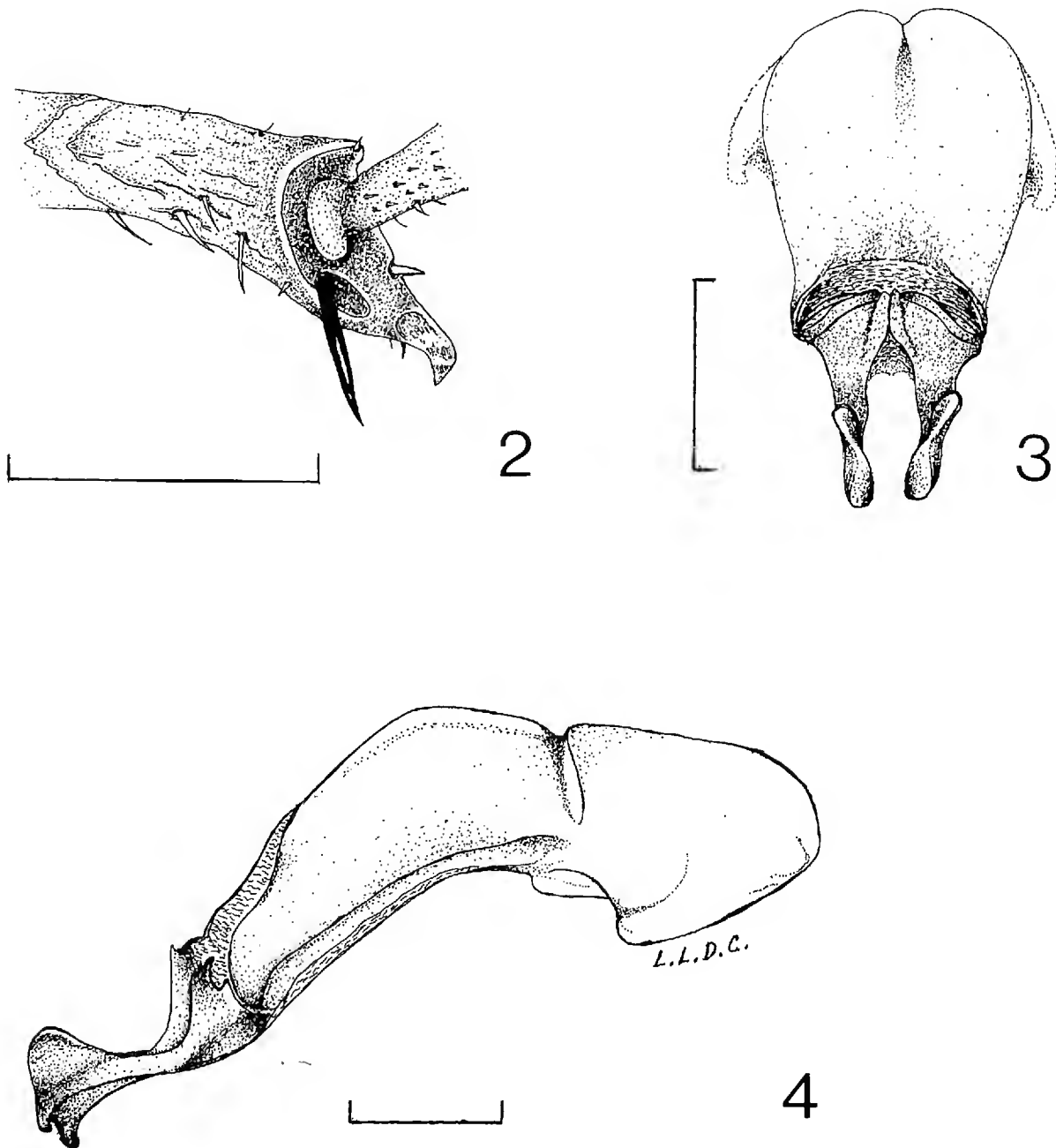


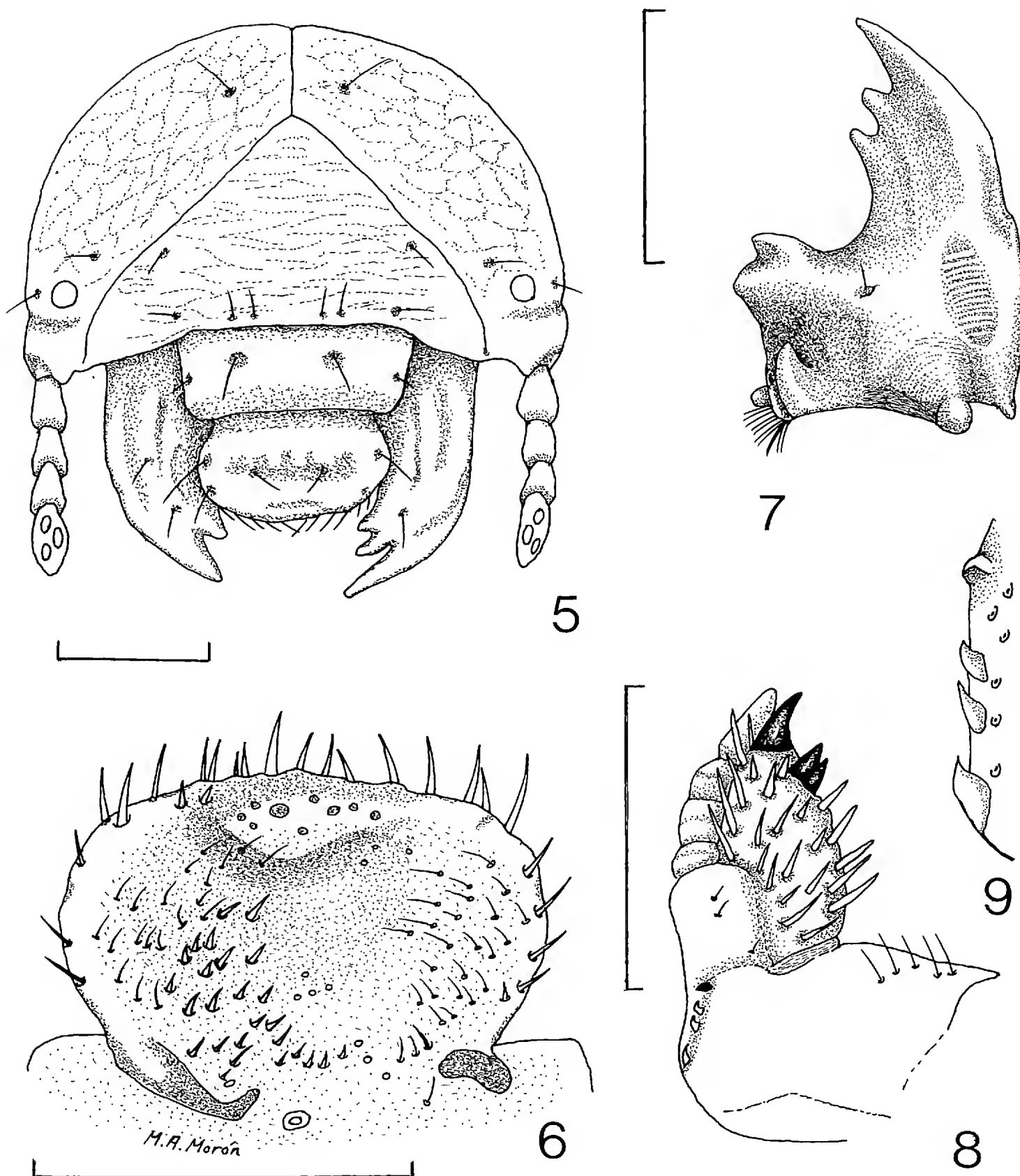
Figure 1. Dorsal view of the holotype of *Iridisoma acahuizotlensis* NEW GENUS, NEW SPECIES. Scale line 5 mm.



Figures 2–4. *Iridisoma acahuizotlensis*. Figure 2. Distolateral view of the apex of left middle tibia. Figure 3. Distal view of the male genital capsule. Figure 4. Lateral view of the male genital capsule. Scale lines are 1 mm.

less acute and prominent pointed calx and short brustia. Stridulatory area of each mandible formed by 13 fine striae. Galea with sharply pointed conical uncus; lacinia with two fused large conical unci; maxillary stridulatory area with only three sharp, anteriorly directed, recurved or angulated teeth, and a prominent distal, rounded process (Figs. 8–9). Labium short, with scarce small setae; hypopharyngeal sclerome strongly developed, prominent and heavily sclerotized (Fig. 10). Dorsal surface of last antennomere with three sensory spots (Fig. 11). *Thorax*. Thoracic spiracles 0.45 mm long and 0.30 mm wide. Respiratory plate with a maximum of 18–20 irregular elongate “holes” along any diameter, but not in definite rows. Arms of respiratory plate nearly contiguous, separated by a distance much less than the dorsoventral diameter of the bulla. Prothoracic sclerome light yellow. Dorsal and lateral setae long, regularly distributed. *Abdomen*. Dorsa of abdominal segments covered with numerous fine, long setae, regularly distributed. Spiracles I–VIII similar in size, 0.40 mm long and 0.30 mm wide. Distance between the two lobes of the respiratory plate much less than the dorsoventral diameter of the bulla (Fig. 12). “Holes” of the plate with irregular, elongate shape, similar to those on thorax (Fig. 13). Upper anal lip with a great number of short and long mixed setae. Septula and palidia absent. Lower anal lip with numerous long scattered setae. *Legs*. Claws falcate, sharp pointed, each bearing two proximal setae (Fig. 14). *Body length* approximately 23 mm.

Diagnosis.—The species presents many unusual characters and is remotely related to other Central American species. One diagnostic feature is the male’s genitalia capsule, with the parameres long, narrow, strongly curved and widened

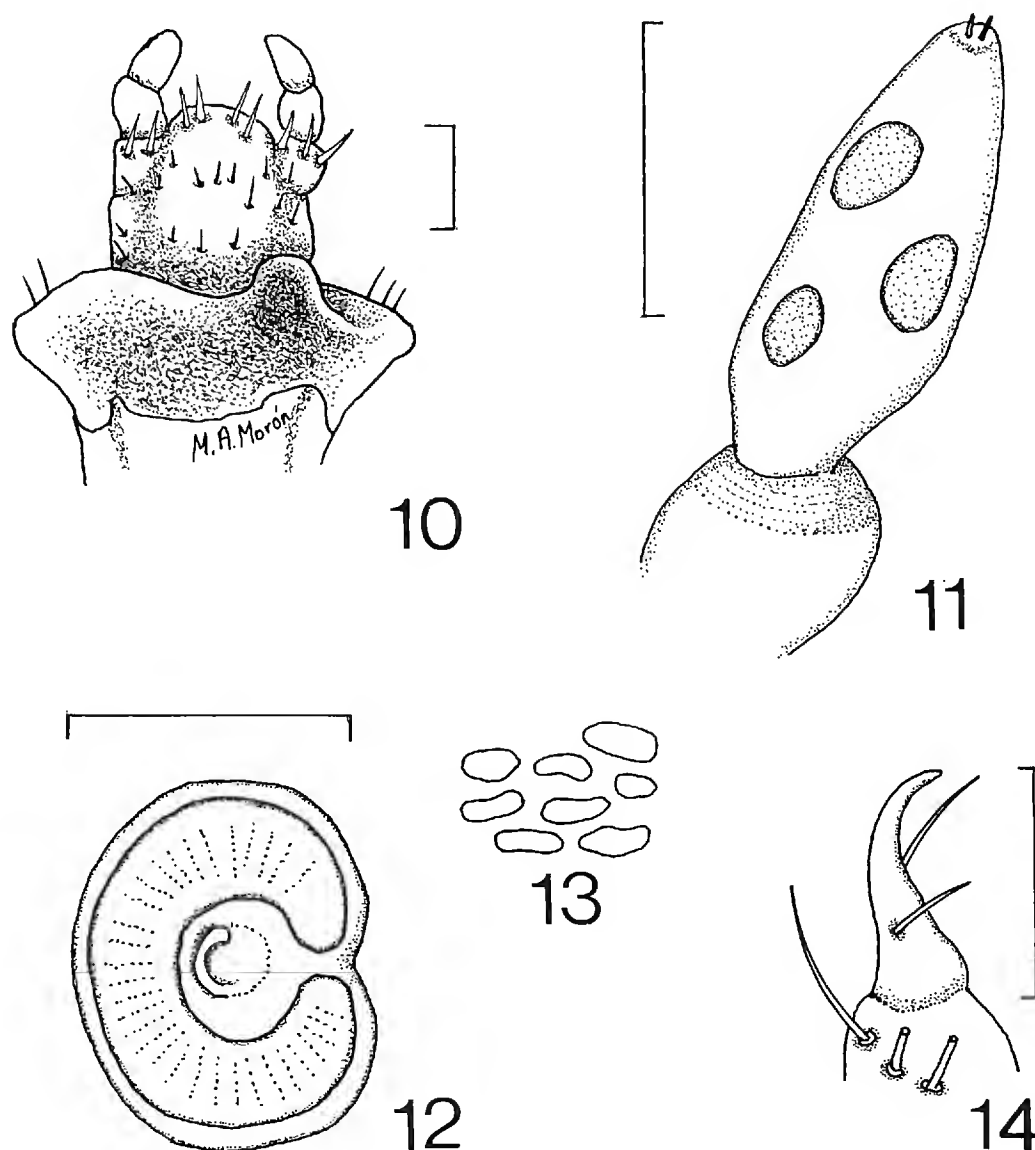


Figures 5–9. *Iridisoma acahuizotlensis* third-instar larva. Figure 5. Frontal view of head. Figure 6. Epipharynx. Figure 7. Inner view of left mandible. Figure 8. Inner view of right maxilla. Figure 9. Detail of right maxillary stridulatory area. Scale lines are 1 mm.

apically, not short, wide, straight or slightly curved and narrowed apically as in *Giesbertiolus* and *Dialithus*.

Etymology.—From the Mexican (Nahuatl) word “*Acahuizotlan*,” translated as “site of spiny reed grass” or “southern site of reed grass,” with the Latin suffix “*ensis*,” belonging to Acahuizotla.

Discussion.—The existence of this species in the Sierra Madre del Sur reinforces the relictual pattern of the montane southern Pacific distribution of these genera of Trichiini. We expect many other surprises in this poorly collected area, es-



Figures 10–14. *Iridisoma acahuizotlensis* third-instar larva. Figure 10. Inner view of hypopharynx. Figure 11. Dorsal view of last antennal article. Figure 12. Third abdominal spiracle. Figure 13. Detail of “holes” in the respiratory plate. Figure 14. Right hind tarsal claw, external view. Scale lines are 0.3 mm.

pecially in small humid, tropical or subtropical canyons, which support remnants of tropical subdeciduous forests. It is interesting that during three years of collecting, we only obtained the type specimen of *Iridisoma*; during that period, only 11 specimens of *Trigonopeltastes discrepans* Howden, *T. s. sallaei* Bates, *T. arquimedes* Schaum, *T. frontalis* Bates and *Apeltastes elongata* Howden were collected, always associated with the lower parts of the vegetation. Perhaps adults of *Iridisoma* are associated with the canopy of the subdeciduous tropical forest, represented in that locality, with trees 18 m high. The larval description is based on a single cast skin of a third instar larva reared to the adult stage.

According with the key to the larvae of American Trichiinae proposed by Morón (1983), *Iridisoma* must be placed near *Inca*, with reference to the absence of clithra, the number of dorsal sensory spots of the antennae, and the haptomerum without mesal tooth-like process. Also it is interesting that *Iridisoma* appears more related to *Trichiotinus* than *Trigonopeltastes*, based upon the mandibular and maxillar structures. It is necessary to know the larval morphology of other Central American genera of Trichiinae to understand their precise relationships.

Material Examined.—Type, reared from third instar larva; data: MEXICO. GUERRERO: Cañada de Rio Escondido, Acahuizotla, Mochitlán, 650 m, 1 Sep 1986, C. Deloya and L. Delgado, ex *Cedrela* sp. (Meliaceae) rotten log.

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DEVELOPMENT AND SURVIVORSHIP OF *CYDIA POMONELLA* (L.) (LEPIDOPTERA: TORTRICIDAE) AT TEN CONSTANT TEMPERATURES

MICHAEL J. PITCAIRN,¹ CAROLYN PICKEL,² LOUIS A. FALCON, AND FRANK G. ZALOM¹
Department of Entomological Sciences, University of California,
Berkeley, California 94720

Abstract.—Development and survivorship of *Cydia pomonella* (L.) immature stages were observed at 10 constant temperatures between 8.9° and 34.4° C. All stages failed to complete development at temperatures below 12.2° C. Fourteen percent of the eggs and no larvae or pupae survived at 34.4° C. The lower developmental thresholds, estimated by regressing developmental rate (1/days) against temperature, ranged between 10.5°–12.5° C. A nonlinear model based on Logan's function was fit to the observed data and provides a more complete description of the developmental rate-temperature relationship than a linear model.

Key Words.—Insecta, *Cydia pomonella*, developmental rates, threshold temperatures, Logan's model

Cydia pomonella (L.), codling moth, is the most destructive insect pest of walnuts, apples, pears and plums in California. Damage is caused by larvae feeding directly on fruit resulting in early fruit drop or unmarketable mature fruit (University of California in press). In the absence of effective biological and cultural controls, damage is prevented by properly timed insecticidal treatments. Spray timing is usually achieved using a degree-day model and pheromone trap catch data (Riedl et al. 1976; University of California 1987, in press).

The relationship between temperature and development of *C. pomonella* has been the subject of several studies (Glenn 1922, Shelford 1927, Hagley 1972, Williams & McDonald 1982, Rock & Shaffer 1983). Early studies were performed in an outdoor insectary under ambient air temperatures; later studies used constant temperature cabinets. However, all these studies investigated temperatures in the middle of the developmental rate curve, a portion that can be reasonably approximated by a straight line. For example, Rock & Shaffer (1983) reared larvae and pupae of moths collected in North Carolina at 16°, 22°, 28°, and 32° C. The lower thermal threshold (9.9° C) was estimated by regressing developmental rate against temperature; the upper thermal threshold was suggested to occur above 32° C.

Studies have shown that the relationship between codling moth developmental rate and temperature is significantly nonlinear (Rock & Shaffer 1983, Gold et al. 1987). Recent field studies in California showed that development under high summer temperatures (> 30°C) was slower than predicted using a linear degree-day model (MJP & FGZ, unpublished data). We suggest that a nonlinear model may better represent moth development, especially when temperatures routinely exceed the upper thermal threshold. Here, we examine the rate of immature

¹ Statewide IPM Project, University of California, Davis, California 95616.

² University of California Cooperative Extension, 142A Garden Highway, Yuba City, California 95991.

development of *C. pomonella* at 10 constant temperatures to provide a more complete description of its developmental rate curve and fit a nonlinear model to the data.

MATERIALS AND METHODS

Cydia pomonella larvae, pupae, and adults were selected from a laboratory colony maintained on artificial diet (modified after Vanderzant & Davich 1958) at about 23° C and natural photoperiod. The colony was initiated with adults collected in apple orchards near Placerville, California. Eggs were obtained by placing 20 adult pairs in a metal rotating oviposition cage (Batiste & Olson 1973) 2–3 h before sunset; eggs were collected 4 h later and put into a vegetable crisper at 100% RH and immediately placed into a temperature cabinet. Sample size varied from 42–89 eggs.

Developing larvae were maintained individually on artificial diet (approximately 10 ml) in 30 ml plastic cups. The end of the larval stage was when larvae began to spin a cocoon. Pupal development was examined using individuals that started cocoons on the same day.

Ten constant temperature regimes were used: 8.9°, 10.0°, 11.1°, 12.2°, 15.6°, 25.6°, 27.8°, 30.0°, and 34.4° C. At 15.6° C and above, egg hatch was checked every 24 h; at 12.2° C and below, egg hatch was checked at 1–3 day intervals. Larvae and pupae were examined for completion of their developmental stage every 1–2 days at 15.6° C and above, and at 1–3 day intervals at temperatures below 15.6° C. The end of a stage was recorded as the midpoint between two observations.

The relationship between temperature and developmental rate (rate = 1/days) was described by linear and nonlinear regression models. Parameter estimates of the linear model were calculated by regressing observations at 15.6°–32.2° C (the X-intercept method of Arnold 1959). Parameter estimates of the nonlinear model were calculated using Marquardt's method of least-squares (SAS Institute 1985).

RESULTS AND DISCUSSION

The survivorship and mean duration of development for the egg, larval, and pupal stages are presented in Table 1. Development was not observed in any stages at 8.9° and 10.0° C but was noted in all stages at 11.1° and 12.2° C. Eggs maintained at 8.9° and 10.0° C remained in the opaque white stage (Richardson et al. 1982), but those at 11.1° and 12.2° C developed to the blackhead stage and then died. Hagley (1972) studied the development of *C. pomonella* eggs at several constant temperatures, and reported that while all eggs failed to hatch at 10.0° C, 27% developed to the blackhead stage before dying. Successful egg hatch, however, did occur at 11° C. In our study, egg survival was highest between 15.6°–27.8° C, was lower at 30.0°–32.2° C and substantially lower at 34.4° C. These results corroborate Hagley's (1972) observations of reduced egg hatch at temperatures above 30° C. Larval survivorship in our study was >80% between 27.8°–32.2° C; pupal survivorship was >80% between 27.8°–30.0° C. No larvae or pupae survived at 34.4° C.

The number of days required to complete embryogenesis declined between 15.6°–27.8° C then increased with increasing temperature. For the larval stage, there was a general increase in developmental rate with increasing temperatures

Table 1. Survivorship and mean days required for development of immature stages of *Cydia pomonella* at different constant temperatures.

Temperature (°C)	Stage												
	Egg				Larva				Pupa				Total
	<i>n</i> ^a	S ^b (%)	Development (mean days ± SE)	Range (days)	<i>n</i>	S (%)	Development (mean days ± SE)	Range (days)	<i>n</i>	S (%)	Development (mean days ± SE)	Range (days)	Development (mean days)
8.9	75	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
10.0	73	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
11.1	78	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
12.2	80	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
15.6	89	77.5	19.26 ± 0.55	18.0–20.5	30	53.3	62.21 ± 2.75	54–82	20	25.0	68.18 ± 1.36	66–75	149.65
25.6	61	78.7	6.47 ± 0.42	5.0–7.0	30	76.7	17.14 ± 0.53	15–23	18	61.1	17.32 ± 0.56	15–21	40.93
27.8	64	79.7	4.21 ± 0.00	—	30	83.3	13.42 ± 0.22	11–17	19	89.5	10.10 ± 0.34	9–14	27.73
30.0	63	58.7	4.27 ± 0.33	3.5–5.5	23	87.0	14.68 ± 0.41	12–19	20	80.0	10.85 ± 0.58	7–15	29.80
32.2	75	49.3	4.56 ± 0.23	4.0–5.0	30	80.0	11.27 ± 0.25	11–14	18	22.2	10.71 ± 1.34	8–14	26.54
34.4	42	14.3	5.40 ± 0.57	5.0–6.0	30	0.0	—	—	30	0.0	—	—	—

^a Sample size.^b Survivorship.

Table 2. Linear regression equations and estimates of lower developmental thresholds using mean developmental rates for immature stages of *Cydia pomonella*.

Stage	Regression equation ^a	SE of regression coefficient	r ²	Lower threshold ^b (°C)
Egg	$Y = -0.121 + 0.0115 \cdot X$	0.0024	0.88	10.56
Larva	$Y = -0.048 + 0.0042 \cdot X$	0.0005	0.96	11.54
Pupa	$Y = -0.065 + 0.0052 \cdot X$	0.0011	0.89	12.49
Egg-to-Adult	$Y = -0.023 + 0.0019 \cdot X$	0.0003	0.94	11.85

^a Regression equation is $Y = a + bX$, where Y is the developmental rate (1/days) and X is temperature (°C).

^b X-intercept.

above 15.6° C, the fastest rate occurring at 32.2° C. Little change in the rate of pupal development was observed at 27.8°–32.2° C. These results suggest that the upper developmental thresholds are near 27.8° C for the egg and pupal stages, and 32.2° C for the larval stage.

The estimated lower thermal thresholds and associated linear regression equations are presented in Table 2. The coefficient of determination, r^2 , was high for all stages. Estimates of the lower thermal threshold ranged between 10.5°–12.5° C and are similar (or slightly lower) to the minimum temperatures for which development was observed. The average number of degree-days (° D) above the estimated threshold of 11.85° C for total development (egg to adult) is 529.45° D.

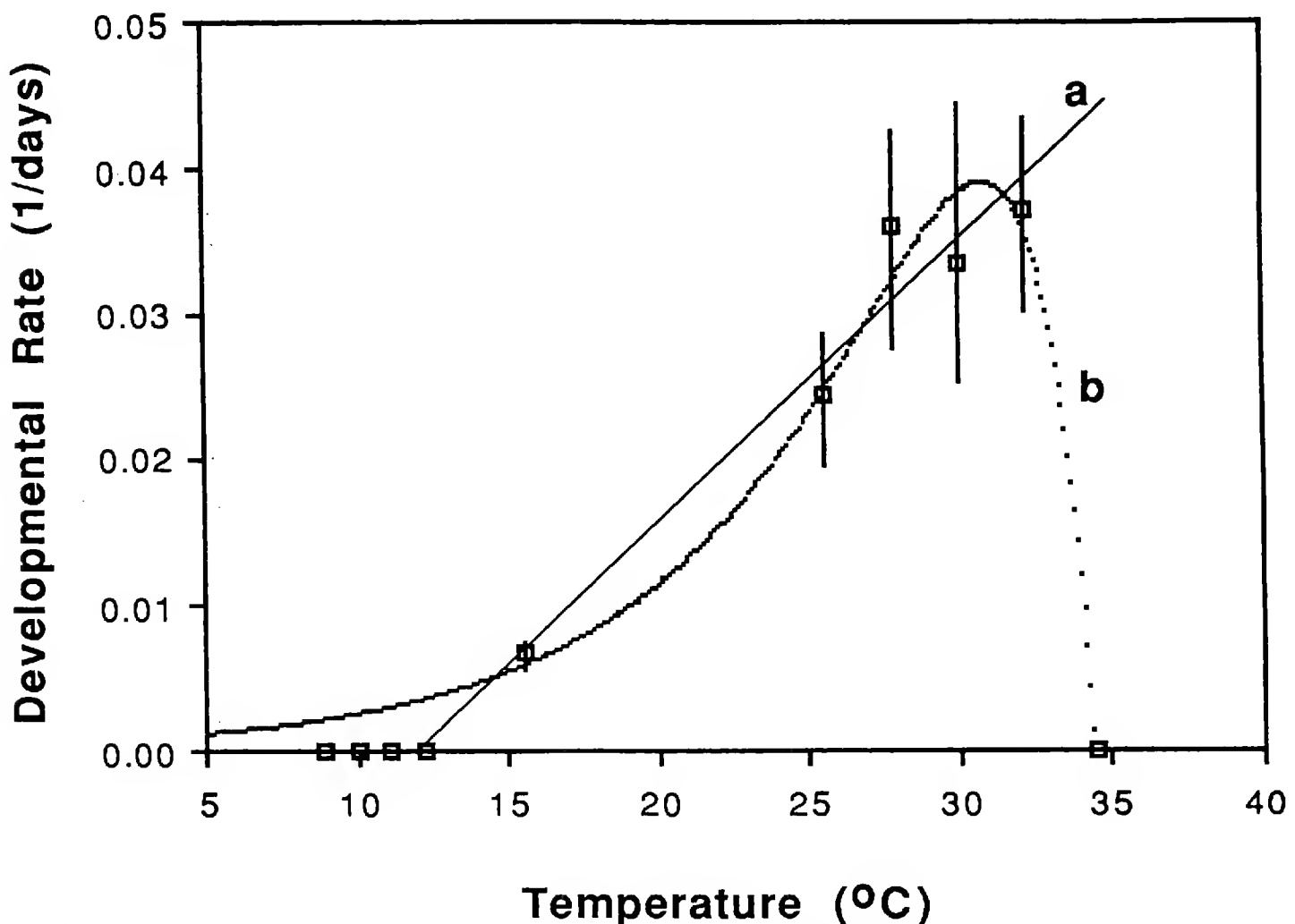


Figure 1. Rate of total (egg to adult) development as a function of temperature for *Cydia pomonella* (a = linear regression for the temperature range of 15.6–32.2° C; b = nonlinear model after Logan et al. 1976; means are given with range of observed values; parameter estimates are given in Tables 2 and 3).

Table 3. Parameter estimates of Logan's model to describe the relationship between *Cydia pomonella* developmental rate and temperature. In the model, rate = $a\{\exp[b \cdot x] - \exp[b \cdot c - (c - x)/d]\}$.

Life stage	Parameter estimates				df ^a
	a	b	c	d	
Eggs	0.0767	0.1921	36.1601	5.1617	265
Larvae	0.0036	0.1067	34.4463	1.2581	129
Pupae	0.0013	0.2443	34.4441	3.8968	61
Total development	0.0006	0.1490	34.4493	2.1796	3

^a Degrees of freedom.

The most commonly reported lower thermal threshold in the literature for *C. pomonella* is 10° C. Using this value for comparison, the average number of degree-days required to complete development of the egg, larval, and pupal stages are 93.87° D, 280.62° D, and 256.93° D, respectively; the mean duration of total development is 631.42° D. Glenn (1922) presented data showing that an average of 645.00° D (base 10° C) were required for total development. In our study, the average number of degree-days from newly emerged larvae to adults was 537.55° D (base 10° C), a value similar to other studies (all base 10° C): 552.78° D (Glenn 1922), 494° D (Williams & McDonald 1982), 514° D (Rock & Shaffer 1983).

The average number of days for the total developmental period was estimated as the sum of the means for the egg, larval, and pupal stages. These data are plotted in Fig. 1 along with the range of observed values. Low or no survival at 34.4° C indicates that high temperature can inhibit *C. pomonella* developmental rate. A nonlinear function based on Logan's model (Logan et al. 1976) was used to describe the rate-temperature relationship (Fig. 1). The parameter estimates for each life stage are given in Table 3. For total development, the calculated lethal maximum temperature with 100% mortality was 34.45° C; the fastest rate of development was calculated to occur at 30.82° C. In contrast with the linear model, Logan's model exhibits a rapid decline at temperatures >31° C and also fits the data well in the intermediate temperature range.

Linear models of development have become widely used in practice because they have worked well for a wide variety of insects, they are easily modified (e.g., adding an upper thermal threshold), and their parameters are easily estimated from developmental data. Our study is significant because not only are the intermediate temperatures examined, but also temperatures at the upper and lower thermal limits of development. When a nonlinear function is fit to our data, a more complete description of the developmental rate curve of *C. pomonella* is presented. Air temperatures exceed 31° C almost daily during July through September in most regions of California where *C. pomonella* is found (University of California 1983) and use of this nonlinear model should improve prediction of immature development during these summer months.

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**DESCRIPTION OF THE LARVA OF *ATRACTELMIS*
(COLEOPTERA: ELMIDAE) AND NEW
INFORMATION ON THE MORPHOLOGY,
DISTRIBUTION, AND HABITAT OF
ATRACTELMIS WAWONA CHANDLER**

WILLIAM D. SHEPARD AND CHERYL B. BARR

Department of Biological Sciences,
California State University, Sacramento,
Sacramento, California 95819

Abstract.—Collection of additional specimens of *Atractelmis wawona* Chandler has allowed descriptions of the female and larva. The species' known geographic distribution is from northern California to southern Oregon and Idaho. Submerged aquatic mosses are the preferred microhabitat.

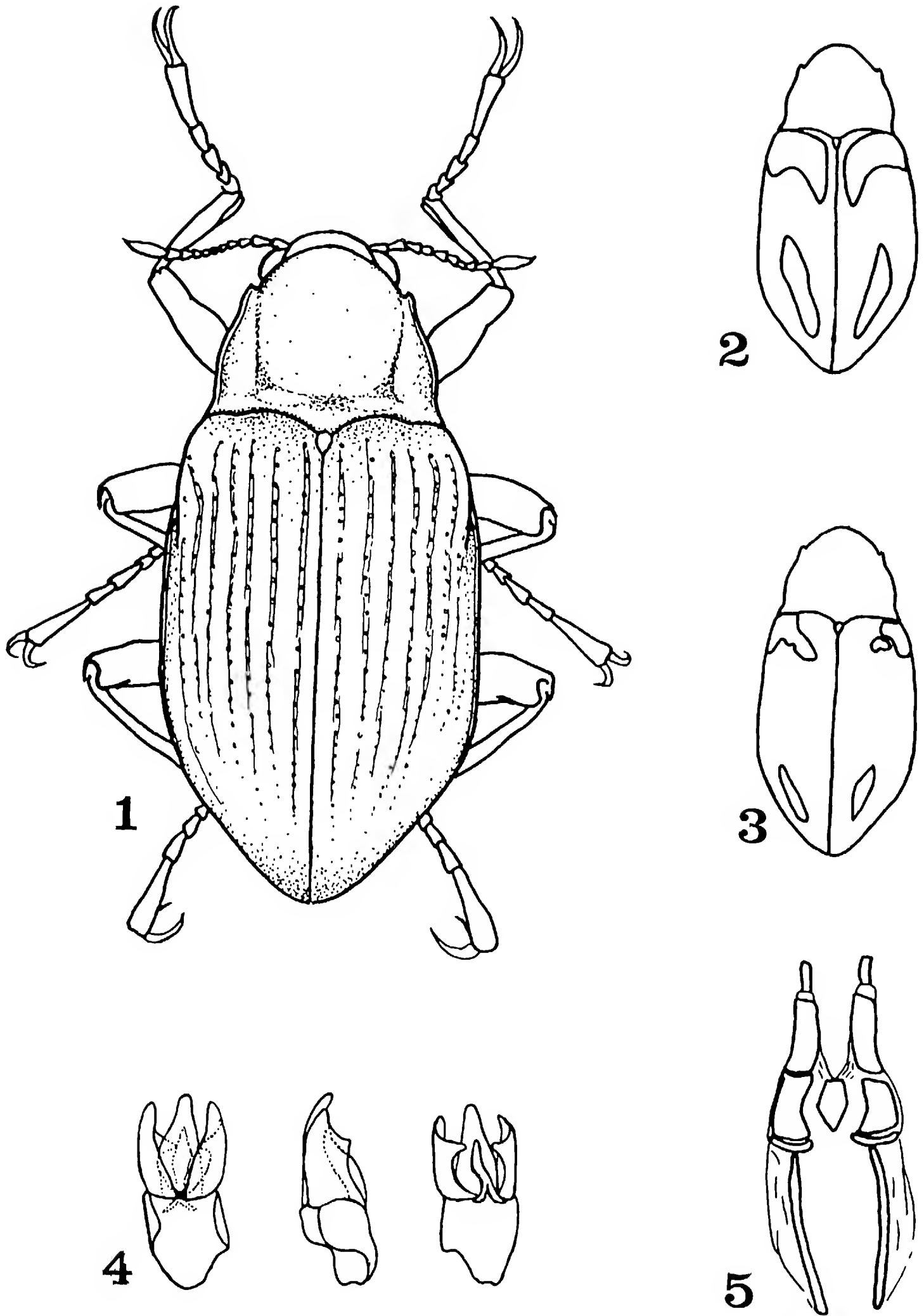
Key Words.—Insecta, Coleoptera, Elmidae, *Atractelmis*, descriptions, distribution, microhabitat

Atractelmis wawona Chandler for many years has been the most elusive riffle beetle in the Nearctic region. This monospecific genus was described from two specimens by Chandler in 1954. Despite serious attempts, it was not collected again until 1969, when Harley P. Brown took a single specimen at Wawona, California, the type locality. Sixteen years later, Brown collected a few more specimens from a new locality near Wildwood, California. We spent several years unsuccessfully searching for the species.

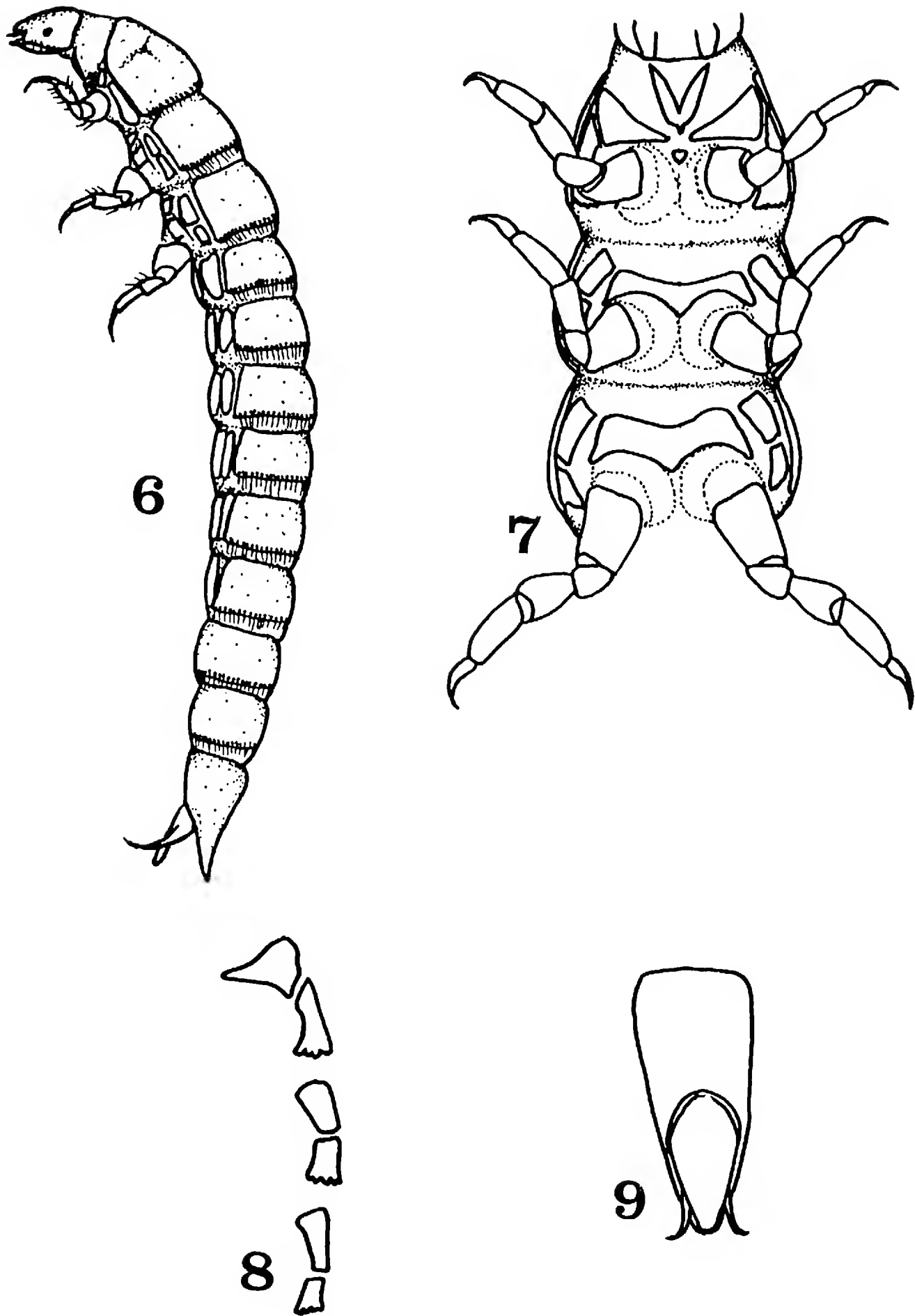
In 1988, a re-examination of the morphology of a specimen showed similarities to *Promoresia*, an eastern Nearctic genus that usually inhabits aquatic mosses. Careful examination of mosses at locations where *Atractelmis wawona* had been previously collected revealed this species to be present, and demonstrated its strong preference for inhabiting aquatic mosses. We now describe the female and larva, both of which were unavailable to Chandler.

ATRACTELMIS CHANDLER

Larva.—Body elongate (Fig. 6), hemicylindrical in cross section; dark brown; sclerites densely tuberculate, intersegmental membranes lightly sclerotized, tan; head prognathous; posterior border of thoracic and abdominal terga I–VIII with numerous tubercles bearing elongate stout plumose setae (giving intersegmental areas a fringed look). Mature length 4.8–5.0 mm. Head highly sclerotized, dark; dorsum very tuberculate; epicranial suture U-shaped with very short stem, arms ending near antennal bases; stemmata distinct; edge of frons straight, smooth. Each antenna three-segmented, each segment with apical setae; segment one as wide as long; segment two 3× as long as wide; segment three 3× as long as wide but one-third the size of segment two. Labrum transversely rectangular, with anterior border of several stout setae. Each mandible bluntly trifold; molar brush present. Each maxilla with galea and lacinia distinct, armed with a brush of stout medially-curved setae; palpus three-segmented, segment one as long as wide, segments two and three longer than wide, segment three with peg-like setae apically. Labium 2× as long as wide, apex truncate, one stout seta present on each side just anterior to middle; each palpus short, two-segmented, segments each as wide as long and having blunt apical setae. Cervical area lightly sclerotized; accessory sclerites (= cervical sclerites) greatly elongate, diverging anteriorly away from a single area (V-shaped) (Fig. 7). Thoracic terga with middorsal suture (or line); prothorax with a transverse triangular depression in anterior one-half on each side. Prosternum



Figures 1–5. Adult *Atractelmis wawona*. Figure 1. Habitus. Figure 2. Normal color pattern. Figure 3. Color pattern variant. Figure 4. Male genitalia in dorsal, lateral and ventral views. Figure 5. Female genitalia.



Figures 6–9. Larval *Atractelmis*. Figure 6. Habitus. Figure 7. Ventral thoracic structures. Figure 8. Left thoracic pleurites. Figure 9. Abdominal segment IX (ventral view) and operculum.

reduced to triangular sclerite between and anterior to procoxae; meso- and metasternum very transverse, lightly tuberculate. Pro-, meso-, and metathoracic pleurites divided into two sclerites (Fig. 8); prothoracic prepleurites with medial extensions that almost meet anterior to procoxae. All legs similar (Fig. 7), all coxal cavities open; each coxa conical, anterolaterally with several stout setae; trochanter well developed, subequal to femur; femur and tibia $2\times$ as long as wide, with numerous setae; tarsungulus bluntly pointed, having one stout seta on medial border. Abdomen nine-segmented; segments

I–VI with separate tergites, pleurites and sternites; segments VII–IX with all sclerites united into a ring. Middorsal line present on segments I–VIII. Segment IX 2× as long as segment VIII, slightly truncate apically, dorsally slightly sinuate (lateral view), having an elongate pentagonal operculum (Fig. 9). Operculum with two posteroventrally directed claws on inner surface, and covering three tufts of perianal tracheal gills each with 7–10 gill filaments. Gill filaments furcate basally (most bifurcate, some trifurcate). Spiracles present on mature larva on sides of mesonotum and abdominal segments I–VIII.

Atractelmis wawona Chandler

Adult Morphology.—The pronotal sculpturing is quite distinct from that of any other Nearctic elmids (Fig. 1), particularly the bulbous disk and the transverse posterior sulcus. The color pattern exhibited by this species is remarkably invariable. Each humerus has a broad comma-shaped macula with the tail near the elytral suture (Fig. 2). The subapical maculae are elongate and directed medially posteriorly. The single variant color pattern we have found has the spots somewhat reduced in size (Fig. 3).

Chandler (1954) described the adult male well, except for one minor detail of the genitalia: the median piece has an elongately sinuate, Y-shaped sclerite on the ventral side (Fig. 4). Chandler's drawing has detail in this area that resembles sutures or folds in the membranes. We have found no external difference between the sexes. The female genitalia are typical for elmids (Fig. 5).

Habitat and Microhabitat

Larvae and adults of *A. wawona* co-occur. They are usually found in cool, small- to medium-sized, mountain streams; in these sites they are most numerous in aquatic mosses. The greatest number of specimens we have collected at once came from the moss *Platyhypnidium riparioides* (Hedwig) Dixon. However, we have also collected specimens from submerged roots of Indian rhubarb, *Peltiphyllum peltatum* (Torrey) Engler, and of riparian trees.

Geographical Distribution

Atractelmis wawona occurs throughout the northern half of California and parts of southern Oregon and Idaho. Although it is probably even more widely distributed, its restricted microhabitat has hidden it from those few who have searched for it, as noted by Chandler (1954).

Distribution Records.—CALIFORNIA. *HUMBOLDT Co.*: 1.6 km (1 mi) west of Dinsmore, Van Duzen River, 13 Jul 1988, W. D. Shepard, 2 adults and 1 larva. *MARIPOSA Co.*: nr Wawona, South fork of Merced River, 17 Jul 1946, H. P. Chandler, 1 adult (holotype); Wawona, South Fork of Merced River, 18 Jul 1969, H. P. Brown, 1 adult. *PLUMAS Co.*: 1.6 km (1 mi) NE of Indian Falls, Indian Creek, 19 Aug 1989, W. D. Shepard and C. B. Barr, 2 larvae. *SHASTA Co.*: Middle Fork of Cottonwood Creek, 24 Jun 1952, H. P. Chandler, 1 adult (paratype). *SHASTA-TEHAMA Co. Border*: Beegum, Beegum Creek, 12 Jul 1988, W. D. Shepard, 10 adults and 25+ larvae; same but 4 Sep 1988, W. D. Shepard and C. B. Barr, 5 adults and 31 larvae; 10.5 km (6.5 mi) S of Platina, North Fork of Beegum Creek, 17 Jul 1990, W. D. Shepard and C. B. Barr, 15 larvae. *SISKIYOU Co.*: 4.8 km (3 mi) SE of Cecilville, South Fork of Salmon River, 21 Jul 1990, W. D. Shepard and C. B. Barr, 11 adults and 1 larva. *TRINITY Co.*: 6.4 km (4 mi) W of Wildwood, Hayfork Creek, 12 Jul 1988, W. D. Shepard, 4 adults and 11 larvae; 3.2 km (2 mi) N of Wildwood, Hayfork Creek, 4 Sep 1988, W. D. Shepard and C. B. Barr, 62 adults and 25+ larvae; same but 17 Jul 1990, W. D. Shepard and C. B. Barr, 24 adults; below Wildwood, Gemmill Gulch, 23 Jun 1985, H. P. Brown, 3 adults; Mad River (town), (on the Mad River, 13 Jul 1988, W. D. Shepard, 1 larva. IDAHO. *ADAMS Co.*: 19.3 km (12 mi) N of New Meadows, Little Salmon River, 17 Aug 1989, W. D. Shepard and C. B. Barr, 3 adults and 11 larvae.

OREGON. CROOK Co.: 4.8 km W of Forest Service Headquarters, Meehan, Ochoco Creek, 26 Jul 1974, R. E. Miller, 1 adult.

DISCUSSION

Brown's (1972:62) key to the genera of aquatic dryopoid larvae of the United States can be modified to include *Atractelmis* as follows (we retain Brown's [1972] style for the key couplets below; the figure numbers listed refer to that work):

- 26 (25) Body robust, broad, subtriangular in cross section; with spatulate spines along lateral margins and mid-dorsal line (Figs. 169, 170):
Ampumixis
 Body long and slender, hemicylindrical; without prominent clusters of spines 26 A
- 26A (26) Abdominal segments 7 and 8 with no longitudinal sutures, segments 1–6 with pleurites; posterior border of nota and terga with tubercles having elongate setae well sclerotized: *Atractelmis*
 Abdominal segments 7 and/or 8 divided by tergo-sternal sutures, pleurites on segments 1–6 or 1–7; posterior border of tubercles with setae not or poorly sclerotized: *Cleptelmis*

Because *Atractelmis* was the last elm mid genus in the United States for which larvae were unknown, we now can concentrate on separating the species in the larval stage.

Adult morphological characters indicate that *Atractelmis* is closely related to *Cleptelmis*, *Rhizelmis* and *Ampumixis*. Externally, adult *Atractelmis* look most similar to adult *Rhizelmis* that are quadrimaculate. This morph of *Rhizelmis*, however, is equally as rare as *Atractelmis*. Fortunately, the two genera do not occur in the same microhabitat. Larval morphology links *Atractelmis* very strongly with *Cleptelmis*, and less strongly with *Ampumixis*. Larval synapomorphies shared with *Cleptelmis* include the number of abdominal pleurites, and the posterior fringe of tubercular setae on thoracic and abdominal segments (weakly developed in *Cleptelmis*). Habitat and/or microhabitat preferences of *Atractelmis* also show similarities to those of *Rhizelmis*, *Ampumixis* and, especially, *Cleptelmis*. In fact, the collection of any of these genera suggests that the others may be present also.

ACKNOWLEDGMENT

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**A NEW SPECIES OF FOSSIL *DASYMUTILLA*
(HYMENOPTERA: MUTILLIDAE) FROM
DOMINICAN AMBER**

DONALD G. MANLEY¹ AND GEORGE O. POINAR, JR.²

¹Department of Entomology, Clemson University,
Pee Dee Research and Education Center,
Florence, South Carolina 29501

²Department of Entomological Sciences, University of California,
Berkeley, California 94720

Abstract.—*Dasymutilla dominica*, a new species of mutillid wasp, is described from a fossil specimen embedded in a piece of Dominican amber estimated to be from 25 to 40 million years old. Very few fossil mutillids have been recorded, and this represents the first description of a fossil mutillid from the New World. This male belongs to the *bioculata* species-group, and can be distinguished from closely related species by its totally black integument.

Key Words.—Insecta, *Dasymutilla dominica*, Mutillidae, new species, fossil, Dominican amber

Fossil velvet ants, or mutillids, are extremely rare and thus far have been limited to Palaearctic forms. Menge (1856) mentioned finding six specimens of this family in Baltic amber and Brischke (1886) cites another three in the same deposits. In addition, Larsson (1978) mentions an additional three in the Copenhagen collection of Baltic amber insects. To our knowledge, none of the above have been described. Scudder (1891) also makes reference to an undescribed *Mutilla* from the mid-Oligocene beds (not amber) located in Brunstatt, Alsatia (now Alsace), in northeastern France.

Bischoff (1915) described seven species of fossil mutillids from Baltic amber, placing them in a new genus, *Protomutilla*. Although Krombein (1979) suggests that at least one of those species may not be correctly assigned to the family Mutillidae, that does, nevertheless, appear to be the first description of a fossil mutillid.

Sharov (1957) described another new species of aculeate Hymenoptera from the Cretaceous of Siberia, which was ultimately assigned to Mutillidae. That fossil specimen, estimated to be about 80 million years old, was called *Cretavus sibiricus* Sharov, for which the author created a new family, Cretavidae. However, Rasnitsyn (1975) determined that the specimen was justified in being placed in the family Mutillidae.

We describe here a mutillid from a piece of Dominican Republic amber. This represents the first record and description of a fossil mutillid from the New World.

METHODS AND MATERIALS

The piece of amber containing the mutillid was lent to GOP for study by Aldo and Didi Costa of Puerto Plata, Dominican Republic. The original piece had to be reshaped in order to better obtain a closer examination of the specimen. It is presently semi-hemispherical, measuring 30 mm in greatest length, 16 mm in

greatest width, 12 mm in greatest depth and weighing 3.5 g. The amber is golden in color with a red tinge on one surface.

The piece of amber originated from mines located in the Cordillera Septentrional mountain ranges in the northern Dominican Republic. An analysis of amber from seven Dominican mines by nuclear magnetic resonance spectroscopy suggests that amber from that area ranges in age from 25 to 40 million years (Lambert et al. 1985).

DASYMUTILLA DOMINICA MANLEY & POINAR, NEW SPECIES

(Figs. 1–3)

Type.—Holotype male, data: DOMINICAN REPUBLIC. Cordillera Septentrional mountains; deposited in the Museum of Dominican Amber, Puerto Plata, Dominican Republic.

Description.—*Male.* Integument black; pubescence sparse, mostly pale, erect or semierect; length about 8 mm. Head black, rounded, sparse pale pubescence throughout; head slightly narrower than thorax. Eyes and ocelli normal; eyes large, not bulging; ocelli small; ocello-ocular distance about $4.0 \times$ greatest width of ocelli. Relatively large, well-separated punctures throughout. Mandibles bidentate, black throughout. Clypeus bidentate (but cannot be seen clearly). Antennae black; flagellomeres subequal in length; scape bicarinate beneath, coarsely punctate; antennal scrobes not carinate (but not clearly visible). Thorax black, longer than broad, predominantly with sparse pale pubescence, with moderately large, well-separated punctures. Pronotum with humeral angles rounded; anterior margin apparently not emarginate (consistent with evenly rounded posterior margin of head). Mesonotum without laterally expanded lobes. Propodeum coarsely reticulate. Tegulae subhemispherical, with moderately large punctures; anterior margin with black pubescence. Pleura coarsely punctate throughout. Prothorax, scutellum, propodeum, and pleura with sparse pale pubescence; mesothorax with black pubescence. Legs black, with sparse pale pubescence; calcaria pale; apices of middle and hind femora rounded; posterior trochanters normal, not toothed; hind tibiae cylindrical, not flattened on inner margin. Wings (badly damaged, clipped off near base) with basal third (right wing) hyaline, dark veins. Abdomen black throughout. Terga and sterna I and II with coarse punctures; apical one-half of remaining segments with smaller, shallower punctures. Tergite I with sparse, pale pubescence; conspicuously lacking an apical fringe of hairs. Sternite I with a longitudinal carina about nine-tenths the length of the segment. Tergite II with anterior two-thirds having sparse, pale pubescence; posterior third with sparse, black pubescence; apical fringe pale. Terga III and IV with sparse, pale pubescence with pale apical fringes of hairs. Terga V and VI with black pubescence throughout, including apical fringes. Felt lines with black pubescence. Sterna I–IV with sparse, pale pubescence; II–IV with apical fringes of pale hairs. Sterna V–VI with black pubescence. Sternite II with a round, median pit filled with hairs (Fig. 3). Pygidium not readily visible, but appears to have an apical fringe of hairs. Hypopygium black, punctation not readily visible; posterolateral angles of last sternite appear to be rounded, not dentate.

Diagnosis.—*Dasymutilla dominica* is placed in the *bioculata* species group. It is easily distinguished from other, closely related members of the *bioculata* species-group by the color of the second abdominal segment. In *D. dominica*, the integument of the second abdominal segment is entirely black. In *D. bioculata* (Cresson), the apical one-half of the second abdominal tergite is ferruginous. *Dasymutilla chiron* (Blake) has a pair of large yellow spots on the posterior one-half of the tergite. In *D. hersilia* Mickel, the second sternite is entirely, and the anterior, posterior, and lateral margins of the second tergite are black, although the remainder is ferruginous; additionally, the integument of the second abdominal segment is entirely ferruginous for *D. lepeletierii* (Fox), *D. pyrrhus* (Fox), and *D. praegrans* Mickel.

Etymology.—The specific name is a Latinized version of the name of the republic from which the specimen was collected.

Distribution.—Known only from the type specimen.

Material Examined.—Type.

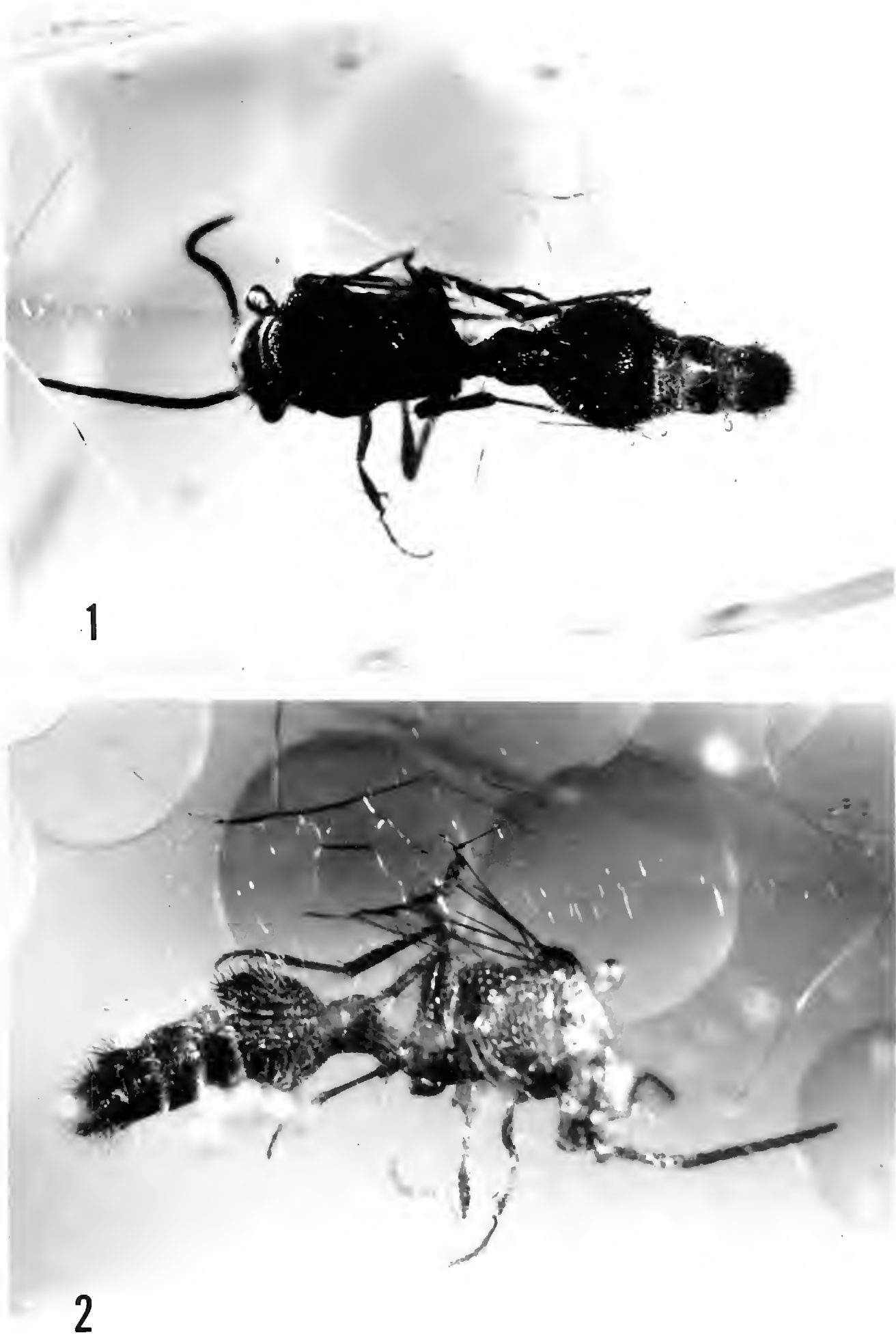
DISCUSSION

The genus *Dasymutilla* was first proposed by Ashmead (1899). The characters that he attributed to the genus included the first abdominal segment being petiolate with the second; rounded or hemispherical, highly polished eyes; males with wings; and the body usually very hairy or pubescent. Inconsistencies in Ashmead's classification were pointed out by subsequent authors. Mickel's (1928) list of diagnostic characters for the group has been generally accepted since its publication. Although his characters included many of the same as Ashmead's, Mickel noted that not all *Dasymutilla* are densely pubescent. Except for characters of the wings (which cannot be seen), the type of *D. dominica* exhibits the characteristics attributed to *Dasymutilla*. The median pit filled with hairs on the second abdominal sternite is an important character, but one that is present only in some male *Dasymutilla*. However, the only other genus in which this character is present is *Traumatomutilla*, and that genus is restricted in distribution to South America. Thus, it seems apparent that, despite its age, this specimen belongs to *Dasymutilla*.

Mickel (1928) points out that many of the characters present in *Dasymutilla* are superspecific; that is, present in more than one species. He uses the term "species group," with members of each group being closely related. Using Mickel's (1928) key to the species, *D. dominica* keys to couplet 54, with species in couplets 54-56 belonging to the *bioculata* species-group. Characters shared by males of this group include the presence of a median pit filled with hairs on the second abdominal sternite, the presence of an apical fringe of hairs on the last tergite, the absence of a prominent tooth on the posterior trochanters, normal size ocelli and eyes, cylindrical posterior tibiae, and rounded apices on the middle and hind femora.

The subfamily Sphaerophthalminae, which contains two tribes, is cosmopolitan in distribution. The tribe Dasylabrini is found primarily in the Old World, and the tribe Sphaerophthalmini occurs primarily in the New World. The New World distribution of the Sphaerophthalmini may have resulted from a single introduction of an ancestral sphaerophthalmine from Africa into South America at about the time that these two continents split apart about 110 million years ago (Brothers 1975). After becoming established in South America, the tribe apparently radiated extensively and rapidly, establishing two basic lines, or subtribes, the Pseudome-thocina and Sphaerophthalmina (to which *Dasymutilla* belongs).

The origin of *Dasymutilla* is not known. However, based upon its present distribution, it may have radiated from an ancestral Sphaerophthalmina in the Central American region after the two continents were reunited during the Cretaceous period (Dietz & Holden 1970), with its distribution being mostly northward into North America. There are at least three extant species of *Dasymutilla* that are found in the Dominican Republic. At least one other species is found in Cuba. There is very little known about how the Caribbean region was formed. However, the land forms presently in the Caribbean, including the Dominican



Figures 1–3. Holotype of *Dasymutilla dominica* Manley & Poinar. Figure 1. Dorsal view. Figure 2. Lateral view. Figure 3. Ventral view of abdomen showing median pit filled with hairs on second sternite (arrow).



Republic, may have separated from the Central American region after the evolution of *Dasymutilla* and prior to their moving to their present location about 120 to 70 million years ago (LePichon 1968). *Dasymutilla* is the most widely distributed and highly radiated (with about 150 species) group of mutillids in North America (at least of the diurnal mutillids). The new *Dasymutilla* we describe here is a relatively highly derived species, because of the pit on the second abdominal sternite. Thus, it seems likely that the genus radiated from a more primitive *Sphaerophthalmina* well over 40 million years ago.

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A BIOGEOGRAPHICALLY BASED ASSESSMENT OF THE POTENTIAL MAYFLY FAUNA OF NEVADA

RICHARD K. ALLEN¹ AND CHAD M. MURVOSH²

¹1048 La Sombra Drive, Lake San Marcos, California 92069

²Department of Biological Sciences, University of Nevada,
Las Vegas, Nevada 89154

Abstract.—A faunal assessment of the mayflies of Nevada is in progress. We hypothesize the number and composition of species and genera expected for Nevada based on the known biogeographical distribution of western species. Sixteen species and 12 genera are presently known from Nevada, but we hypothesize the total number of species and genera will be 74 and 32, respectively. Biogeographical patterns reveal where in the state species should be found.

Key Words.—Insecta, mayflies, Nevada, geographic distribution, biogeography, Ephemeroptera

The mayflies (Ephemeroptera) of North and Central America are now well known and the species composition of only a few areas on the continent are poorly reported. The most poorly known region of the Nearctic is Nevada, where only 15 species have been reported. Mayflies of most states surrounding Nevada (Arizona, California, Idaho, Oregon and Utah) had been thoroughly studied. Much of this literature is scattered in many individual papers, but some summary references include Allen & Edmunds (1956) for Oregon, Day (1956) for California, Edmunds (1954) for Utah, Edmunds et al. (1976) and Edmunds (1984) for North America, Jensen (1966) for Idaho and Kilgore & Allen (1973) for Arizona. We predict the potential mayfly fauna for Nevada based upon the biogeographic distribution of species in western North America. Allen (1990) has published the distribution patterns of North and Central American mayflies; we refer to his distribution patterns in this paper.

Collections of Nevada mayflies are now in progress to corroborate our hypothesis and also to extend the distributional range and limits of western North American species.

Physiography of Nevada.—Nevada is a large state which has been poorly collected. The state is about 790 km long and 512 km wide. Drainage from the southeastern corner of Nevada is to the Gulf of California via the Colorado River, but most of the remainder of the state lies within The Great Basin. This is a geographic/hydrologic region where no surface water leaves except by evaporation. The usage of the term “Great Basin” has been confused at times by biologists and anthropologists (Fiero 1986). The Great Basin lies in the northern part of a much larger geologic province called the Basin and Range. A bird’s eye view of Nevada would see many uplifted blocks (horsts) forming the mountain ranges separated by broad elongated valleys or basins formed by down dropped blocks (grabens). The long axes of the valleys and ranges generally trend north-south. The valley floors are quite high, generally between 1200 and 1500 m above sea level. The mountains may be 3900 m high (Fiero 1986).

Lentic habitats dominated the landscape during former pluvial periods (Hubbs & Miller 1948), but these ecosystems are relatively uncommon today compared

to the many lotic systems present. Two important river systems include the Humboldt River in northern Nevada and the Colorado River in southern Nevada but the latter has been largely transformed into a lentic habitat (Lake Mead). There are some smaller rivers, but these are overshadowed in number by the numerous small streams that flow down the mountain canyons. Few of these can be seen from the basin highways and many are difficult to get to, often requiring high clearance vehicles and/or four wheel drive. As a result, it may be a long time before we have an accurate picture of the aquatic insect fauna of the state.

Mayfly Distribution Patterns. — The distributions of mayflies suggest that North and Central America can be divided into five biogeographic subdivisions with regard to Ephemeroptera (Allen 1990): Arctic, Northern American, Western North American, Eastern North American, and Mesoamerican. The “Arctic Subdivision” includes species that are distributed about 58° North Latitude. The “North American Subdivision” includes species that are widely distributed in all of North America. The “Eastern North American Subdivision” includes species that are restricted to western or eastern North America in Mexico, the United States, and Canada. The “Mesoamerican Subdivision” includes species that are distributed mainly in tropical Mexico and Central America, but may occur as far north as the southern U.S.

NORTH AMERICAN SUBDIVISION

This subdivision includes two distinct distribution patterns, the “Pancontinental” and the “Widespread North American.” Both patterns include species known in Nevada, and species expected there.

Pancontinental Distribution Pattern. — Ten species occur across North America, except in the southwest deserts of the U.S. *Stenonema terminatum* (Walsh) is now known from Elko Co., *Caenis latipennis* Banks, which is presently known from only western Oregon and Washington, is not expected to occur in Nevada. *Baetis hageni* Eaton and *B. tricaudatus* Dodds eventually should be found widely distributed in the state. *Attenella margarita* (Needham), *Caenis simulans* McDunnough, *Ephemerella simulans* Walker, and *Hexagenia limbata* (Serville) should be found in the northern parts of the state. *Ephemerella aurivillii* Bengtsson and *Paraleptophlebia debilis* (Walker) should be found in the western and northern parts of Nevada.

Widespread North American Distribution Pattern. — Four species are widely distributed in the United States and Canada, but have narrower distributional limits than the pancontinental species. These species are also absent from the southwest deserts. *Ephoron album* (Say) and *Heptagenia elegantula* (Eaton) are presently known in Nevada. *Baetis quilleri* Dodds, which has been reported from California, Arizona, Utah and Idaho, should be found in Nevada. *Pseudiron centralis* McDunnough is known from only southern Canada, eastern Utah and Wyoming, and the species is not expected in Nevada.

WESTERN NORTH AMERICAN SUBDIVISION

This subdivision includes nine distribution patterns which include species that are presently known to occur in Nevada, and/or expected to occur in the state.

Widespread Western Distribution Pattern. — This pattern (Fig. 1) includes seven species, of which six are known in Nevada: *Drunella* (*Myllonella*) *coloradensis*

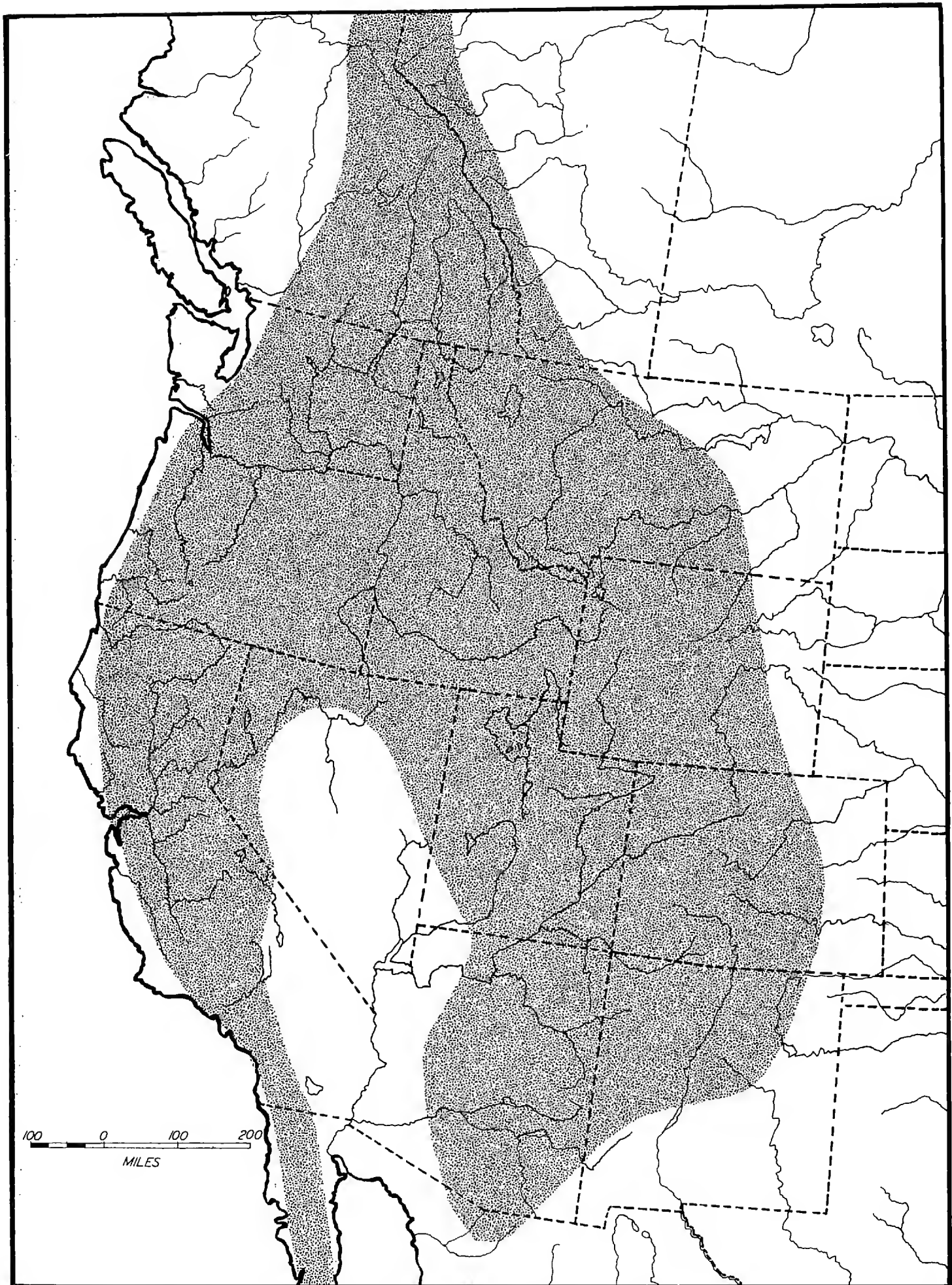


Figure 1. Composite pattern for the following mayfly distributions: *Widespread Western* (southeastern Alaska, southern Yukon Territory, western Northwest Territories, British Columbia, parts of southwestern Alberta, Washington, most of Oregon, eastern California except for southern desert, Idaho, western Montana, Wyoming, western Colorado, and New Mexico, eastern Arizona, northeastern and northwestern Nevada, and most of Utah), *Western United States* (Washington, Oregon, and California, south to near Los Angeles, northern Nevada, most of Idaho, western Montana, Wyoming, Colorado and New Mexico, eastern Arizona and most of Utah, southern British Columbia and southwestern Alberta), *Northwest and Coast Ranges* (Washington, Oregon, most of California south to about

(Dodds), *D. (Eatonella) doddsi* Needham, *D. (Drunella) grandis* (Eaton), *Ephemerella inermis* Eaton, *Iron longimanus* (Eaton), and *Tricorythodes (Tricorythodes) minutus* Traver. The distribution of *Baetis bicaudatus* Dodds (California, Idaho, Oregon, and Utah) suggests it will eventually be found in Nevada.

Western United States Distribution Pattern. — This (Fig. 1) is composed of eight species with four known from Nevada: *Rhithrogena hageni* Eaton, *R. morrisoni* (Banks), *Serratella tibialis* (McDunnough), and *Timpanoga hecuba* Eaton, are presently known from Nevada. *Baetis insignificans* McDunnough and *Paraleptophlebia memorialis* (Eaton) occur in all of the western states surrounding Nevada, and *Ephemerella infrequens* McDunnough and *Iron albertae* McDunnough occur in all of the surrounding states except Arizona. Eventually, all of these species are expected to be found in Nevada.

Northwest Distribution Pattern. — This (Fig. 2) includes 71 species, none of which are known in Nevada. As the name suggests, all species are distributed in the northern reaches of western North America. Four are known to occur in southern Idaho and Oregon and should occur in Nevada: *Choroterpes albiannulatus* McDunnough, *Paraleptophlebia heteronea* (McDunnough), *Rhithrogena futilis* (McDunnough), and *Dactylobaetis cepheus* Traver & Edmunds.

Southwest Distribution Pattern. — This (Fig. 2) includes 42 species from the southwest deserts to west-central Mexico. It is impossible to hypothesize which of these species will eventually be found in Nevada. Only three species of *Leptohyphes* (*L. apache* Allen, *L. packeri* Allen, and *L. quercus* Allen) are possible contenders, because they occur in central Arizona. *Leptohyphes apache* also occurs in the southwest corner of Utah.

Coast Ranges Distribution Pattern. — This (Fig. 3) includes 46 described species, of which two, *Baetis parallelus* Banks and *Ephemerella rama* Allen, were described from Nevada. Fourteen of the other 44 species, all of which are presently known from the Sierra Nevada Mountains in California, are expected to be found, eventually, in western Nevada: *Ameletus amator* Mayo, *Attenella delantala* (Mayo), *Baetis palisadi* Mayo, *Cinygmula tioga* Mayo, *Edmundsius agilis* Day, *Eurylophella lodi* (Mayo), *Iron dulciana* (McDunnough), *I. lepidus* (Traver), *Paracloeodes abditus* Day, *Paraleptophlebia placeri* Mayo, *Serratella levis* (Day), *S. sequoia* (Allen & Collins), *S. velmae* (Allen & Edmunds), and *Siphonurus spectabilis* Traver. The remaining species are not expected to occur in Nevada and are known only from the coast ranges of the Pacific.

Rocky Mountain Distribution Pattern. — This (Fig. 3) is composed of 11 species, and only *Heptagenia solitaria* (McDunnough) is expected in Nevada. This species is known as far west as southern Oregon. The other species are widely distributed in the Rocky Mountains from New Mexico to Canada, but do not occur west of eastern Utah.

←

half of Baja California, Idaho, western Montana, northwestern Wyoming, southeastern British Columbia and southwestern Alberta), and the *Northwest and Rocky Mountain* (western Northwest Territories south, through eastern British Columbia and western Alberta, Oregon, northern California and eastern Washington, Idaho, western Montana, Wyoming, Colorado and New Mexico, very northern Mexico, eastern Arizona and northern and eastern Utah).

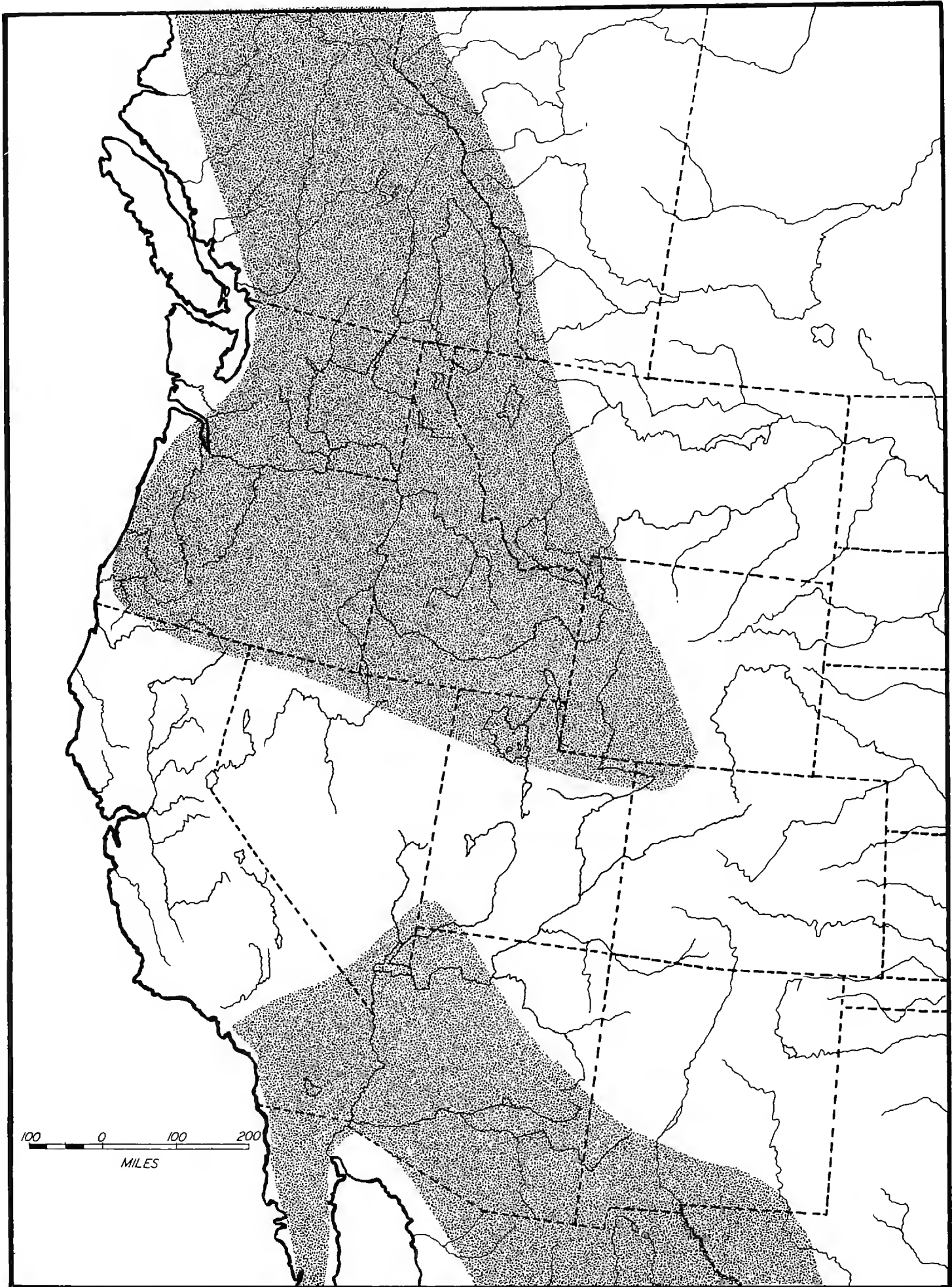


Figure 2. Composite patterns for the following mayfly distributions: *Northwest* (Washington, Oregon, Idaho, western Montana and Wyoming, northern Nevada, Utah, and northwestern Colorado, British Columbia, western Alberta and Northwest Territories), *Southwest* (Southern California and Nevada, Arizona, southern New Mexico, Baja Mexico and northwestern Mexico), *Widespread Meso-american* (southeastern Arizona, western New Mexico, western Mexico, most of Central America to South America, eastern Mexico into south central Texas).

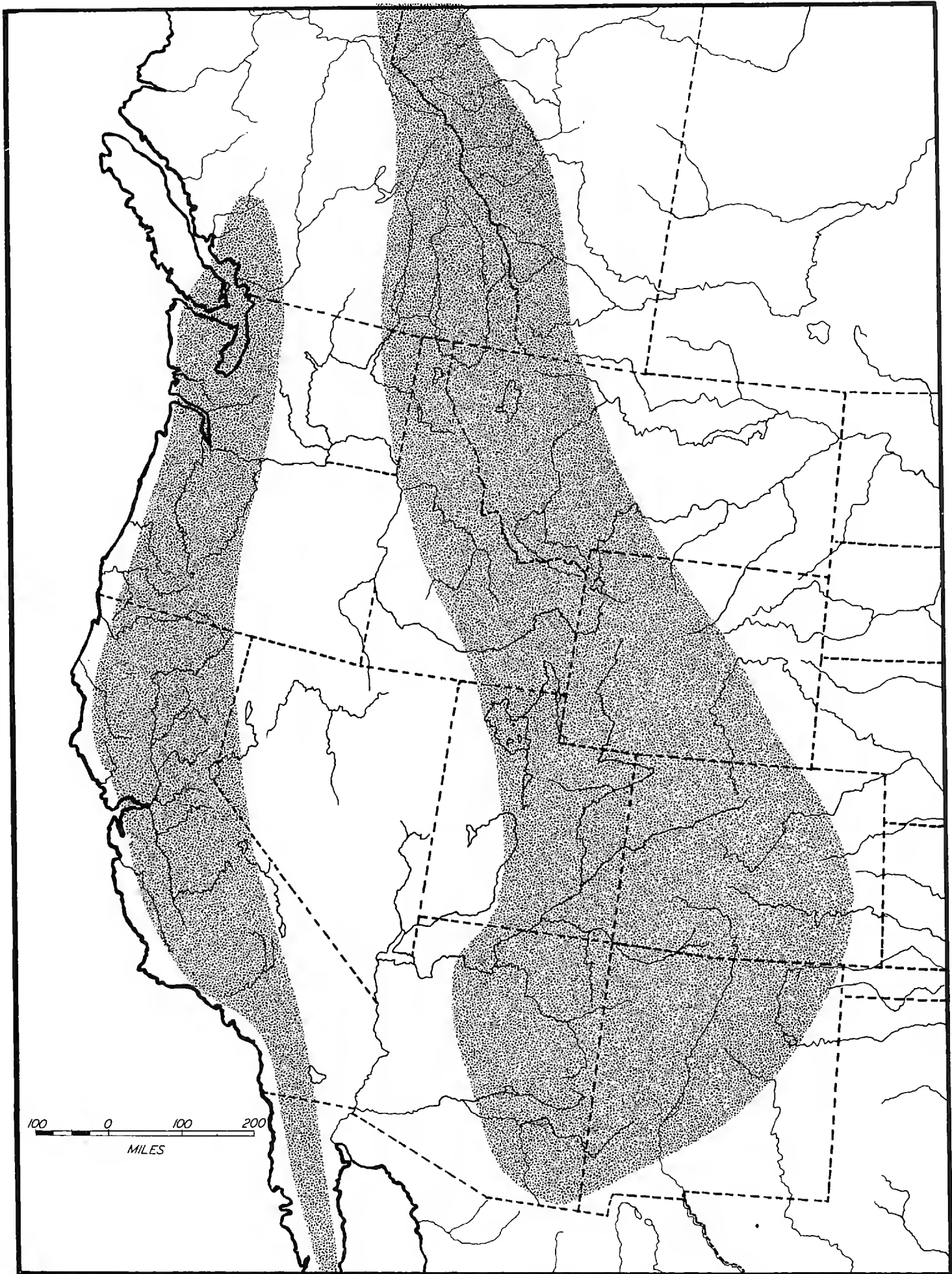


Figure 3. Composite patterns for the following mayfly distributions: *Coast Ranges* (western Washington and Oregon and California south to near Los Angeles, part of central western tip of Nevada, southwestern British Columbia), *Rocky Mountain* (western Northwest Territories, Alberta, Montana, Wyoming, Colorado, and New Mexico, eastern British Columbia, Washington, Idaho, Utah and Arizona), and *Disjunct Western* (southwestern Washington and Oregon, California south to most of Baja California, parts of central and southeastern Arizona, central New Mexico, most of Colorado, Wyoming and parts of central Montana into southwestern Alberta).

Table 1. List of the mayflies currently reported from Nevada.

Family	Species	Locality
Baetidae	<i>Baetis parallelus</i> Banks	Reno (Type Locality)
Ephemerellidae	<i>Drunella (Myllonella) coloradensis</i> (Dodds)	Elko Co., Washoe Co.
	<i>Drunella (Eatonella) doddsi</i> Needham	Elko Co., Washoe Co.
	<i>Drunella (Drunella) grandis</i> (Eaton)	Elko Co., Washoe Co.
	<i>Ephemerella inermis</i> Eaton	Elko Co.
	<i>Ephemerella rama</i> Allen	Reno (Type Locality)
	<i>Serratella tibialis</i> (McDunnough)	Elko Co.
	<i>Timpanoga hecuba</i> (Needham)	Carson River
Heptageniidae	<i>Heptagenia elegantula</i> (Eaton)	Reno
	<i>Iron longimanus</i> (Eaton)	Washoe Co.
	<i>Rhithrogena hageni</i> Eaton	Reno
	<i>Rhithrogena morrisoni</i> (Banks)	Reno
	<i>Stenonema terminatum</i> (Walsh)	Elko Co.
Oligoneuridae	<i>Isonychia intermedia</i>	Clark Co. Moapa River (unpublished)
Palingeniidae	<i>Ephoron album</i> (Say)	Elko Co.
Tricorythidae	<i>Tricorythodes (Tricorythodes) minutus</i> Traver	Elko Co.

Northwest and Coast Ranges Distribution Pattern.—This (Fig. 1) also includes 11 species, and two, *Ametropus ammophilus* Allen & Edmunds, and *Centroptilum conturbatum* McDunnough, are not expected in Nevada; their known distribution is from the coast ranges in the U.S. and Canada. The following species are known to occur in the Sierra Nevada of California and should eventually be found in the western part of Nevada: *Ameletus validus* (McDunnough), *Caudatella heterocaudata* (McDunnough), *C. hystrix* (Traver), *Drunella (Myllonella) flavilinea* (McDunnough), *Drunella (Drunella) spinifera* (Needham), *Ironodes nitidus* (Eaton), *Ironopsis grandis* (McDunnough), *Serratella teresa* (Traver), and *Siphonurus columbianus* McDunnough.

Northwest and Rocky Mountain Pattern.—This (Fig. 1) includes eight species distributed within its geographical limits, and all of them are expected in Nevada. Five species, *Callibaetis coloradensis* Banks, *Iron deceptivus* (McDunnough), *Nixe (Akkarrion) criddlei* (McDunnough), *Rhithrogena undulata* (McDunnough), and *Siphonurus occidentalis* Eaton, occur in southern Idaho and southern Oregon. *Callibaetis nigrinus* Banks is known from southern Idaho, but not from Oregon, and *Nixe (Akkarrion) simplicioides* (McDunnough) occurs in southern Idaho and northern Oregon. *Traverella albertana* (McDunnough) occurs in southern Idaho and also north central Arizona, and southeastern Utah. *Siphonurus occidentalis* also occurs in northern California, Utah and central Arizona.

Disjunct Western Distribution Pattern.—This (Fig. 3) presently includes six species, of which four, *Cinygmula par* (Eaton), *C. mimus* (Eaton), *Rhithrogena flavianula* (McDunnough) and *Serratella micheneri* (Traver), occur in the Sierra Nevada of California. These species should eventually be found in western Nevada. *Baetis adonis* Traver, known from New Mexico and southern California, and *Tricorythodes (Homoleptohyphes) dimorphus* Allen, known from eastern Arizona and southern California, are not expected in Nevada.

Table 2. List of the mayflies predicted to be collected in Nevada.

Family	Species	Area of State	
Baetidae	<i>Baetis bicaudatus</i> Dodds	Widespread	
	<i>Baetis hageni</i> Eaton	Widespread	
	<i>Baetis insignificans</i> McDunnough	Widespread	
	<i>Baetis palisadi</i> Mayo	Western	
	<i>Baetis quilleri</i> Dodds	Widespread	
	<i>Baetis tricaudatus</i> Dodds	Widespread	
	<i>Callibaetis coloradensis</i> Banks	Northern	
	<i>Callibaetis nigrinus</i> Banks	Northern	
	<i>Dactylobaetis cepheus</i> Traver & Edmunds	Northern	
	<i>Paracloeodes abditus</i> Day	Western	
Caenidae	<i>Caenis simulans</i> McDunnough	Northern	
Ephemerellidae	<i>Attenella delantela</i> (Mayo)	Western	
	<i>Attenella margarita</i> (Needham)	Northern	
	<i>Caudatella heterocaudata</i> (McDonnough)	Western	
	<i>Caudatella hystrix</i> (Traver)	Western	
	<i>Drunella (Myllonella) flavilinea</i> (McDunnough)	Western	
	<i>Drunella (Drunella) spinifera</i> Needham	Western	
	<i>Ephemerella aurivillii</i> Bengtsson	Northern & Western	
	<i>Ephemerella infrequens</i> McDunnough	Widespread	
	<i>Eurylophella lodi</i> (Mayo)	Western	
	<i>Serratella levis</i> (Day)	Western	
	<i>Serratella micheneri</i> (Traver)	Western	
	<i>Serratella sequoia</i> (Allen & Collins)	Western	
	<i>Serratella teresa</i> (Traver)	Western	
	<i>Serratella velmae</i> (Allen & Edmunds)	Western	
	Ephemeridae	<i>Ephemerella simulans</i> McDunnough	Northern
		<i>Hexagenia limbata</i> (Serville)	Northern
	Heptageniidae	<i>Cinygmula mimus</i> (Eaton)	Western
		<i>Cinygmula par</i> (Eaton)	Western
		<i>Cinygmula tioga</i> Mayo	Western
<i>Heptagenia solitaria</i> (McDunnough)		Northern	
<i>Iron albertae</i> (McDunnough)		Widespread	
<i>Iron deceptivus</i> (McDunnough)		Northern	
<i>Iron dulciana</i> (McDunnough)		Western	
<i>Iron lepidus</i> (Traver)		Western	
<i>Ironodes nitidus</i> (Eaton)		Western	
<i>Ironopsis grandis</i> (McDunnough)		Western	
<i>Nixe (Akkarrion) criddlei</i> (McDunnough)		Northern	
<i>Nixe (Akkarrion) simplicioides</i> (McDonnough)		Widespread	
<i>Rhithrogena flavianula</i> (McDunnough)		Western	
<i>Rhithrogena futilus</i> McDunnough		Northern	
<i>Rhithrogena undulata</i> Banks		Northern	
Leptophlebiidae		<i>Choroerpes albiannulatus</i> McDunnough	Northern
	<i>Choroerpes intermedia</i> McDunnough	Southern	
	<i>Paraleptophlebia debilis</i> (Walker)	Northern & Western	
	<i>Paraleptophlebia heteronea</i> (McDunnough)	Northern	
	<i>Paraleptophlebia memorialis</i> (Eaton)	Widespread	
	<i>Paraleptophlebia placeri</i> Mayo	Western	
	<i>Traverella albertana</i> (McDunnough)	Widespread	
Siphonuridae	<i>Ameletus amator</i> Mayo	Western	
	<i>Ameletus validus</i> McDunnough	Western	
	<i>Edmundsius agilis</i> Day	Western	
	<i>Siphonurus columbianus</i> McDunnough	Northern	

Table 2. Continued.

Family	Species	Area of State
Tricorythidae	<i>Siphonurus occidentalis</i> Eaton	Widespread
	<i>Siphonurus spectabilis</i> Traver	Western
	<i>Leptohyphes apache</i> Allen	Southern
	<i>Leptohyphes packeri</i> Allen	Southern
	<i>Leptohyphes quercus</i> Allen	Southern

MESOAMERICAN SUBDIVISION

This subdivision includes two patterns the "Mesoamerican" and the "Widespread Mesoamerican," the latter may include species that eventually will be found in Nevada.

Widespread Mesoamerican Distribution Pattern.—This (Fig. 2) includes nine species that are distributed from tropical Mexico and Central America to the southern United States. Two of these, the boreal *Choroterpes intermedia* McDunnough and the austral *Leptohyphes packeri* Allen, are expected to be found, eventually, in Nevada. The former species is known from western Arizona to Mexico. The latter is the most widely distributed species in the Americas, from Honduras to southwestern Arizona. The other species that are distributed in this pattern do not occur north of southern Arizona and New Mexico and have not been found north of their presently known distributional limits.

CONCLUSIONS

The mayfly fauna of Nevada (Table 1) presently includes 16 species in 12 genera. We postulate that an additional 20 genera and 58 species will be found in the state (Table 2) based upon biogeographic assessments of surrounding states. The order of listing in Tables 1 and 2 are alphabetical, not phylogenetic. The total potential number of genera and species should be 32 and 74, respectively. We further hypothesize that 26 species will be found in western Nevada; 15 in northern Nevada; four in the southern part of the state; two in the north and west; and 11 species will be found to be widespread. Future collections are expected to corroborate these predictions confirming the use of biogeographic information in assessing the state's fauna as a whole, and that of its partitioned regions.

Species of different genera and subgenera can be expected to be found in the following habitats: *Ameletus*, *Heptagenia*, *Iron*, and *Rhithrogena* in small rapid streams; *Edmundsius* in slow flowing, shallow streams; *Caenis*, *Callibaetis*, and *Siphonurus* in lentic situations; *Attenella*, *Choroterpes*, *Ephemerella*, *Caudatella*, *Drunella*, *Eurylophella*, *Serratella*, *Ephemerella*, and *Hexagenia* in a variety of lotic and lentic habitats; *Dactylobaetis*, *Cinygmula*, *Paraleptophlebia*, and *Leptohyphes* in a variety of lotic habitats; *Paracloeodes* in large streams; *Baetis* species in streams that range from slow flowing to torrential. Detailed habitat descriptions can be found in Edmunds et al. (1976) and Edmunds (1984).

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A NEW SPECIES OF *UROLEUCON* (*UROLEUCON*) AND COMMENTS ON *UROLEUCON* (*UROLEUCON*) *TUCUMANI* (ESSIG) (HOMOPTERA: APHIDIDAE)¹

MIGUEL ANGEL DELFINO

Instituto Superior de Entomología, Facultad de Ciencias Naturales,
Universidad Nacional de Tucumán,
Miguel Lillo 205, 4000–Tucumán, Argentina

Abstract.—*Uroleucon* (*Uroleucon*) *garnicai* NEW SPECIES on *Eupatorium buniifolium* Hooker & Arnold from Argentina is described. Morphological and biological aspects were analyzed together with those of its closely related species *Uroleucon* (*Uroleucon*) *tucumani* (Essig). The study of the type specimens of *U. tucumani* shows that they could belong to two different species; those collected in Tucumán are true *U. tucumani*.

Key Words.—Insecta, *Uroleucon garnicai*, *Uroleucon tucumani*, Aphididae, morphometrics, discriminant analysis

Uroleucon live on plants in the Asteraceae (= Compositae), and are broadly distributed throughout the world with some almost cosmopolitan species. Smith & Cermeli (1979) list 23 species in the Neotropical region, seven of which were described from Argentina. Of these, *Uroleucon* (*Uroleucon*) *tucumani* (Essig) was described by Essig (1953) as a *Macrosiphum* from specimens collected on *Baccharis* sp. in Huanta (Guanta), Chile and on *Baccharis* sp. (?) in Tucumán province, Argentina by Michelbacher.

All the aphids collected on *Baccharis coridifolia* De Candolle in Córdoba province, Argentina, as well as those collected on *Eupatorium buniifolium* Hooker & Arnold in Córdoba and Tucumán provinces, had been previously considered to be *U. tucumani*. Essig's description is very brief and generalized, making it impossible to recognize accurately this, and related, species.

To solve this problem, a detailed study of the *Uroleucon* collected on *B. coridifolia* and *E. buniifolium* was undertaken, and showed two species exist with one described as new here.

MATERIALS AND METHODS

Aphids belonging to the genus *Uroleucon* were collected on *E. buniifolium* and *B. coridifolia* in Tafi del Valle (Tucumán, Argentina) and Cabana (Córdoba, Argentina). Adult aphids were mounted on slides in Hoyer's mountant. Nineteen body structures (Table 1) were measured from 60 apterae (30 of each host plant). The data were analyzed on a VAX-11 computer using the discriminant analysis program in the BMDP statistical package, at the University of California.

During comparative studies, the types of *U. tucumani* (Essig) were analyzed. Their data follow: "Type," ARGENTINA. TUCUMÁN: 11 Feb 1951, Michelbacher, *Baccharis* sp.?, 1 alate viviparous female. Paratypes: same data as type, 4 apterous viviparous females; CHILE. HUATA (GUANTA): 4 Dec 1950, Michelbacher, *Baccharis* sp., 4 apterous viviparous females, 3 alate viviparous females.

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Table 1. Morphometric data for *U. garnicai* and *U. tucumani*. All measurements are in mm as range, followed by the mean in parentheses.

Character	<i>U. garnicai</i>	<i>U. tucumani</i>
Body length	1.92–2.67 (2.30)	1.86–2.59 (2.14)
Metatibia length	1.30–1.68 (1.51)	1.13–1.70 (1.41)
Metafemor length	0.75–0.85 (0.82)	0.65–0.93 (0.77)
Siphunculus length	0.49–0.62 (0.55)	0.44–0.60 (0.54)
Cauda length	0.31–0.38 (0.34)	0.24–0.31 (0.13)
Decimal proportion of reticulated part of the siphunculus	0.21–0.27 (0.24)	0.20–0.29 (0.24)
Length of ant. seg. III	0.55–0.73 (0.64)	0.51–0.68 (0.61)
Length of ant. seg. IV	0.50–0.62 (0.58)	0.33–0.53 (0.45)
Length of ant. seg. V	0.44–0.59 (0.50)	0.30–0.44 (0.40)
Length of base of ant. seg. VI	0.14–0.18 (0.17)	0.12–0.17 (0.14)
Length of processus terminalis	0.71–0.87 (0.80)	0.54–0.76 (0.67)
Length of ultimate rostral segment	0.13–0.15 (0.14)	0.13–0.15 (0.14)
Length of hind distitarsus	0.14–0.17 (0.16)	0.12–0.14 (0.13)
Diameter of ant. seg. III	0.032–0.035 (0.034)	0.030–0.037 (0.033)
Length of setae on ant. seg. III	0.030–0.040 (0.034)	0.017–0.027 (0.023)
Number of sensoria on ant. seg. III	4–13 (9)	7–15 (11)
Number of rostral setae	6–10 (8)	7–13 (9)
Number of caudal setae	9–12 (11)	8–11 (10)

UROLEUCON (UROLEUCON) GARNICAI DELFINO, NEW SPECIES

Types.—Holotype: apterous viviparous female; data: ARGENTINA. *CÓRDOBA PROVINCE*: Cabana, 27 Jan 1988, M. A. Delfino, *Eupatorium buniifolium*; deposited: Instituto Miguel Lillo, Tucumán. Paratypes: same data as holotype, 3 apterous viviparous females, 2 alate viviparous females; same data as holotype except 28 Jan 1985, 17 apterous viviparous females. ARGENTINA. *TUCUMÁN PROVINCE*: Tafi del Valle, 2 Mar 1985, M. A. Delfino, *Eupatorium buniifolium*, 9 apterous viviparous females. All paratypes deposited: British Museum (Natural History), London.

Apterous Viviparous Female.—($n = 30$) *Color*: Living specimens with entire body brown. Cleared specimens with dorsum colorless, bearing distinct separate brown sclerites; weakly sclerotized specimens with the sclerites poorly defined; head, antennal segments I, II and base of III brown; antennae flagellum, rostrum, distal halves of the femora, distal fourth part of the tibiae, tarsi and siphunculi dark brown to nearly black; cauda pale to slightly smoky. *Morphological characters*: Body length 1.92–2.67 mm (Fig. 1A). Head smooth with antennal tubercles well developed, diverging; median frontal tubercle inconspicuous (Fig. 1E). Antennae with processus terminalis $4.28\text{--}5.31\times$ the base of segment VI; flagellum almost smooth in the basal one-half of segment III and imbricate distally. Antennae hairs on segment III 0.030–0.040 mm long, about $0.86\text{--}1.14\times$ as long as the basal diameter of segment. Secondary rhinaria 6–13, distributed on nearly the whole length of antennal segment III (Fig. 1B). Rostrum reaching the hind coxae; ultimate rostral segment 0.13–0.15 mm; $0.81\text{--}1.00\times$ as long as the hind distitarsus (Fig. 1H), with 7–10 additional hairs. Hind tibiae and femur $0.56\text{--}0.76$ and $0.31\text{--}0.40\times$ body length, respectively. First tarsal chaetotaxy usually 5:5:5. Dorsal hairs of abdomen on small sclerites (Fig. 1D); tergite VIII with 4 hairs. Postsiphuncular sclerites distinct, sometimes very small; antesisiphuncular sclerites not developed. Frequently small marginal tubercles, irregularly present on segments II–IV. Siphuncular length $0.22\text{--}0.27\times$ body length (Fig. 1G), distinctly shorter than antennal segment III, reticulated on distal 0.21–0.29, remainder imbricate. Cauda with distal two-thirds rather slender, acuminate, bearing 9–12 hairs; about $0.56\text{--}0.68\times$ as long as the siphuncular length. Genital plate with 2–4 (usually 2) hairs on anterior half and 8–12 hairs on the hind margin. *Measurements*: See Table 1.

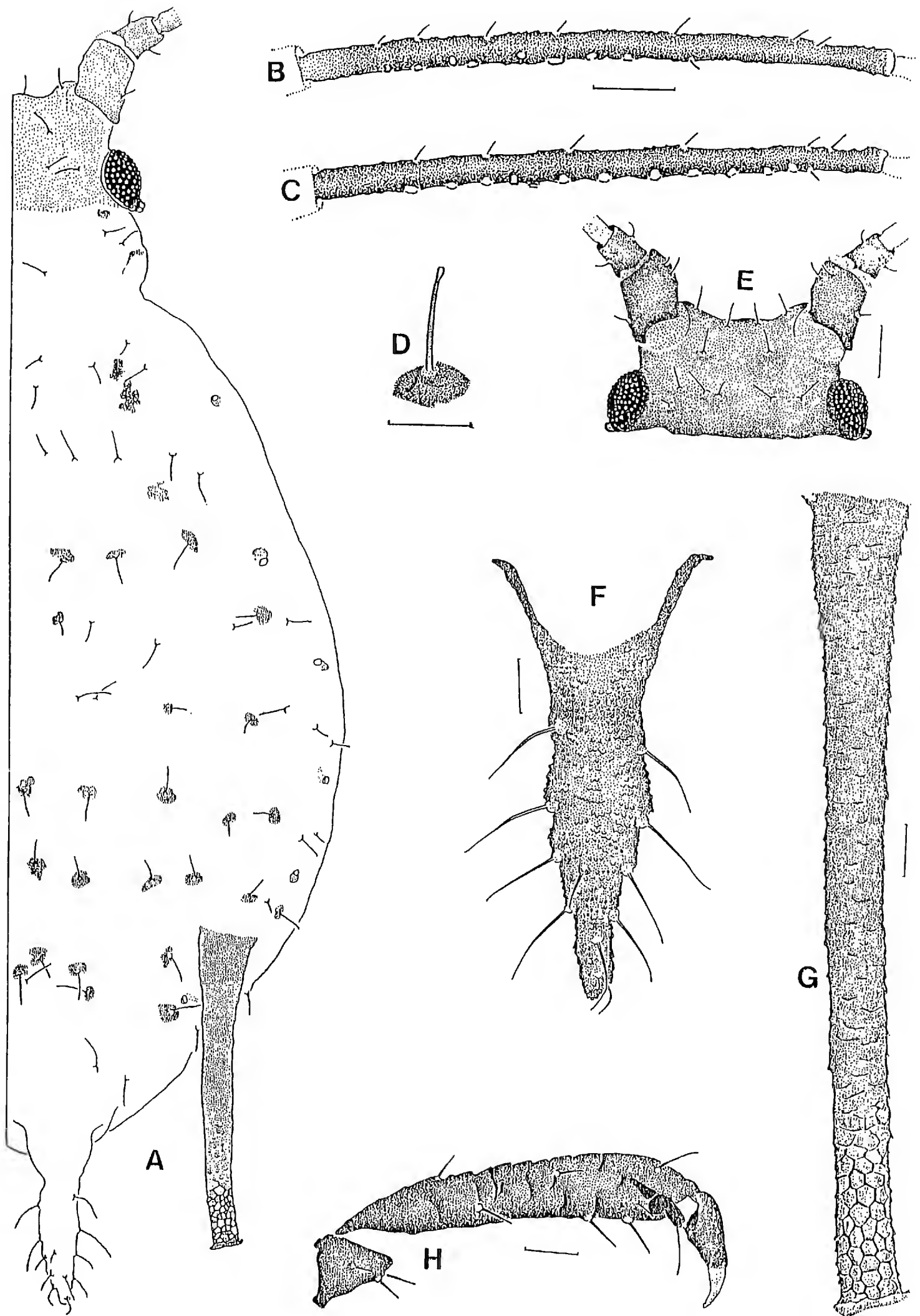


Figure 1. *Uroleucon garnicai*, NEW SPECIES. A. Body dorsum, right half (aptera). B. Secondary rhinaria on antennal segment III (aptera), scale bar = 98μ . C. Secondary rhinaria on antennal segment III (alate). D. Dorsal hair on abdomen with sclerite base (aptera), scale bar = 24μ . E. Frontal area of head showing median frontal tubercle (aptera), scale bar = 98μ . F. Cauda (alate), scale bar = 40μ . G. Siphunculus (aptera), scale bar = 40μ . H. Hind distitarsus (aptera), scale bar = 24μ .

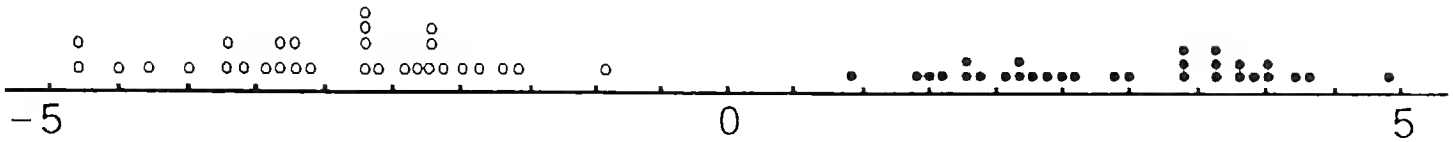


Figure 2. Standardized discriminant function showing canonical variable distributions for *U. tucumani* and *U. garnicai*. On this function, the unstandardized discriminant index, L_o , of 3.33 equals 0 on this standardized function. Black = *U. garnicai*, white = *U. tucumani*.

Alate Viviparous Female.—($n = 2$) *Color:* Living specimens with head, antennae, thorax and legs dark brown, abdomen brown. Cleared specimens with head and thorax brown; antennal segment I, II and base of III concolorous with the head, remainder dark brown; legs with basal one-half of femora pale, distal one-half dark brown; tibiae dark brown except basally slightly pale; tarsi concolorous with apical tibiae; marginal sclerites small, on poorly pigmented specimens; siphunculi uniformly dark brown; cauda, genital, and anal plates dusky, or slightly darker than abdomen. *Morphological characters:* Body length 2.39–2.48 mm. Antennae with processus terminalis $4.14\text{--}4.61 \times$ the base of segment VI. Hairs of antennal segment III 0.030–0.032 mm long, about $0.94\text{--}1.07 \times$ the length of the basal diameter of segment. Secondary rhinaria on segment III about 8–14 in number covering almost its entire length (Fig. 1C). Ultimate rostral segment 0.14 mm; $0.78\text{--}0.86 \times$ the length of the hind distitarsus, with 7–8 additional hairs. Hind tibiae and femur $0.62\text{--}0.73$ and $0.32\text{--}0.37 \times$ body length, respectively. Dorsal hairs of abdomen on small sclerites poorly pigmented. Siphunculi $0.22\text{--}0.26 \times$ body length, reticulated over apical $0.23\text{--}0.24$, remainder imbricate. Cauda about $0.53\text{--}0.60 \times$ siphuncular length (Fig. 1F). Otherwise like apterous viviparous females.

Diagnosis.—Because *U. garnicai* overlaps morphologically with *U. tucumani*, a discriminant function must be calculated to separate these species reliably. See Table 2, the discussion for character overlap and the diagnostic function.

Etymology.—This species is named after Rafael Garnica, Universidad de Leon, Spain, who taught me so much on our field trips in that country.

Material Examined.—See types.

DISCUSSION

Morphology.—The correlation matrices for both *U. garnicai* and *U. tucumani* show that the lengths of the metafemur, antennal segment III and cornicle (siphunculus) are highly correlated; therefore, I consider only one of these characters for the morphological analysis of the specimens. The use of discriminant analysis between the two species shows that the lengths of the cauda, antennal segment III, antennal segment IV, setae on antennal segment III and the base of antennal segment VI are five characters that could differentiate the two species.

Table 2. Differences between *U. garnicai* and *U. tucumani*. Measurements are in mm as range followed by the mean within parentheses.

Character	<i>U. garnicai</i>	<i>U. tucumani</i>
Color in life	brown	black
Cauda length	0.31–0.38 (0.34)	0.24–0.31 (0.28)
Processus terminalis length	0.71–0.87 (0.80)	0.54–0.76 (0.67)
Hind distitarsus length	0.14–0.17 (0.16)	0.12–0.14 (0.13)
Setae length of ant. seg. III	0.030–0.040 (0.034)	0.017–0.027 (0.023)
Host plant	<i>E. buniifolium</i>	<i>B. coridifolia</i>
Linear discriminant function (L_o 3.33) (see discussion section).	$L_g = 3.96$	$L_t = 2.69$
Ratio (see Fig. 3)	13.23–18.82	8.50–12.96

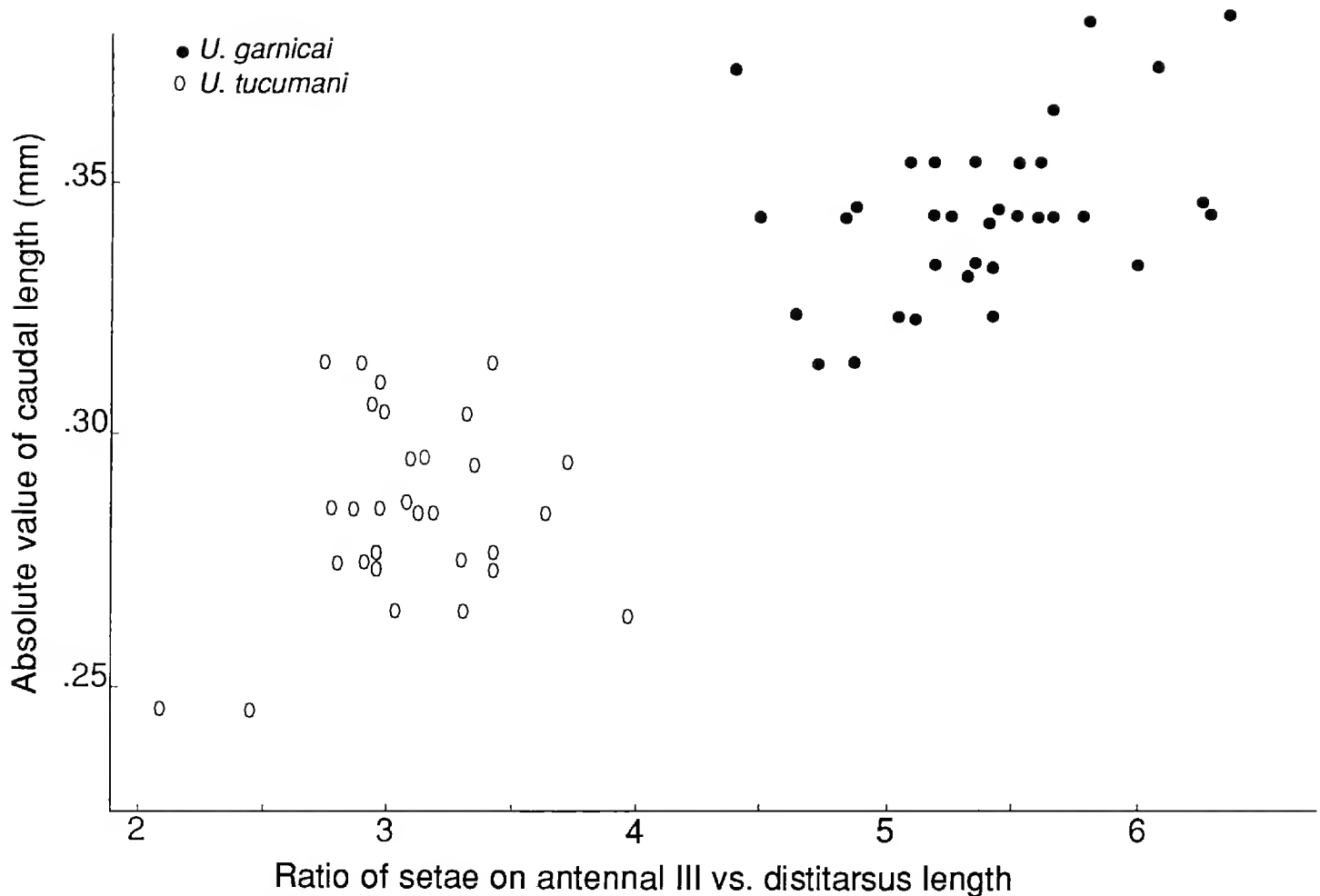


Figure 3. Regression of caudal length plotted against a ratio of the number of setae on antennal segment III versus distitarsal length. White = *U. tucumani*, black = *U. garnicai*.

A linear discriminant function (L) distinguishes these species; for *U. garnicai*, $L_g = 3.96$; for *U. tucumani*, $L_t = 2.69$; with discriminant index (L_o) of 3.33. Starting from these values specimens belonging to these species could be correctly classified according to the following function, L_i .

$$L_i = (7.4883 \times X_1) - (4.2548 \times X_2) + (1.8261 \times X_3) \\ + (7.9576 \times X_4) + (53.5169 \times X_5)$$

where: X_1 = cauda length; X_2 = length of antennal segment III; X_3 = length of antennal segment IV; X_4 = length of base of antennal segment VI; X_5 = setae length of antennal segment III. (Lengths are in mm.) The specimens are *U. garnicai* if $L_i > 3.33$, as L_o , or are *U. tucumani* if $L_i < 3.33$.

The histogram of the canonical variates (Fig. 2) shows the separation between these two species. The setae length on antennal segment III \times length of hind distitarsus I also obtained values that discriminate these species; that value in *U. garnicai* ranges from 4.8–6.4 and in *U. tucumani* it is 2.0–3.9. The ratio: (ant. seg. III) \times (hind distitarsus)/(cauda length), is 13.23–18.82 for *U. garnicai* and 8.50–12.96 for *U. tucumani*. These values are plotted in Fig. 3.

The length of hind distitarsus (Table 1) also seems to be a useful character to separate these species univariately. However, three alatae and four apterae from Chile ("Paratype" of *U. tucumani*) have tarsal lengths of 0.16–0.18 mm, similar to *U. garnicai*; however, one alatae from Tucumán ("Type" of *U. tucumani*) and four apterae also from Tucumán ("Paratype" of *U. tucumani*) have tarsal lengths of 0.11–0.13 mm, as do the specimens that I collected on *B. coridifolia*. Because of this, although Essig's "Type" and "Paratype" from Tucumán are necessarily

“true” *U. tucumani*, as I collected on *B. coridifolia*, Essig’s “Paratype” from Chile could be another very closely related species.

Furthermore, the apterae from Chile have a few secondary rhinariae (2–6) on the antennal segment III and the processus terminalis is short in relation at the base of antennal segment VI. Curiously, Essig drew two antennal segments III of apterae and alatae when he described *U. tucumani*, one set with long setae and the other with shorter ones. He obviously observed some differences in his material that he did not explain in the description.

Biology. — *Uroleucon garnicai* colonizes the young shoots and stems of the inflorescences of *E. buniifolium*, a shrub widely distributed in Argentina. In Tafi del Valle (1972 m el) this species forms crowded colonies that often cover several stems; whereas, in Cabana (500–600 m el) it forms disperse and small groups of 1–3 adult aphids per group. This suggests that there could be different ecotypes which are more or less suitable to *U. garnicai*, according to the geographic distribution of *E. buniifolium*.

No sexuals of *U. garnicai* were found on this plant. Alate males were captured in Moericke traps placed in Tafi del Valle; morphologically these males are fairly similar to *U. garnicai* females. If the males are actually *U. garnicai*, considering the abundance on *E. buniifolium* there, the possible origin of *U. garnicai* could be in the highlands (e.g., Tafi del Valle) where its host plant is common. *Uroleucon garnicai* seems to be completely monophagous on this single host species year-round. It may be a holocyclical and monoecious species on *E. buniifolium*.

Uroleucon tucumani colonizes twigs and shoots on *B. coridifolia*, a shrub also widely distributed in Argentina. In Cabana, its colonies contain only a few adults, which fall readily when disturbed.

Both species are very closely related but are easily distinguished in nature by their body color and host plant; *U. garnicai* is brown and lives on *E. buniifolium*, whereas *U. tucumani* is black and lives on *B. coridifolia*.

Conclusions. — *Uroleucon (Uroleucon) garnicai* is a new species closely related to *Uroleucon (Uroleucon) tucumani* (Essig). Both may be distinguished by biological and morphological characters. The *U. tucumani* paratypes labelled by Essig with specimens collected in Argentina and Chile could belong to two different species. The specimens collected in Tucumán are the true *U. tucumani*.

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Scientific Note

NOCTURNAL CLUSTERING OF THE SOLITARY WASP, *CHALYBION CALIFORNICUM* (SAUSSURE) (HYMENOPTERA: SPHECIDAE)

Chalybion californicum (Saussure) is a solitary wasp that provisions its nest with spiders. It appears to make its nest in preexisting cavities, especially in abandoned nests of the sphecid mud-daubers, *Sceliphron*. After provisioning the nests, females close the entrance with mud (Bohart, R. M. & A. S. Menke. 1976. Sphecid wasps of the world, a generic revision. University of California Press, Berkeley). *Chalybion californicum* occurs throughout most of the United States, and also has been reported from southern Canada, northern Mexico, Hawaii and Bermuda (Bohart, R. M. & A. S. Menke. 1963. Univ. Calif. Publ. Entomol., 30: 91–182). This note confirms previous reports (Weiss, H. B. 1944. Entomol. News, 55: 270–271, Ward, G. L. 1972. Proc. Indiana Acad. Sci., 81: 177–181) that *C. californicum* aggregates nightly in the same location in successive seasons.

We observed a dense cluster or “sleeping aggregation” (Evans, H. E. & E. G. Linsley. 1960. Bull. So. Calif. Acad. Sci., 59: 30–37) of *C. californicum* that appeared nightly beneath an overhanging eave of a ground-level apartment in Riverside, California. The aggregation was first noticed in mid-June 1989 and the number of individuals in the aggregation during the summer was estimated to be about 50. This number declined noticeably in September, and the last individual was seen on 13 Oct 1989. In late April 1990, the aggregation site was examined nightly; no wasps were seen until 8 May when approximately 12 individuals aggregated. The synchronous reappearance of the wasps after the long winter absence was striking. The number of individuals fluctuated between three and 16, during 8–29 May. On 2 June the number increased abruptly to 27, then to 45–50 on 3 June. Through the remainder of June and July, the number of individuals in the aggregation was estimated as 65–70. The number began to decrease gradually in August; the rate of decrease was more rapid later in the month than earlier. Between late September and mid October, the number of individuals was down to about 20 and fluctuated up and down nightly. Between the evenings of 14 and 15 Oct, the number dropped sharply from approximately 15 to seven. On the morning of 16 Oct, we marked the remaining wasps with paint to see if they would overwinter and return again next year. This was the last that the wasps were seen in 1990; however, it is uncertain if the disturbance that we caused the wasps when we marked them hastened their departure from the aggregation site.

Each year the aggregation site was the exact same spot on a 15 × 15 cm wooden pillar where it joined with an eave approximately 2.4 m above the ground (Fig. 1). The eave was on the east side of the apartment and the wasps aggregated on the north side of the pillar. In late afternoon, the wasps flew around the aggregation site and some landed. Gradually more landed until all were settled one to several hours before dark. In cooler weather (e.g., 8 May–1 June 1990, with daily max-



Figure 1. Aggregating *Chalybion californicum*.

imum temperatures between 19 and 30° C), they generally aggregated earlier (approximately 16:00–16:30 h); in hotter weather (e.g., 2–4 June 1990, maximum temperatures between 35 and 38° C), they aggregated later, about 18:00–18:30 h. During the period 8 May–4 June, the morning dispersal was not observed; however, on cooler days they usually were not dispersed before 07:30 h, although on hot days most had dispersed by 07:30.

At 22:00 h, 7 Sep 1989, the aggregation contained roughly 40–50 individuals and we collected 10 for sex determination; of these, six were male and four were female, demonstrating that both sexes were present. We did not observe any mating behavior; however, because our observations were not continuous, we cannot say for certain that mating did not occur.

Weiss (1944) initially documented the reappearance of *C. californicum* at the same aggregation site in New Jersey in five successive summer seasons with intervening winters when the wasps were absent. Weiss (1944) suggested that a chemical aggregation cue (pheromone) persisted at the site from autumn to spring. However, this does not seem likely because the pheromone would have to persist throughout the winter and remain potent enough to attract wasps from a distance in the spring. Nonchemical aggregation cues, such as visual cues, would be more likely to persist from one season to the next. Alternatively, we suggest that the aggregation in the spring may consist of the same individuals that were present in the fall and that the overwintered wasps remembered the aggregation site in the same manner that wasps learn and remember the location of nesting sites (Evans, H. E. & M. J. W. Eberhard. 1970. *The wasps*. University of Michigan Press, Ann Arbor). This may provide a more likely explanation for the synchronous reappearance of 12 wasps on 8 May 1990, as opposed to a scenario where newly emerged wasps were searching for a nocturnal resting site and 12 wasps were attracted to the same physical cue for the first time on the same night. However, a weakness in our hypothesis is that *C. californicum* is reported to overwinter as a prepupa (Rau, P. & N. Rau. 1916a. *J. Anim. Behavior*, 6: 27–

63). To test our hypothesis, we marked some individuals in autumn 1990 and will watch for their reappearance in the spring of 1991.

Nocturnal aggregations of several species of *Chalybion* have been reported: *C. californicum* (= *C. caeruleum* [L.]) (Rau, P. & N. Rau. 1916b. Ann. Entomol. Soc. Am., 9: 227–274; Rau, P. 1938. Ann. Entomol. Soc. Am., 31: 540–556; Weiss 1944; Ward 1972), *C. zimmermanni* Dahlbom (Rau, P. 1942. Can. Entomol., 74: 196), *C. bengalense* (Dahlbom) (= *C. violaceum* [Fabr.]) (Williams, F. X. 1928. Hawaiian Sugar Planters' Assoc., Entomol. Ser. Bull., 19: 1–179; Jayakar, S. D. & R. S. Mangipudi. 1965. J. Bombay Nat. Hist. Soc., 61: 708–711), and *C. japonicum* (Gribodo) (= *Sceliphron inflexum* Sickmann) (Iwata, K. 1963. Trans. Shikoku Entomol. Soc., 7: 114–118). All four species are in the subgenus *Chalybion*; *C. californicum* and *C. zimmermanni* are New World species, and *C. bengalense* and *C. japonicum* are Old World species (Bohart & Menke 1976). The aggregations of these four species consisted of both sexes although no mating behavior was observed by Rau & Rau (1916b) or Ward (1972) or by us. Therefore, the aggregations do not appear to facilitate mating. By day, *Chalybion* spp. are solitary wasps; why they aggregate at night has remained a mystery since Rau & Rau first described this behavior in 1916.

Acknowledgment.—We thank R. M. Bohart for his identification; a voucher specimen from this study is deposited in the UCR Entomological Teaching and Research Collection, University of California, Riverside.

T. R. Prentice and G. P. Walker, *Department of Entomology, University of California, Riverside, California 92521.*

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Scientific Note

OCCURRENCE OF *COCCINELLA SEPTEMPUNCTATA* (L.) (COLEOPTERA: COCCINELLIDAE) IN CENTRAL BRITISH COLUMBIA

Coccinella septempunctata (L.), the seven spotted lady beetle (C7), is a Palearctic predator intentionally introduced into North America numerous times since 1956 for the biological control of aphids (Angalet, G. W., J. M. Tropp & A. N. Eggert. 1979. Environ. Entomol., 896–901; Schaefer, P. W., R. J. Dysart & H. B. Specht. 1987. Environ. Entomol., 16: 368–373). During 1973 it was found to be established in both northern New Jersey and Quebec (Angalet, G. W. & R. L. Jacques. 1975. USDA Coop. Econ. Insect Rep., 25: 883–884; Laroche, A.

1979. *Bull. Invert. Ins. Québec*, 1: 68–73). Since then, its range in North America has rapidly expanded, both as a result of natural dispersal and redistribution by biocontrol workers (Schaefer et al. 1987). This article reports a significant expansion of the known range of *C. septempunctata* to central British Columbia.

In early August, 1990, large numbers of beetles were noted on bareroot spruce (*Picea*) seedlings, caragana (*Caragana arborescens* Lamarck) windbreaks, and weeds alongside a greenhouse at a commercial conifer seedling nursery located at Ness Lake near Prince George, British Columbia. Because of a concern for potential damage to the seedlings, adults were collected and submitted to Pacific Forestry Centre, Forestry Canada, for identification. Seven of these adults were *C. septempunctata*. This identification was later confirmed by J. McNamara of Biosystematics Research Centre, Agriculture Canada, Ottawa, who also determined the remaining beetles in the collection (2 females) to be *Hippodamia* sp. prob. *quinesignata* (Kirby). Voucher specimens of C7 (7 adults) and *Hippodamia* sp. (2 adults) are deposited in the Forestry Canada, Forest Insect and Disease Survey insect reference collection, Victoria, British Columbia.

The origin of this C7 population is enigmatic. As there have been no intentional releases of C7 in central British Columbia, its presence at Ness Lake could have resulted from either an adventive introduction or natural dispersal. Although an adventive introduction cannot be ruled out, other isolated recoveries of C7 in North America indicate that natural dispersal is a credible mechanism to account for its presence in the Prince George area. *Coccinella septempunctata* is an active flier capable of long distance dispersal from release sites. It has been found on Sable Island, Nova Scotia, more than 175 km from the nearest land (Schaefer et al. 1987). As well, recent surveys in Saskatchewan and Manitoba have shown it to be present in most agricultural areas of both provinces, with dispersal as far north as Ile-a-La-Crosse (55°30'N) in the boreal forest of Saskatchewan, more than 360 km from the nearest release site (Turnock, W. J., B. Timlick, J. F. Doane & J. Soroka. 1990. *Ag. Can. Res. Br. Biocontrol News*, 3: 25–30). Further surveys should be conducted in British Columbia to determine the distribution of C7.

Because releases of *C. septempunctata* in the Pacific Northwest have been confined to the Vancouver area of British Columbia, more than 520 km to the south (Schaefer et al. 1987; B. D. Fraser, personal communication), and in agricultural areas of Washington and Oregon, at least 750 km to the SSE (Schaefer et al. 1987; Olkowski, W., A. Zhang & P. Thiers. 1990. *IPM Practitioner*, 12: 1–12) surveys along the major drainages to the south (e.g., Fraser, Thompson, Okanagan and Columbia rivers) would indicate if C7 has spread from more southerly populations. Although dispersal from more southerly populations is more likely, the recovery of C7 from a more northerly latitude in the boreal forest of Saskatchewan indicates that dispersal into British Columbia from the northeast through the Peace River drainage system cannot be discounted.

Material Examined.—*Coccinella septempunctata*: BRITISH COLUMBIA. Ness Lake (54°N, 123°05'W), about 25 km NW of Prince George, 16 Aug 1990, F. Donnelly, ex *Picea* and *Caragana arborescens*, FIDS 90-1305-01.

Acknowledgment.—The cooperation of the staff of Ness Lake Nursery, Industrial Forest Services, Prince George and the assistance of Mr. R. Turnquist, Forestry Canada, Forest Insect and Disease Survey, Victoria, B.C., in surveying the

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L. M. Humble, *Forestry Canada, Pacific Forestry Centre, 506 West Burnside Road, Victoria, British Columbia, Canada V8Z 1M5.*

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Scientific Note

NOTES ON TWO PACIFIC COASTAL SPECIES OF TENEBRIONIDAE (COLEOPTERA)

Scaphidema pictum Horn was transferred (Triplehorn, C. A. 1961. *Coleopt. Bull.*, 15: 125–127) into *Phaleromela*, receiving the new name *variegata* Triplehorn, because *pictum* was preoccupied. At the time *Phaleromela variegata* was known only from Oregon. Shortly thereafter, its range was reported as southwestern British Columbia to Oregon, in sandy areas along river banks (Hatch, M. 1965. *Beetles of the Pacific Northwest. Part IV.* University of Washington Press, Seattle). Subsequent collection records show that the range is more extensive, including Idaho and California. The Idaho collections are from the western edge (Idaho Co.) and the south central part (Blaine Co.) of that state (data below). Probably, the beetles occur throughout the Snake River drainage, including the western parts of Wyoming and Montana.

In California, several collections have been made (data below), where specimens were taken from fine, dry, partially shaded sand near rivers or streams. Although the beetles and their larvae inhabit dry sand, they are never more than a few inches from moist sand and do not live long in the laboratory if water is withheld. The sand bars and banks where they occur are often flooded during winter. It is unknown how they survive this period. Collection localities include both the coastal mountains and the Sierra Nevada, at elevations near sea level to almost 2000 m.

Phaleromela variegata (as *Scaphidema pictum*) and *P. globosa* (LeConte) (as *Phaleria*) were included in a list of Tenebrionidae (Papp, C. S. & W. D. Pierce. 1960. *J. Kansas Entomol. Soc.*, 33: 154–156) found to be associated with stored animal food in the Antelope Valley on the western edge of the Mojave Desert. *Phaleromela variegata* appears to be strictly limited to the montane riparian habitat described above and has not been recorded in barnyard situations. Moreover, the closest geographic records are about 500 miles north. *Phaleromela globosa* occurs strictly on maritime sand dunes from British Columbia to approxi-

mately San Luis Obispo in central California, with no other records from interior localities. Thus, both the occurrence of these species in the Mojave Desert and their association with stored products need verification.

Diaperis californica Blaisdell, described in 1929, has remained rare in collections. In a revisionary treatment (Triplehorn, C. A. 1965. Proc. U.S. Nat. Mus., 117: 349–458) only 14 specimens were recorded from four localities in Calaveras, Placer, Madera and Fresno Counties. We provide additional locality records (see below), with localities from the San Bernardino Mountains being outside the Sierra Nevada and about 300 miles south of the previously known range.

Records.—*Phaleromela pictum*: CALIFORNIA. MENDOCINO Co.: Eel River Ranger Station, nr Covelo, 9 Jun 1972; 4.8 km (3 mi) N of Branscomb, 18 May 1984. PLUMAS Co.: Humbug Creek, 4.8 km (3 mi) NW of Portola, 1584 m (5200 ft), 18 May 1982; 1.6 km (1 mi) S of Meadow Valley, 1173 m (3850 ft), 14 May 1982. SISKIYOU Co.: 14.4 km (9 mi) E of McCloud, 1067 m (3500 ft), 10 Jun 1974. TRINITY Co.: Hayfork Ranger Station, nr Hayfork, 23 May 1973; Forest Glen, 5 Jun 1988. IDAHO. BLAINE Co.: Big Woods River, 32 km (20 mi) N of Shoshone, 1 Jul 1966. IDAHO Co.: Stites, 31 May 1975.

Diaperis californica: CALIFORNIA. CALAVERAS Co.: 6.4 km (4 mi) E of Murphy's, 914 m (3000 ft), 12 Jul 1963. EL DORADO Co.: Blodgett Experimental Forest, 20.8 km (13 mi) E of Georgetown, 21 Jun 1981, blacklight. MARIPOSA Co.: El Portal, 16 Jun 1961, ex *Laetoporus sulphureus* (Bulliard ex Fries). Yosemite National Park, Tenaya Canyon, 960 m (3150 ft), 17 May 1928. SAN BERNARDINO Co.: Crestline, 1494 m (4900 ft), 5 Jul 1968; Lake Arrowhead, 2 Jul 1949. TUOLUMNE Co.: Twain Harte, 21 Jun 1961.

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John T. Doyen¹ and F. T. Hovore,² ¹*Department of Entomological Sciences, University of California, Berkeley, California 94720;* ²*Placerita Canyon Nature Center, Newhall, California 91321.*

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THE PAN-PACIFIC ENTOMOLOGIST

Volume 67

July 1991

Number 3

Contents

THOMAS, D. B.—The Acanthosomatidae (Heteroptera) of North America	159
BULLOCK, S. H., R. AYALA, G. RODRÍGUEZ-GONZALEZ, R. PALACIOS-CHÁVEZ, D. ROMAS-ZAMORA, D. L. QUIROZ-GARCÍA, & M. DE LA LUIZ ARREGUÍN-SANCHEZ—Nest provision and pollen foraging in three Mexican species of solitary bees (Hymenoptera: Apoidea)	171
O'NEILL, K. M. & W. P. KEMP—Foraging of <i>Stenopogon inquinatus</i> (Loew) (Diptera: Asilidae) on Montana rangeland sites	177
DELGADO-CASTILLO, L. & M. A. MORÓN—A new genus and species of Trichiini from Mexico (Coleoptera: Melolonthidae)	181
PITCAIRIN, M. J., C. PICKEL, L. A. FALCON & F. G. ZALOM—Development and survivorship of <i>Cydia pomonella</i> (L.) (Lepidoptera: Tortricidae) at ten constant temperatures	189
SHEPARD, W. D. & C. B. BARR—Description of the larva of <i>Atractelmis</i> (Coleoptera: Elmidae) and new information on the morphology, distribution, and habitat of <i>Atractelmis wawona</i> Chandler	195
MANLEY, D. G. & G. O. POINAR, JR.—A new species of fossil <i>Dasymutilla</i> (Hymenoptera: Mutillidae) from Dominican amber	200
ALLEN, R. K. & C. M. MURVOSH—A biogeographically based assessment of the potential mayfly fauna of Nevada	206
DELFINO, M. A.—A new species of <i>Uroleucon</i> (<i>Uroleucon</i>) and comments on <i>Uroleucon</i> (<i>Uroleucon</i>) <i>tucumani</i> (Essig) (Homoptera: Aphididae)	216
SCIENTIFIC NOTES	
PRENTICE, T. R. & G. P. WALKER—Nocturnal clustering of the solitary wasp, <i>Chalybion californicum</i> (Saussure) (Hymenoptera: Sphecidae)	222
HUMBLE, L. M.—Occurrence of <i>Coccinella septempunctata</i> (L.) (Coleoptera: Coccinellidae) in central British Columbia	224
DOYEN, J. T. & F. T. HOVORE—Notes on two Pacific coastal Species of Tenebrionidae (Coleoptera)	226

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**NEW SPECIES OF *NOTASPIDIUM* DALLA TORRE
FROM THE NEARCTIC AND NEOTROPICAL REGIONS
(HYMENOPTERA: CHALCIDIDAE)**

JEFFREY A. HALSTEAD¹

296 Burgan, Clovis, California 93612

Abstract.—Eleven new species of *Notaspidium* are described from the Nearctic and Neotropical regions: *N. acutum* NEW SPECIES, *N. boharti* NEW SPECIES, *N. braziliense* NEW SPECIES, *N. burdicki* NEW SPECIES, *N. giganteum* NEW SPECIES, *N. hansonii* NEW SPECIES, *N. lineatum* NEW SPECIES, *N. mexicanum* NEW SPECIES, *N. minutum* NEW SPECIES, *N. truncatum* NEW SPECIES, and *N. villegasi* NEW SPECIES. *Notaspidium formiciforme* (Walker), the only species previously described from these regions, is redescribed and its female is described for the first time. The taxonomic history of *Notaspidium* is discussed, and characters to distinguish it from other New World Chalcididae are presented. The first host information is presented for *Notaspidium*.

Key Words.—Insecta, *Notaspidium*, Nearctic, Neotropical, Chalcididae, Chalcidoidea, Hymenoptera

Notaspidium are small (1 to 4 mm) metallic green to black chalcidid wasps which have blue, violet, gold, or silver iridescence on the mesosoma, and orange or brown antennae, tegulae, or legs. The metallic green color is unique in the Chalcididae except for some Australian and Oriental species of *Steninvreia* and *Notaspidiella*. Most chalcidid species are black, brown, yellow, red, orange, or a combination of these colors.

Four species of *Notaspidium* have been described: *N. bakeri* Narendran (1989) from Mindanao, the Philippines; *N. formiciforme* (Walker) (1834) from Saint Vincent Island, West Indies; *N. grisselli* Narendran (1987) from Kerala, India; and *N. papuanum* Boucek (1988) from the Aieme River, Papua New Guinea. Walker (1871) illustrated the habitus, mesosoma, gaster, and head of *N. formiciforme*, but Narendran (1987) erroneously illustrated a male of *N. giganteum* as *N. formiciforme*. These are the only publications dealing with *Notaspidium*.

This paper clarifies *N. formiciforme* by redescribing the male and describing the female, describes new species, and diagnoses the *Notaspidium*. Eleven species of *Notaspidium* from the Nearctic and Neotropical regions are described and illustrated. A key is omitted here, because many descriptions of additional new species and a key to all of the American species are forthcoming (unpublished data).

The only existing biological information on *Notaspidium* is that Central American species are found on twigs infested by bark beetles (Scolytidae) (Boucek 1988). New host information indicates that specimens have emerged from an unidentified dead branch, and from an unidentified lepidopterous pupa (attached to specimen) in U. S. quarantine of a Jamaican shipment. Biological control benefits and possibilities of *Notaspidium* are unknown.

¹ Correspondence: % Kings River Conservation District, 4886 E. Jensen Avenue, Fresno, California 93725.

Distributional information on *Notaspidium* was previously restricted to India, Papua New Guinea, the Philippines and the West Indies (Boucek 1988, Narendran 1989), but is currently expanded to include Argentina, Belize, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, and Peru. The examination of museum collections and additional collecting in Central and South America will undoubtedly further improve our knowledge and produce many more undescribed species.

Useful species characters include the length of tergum I in relation to that of the gaster; the shape of the gaster, especially the terga and the basal sterna; the shape and sculpture of the scrobe cavity, scutellum, mesopleural acetabulum, metapleuron, hind femur, propodeum, and tergum I; the morphology of the pre-orbital carina; and body color.

Notaspidium may be distinguished from other genera of New World Chalcididae by the following characters: a hind tibia that is truncate distally with two apical spurs (Haltichellinae); a marginal vein of the forewing that does not reach the anterior margin of wing, but is separated from it by a short distance; postmarginal and stigmal veins which are absent (Hybothoracini); a tergum I with a lateral carina dorsally, and occasionally with longitudinal carinae and/or a median carina; a scutellum that is broadly rounded, subacuminate, or with a long, projecting, finger-like process; preorbital carina in some species that form an arch just below anterior ocellus, but which is absent in others; color that is predominantly metallic green or at least metallic green on the mesosoma; and wings that are hyaline.

A mylar glare-reducing screen was used when studying specimens. Abbreviations include: T1 for tergum I, etc., and S1 for sternum I. Museum acronyms are: American Museum of Natural History, New York (AMNH); British Museum of Natural History, London (BMNH); Canadian National Collection, Ottawa (CNC); California State University, Fresno (CSUF); United States National Museum of Natural History, Washington, D.C. (USNM); Utah State University, Logan (USU).

NOTASPIDIUM FORMICIFORME (WALKER)

(Figs. 3, 15, 27, 39, 51, 61)

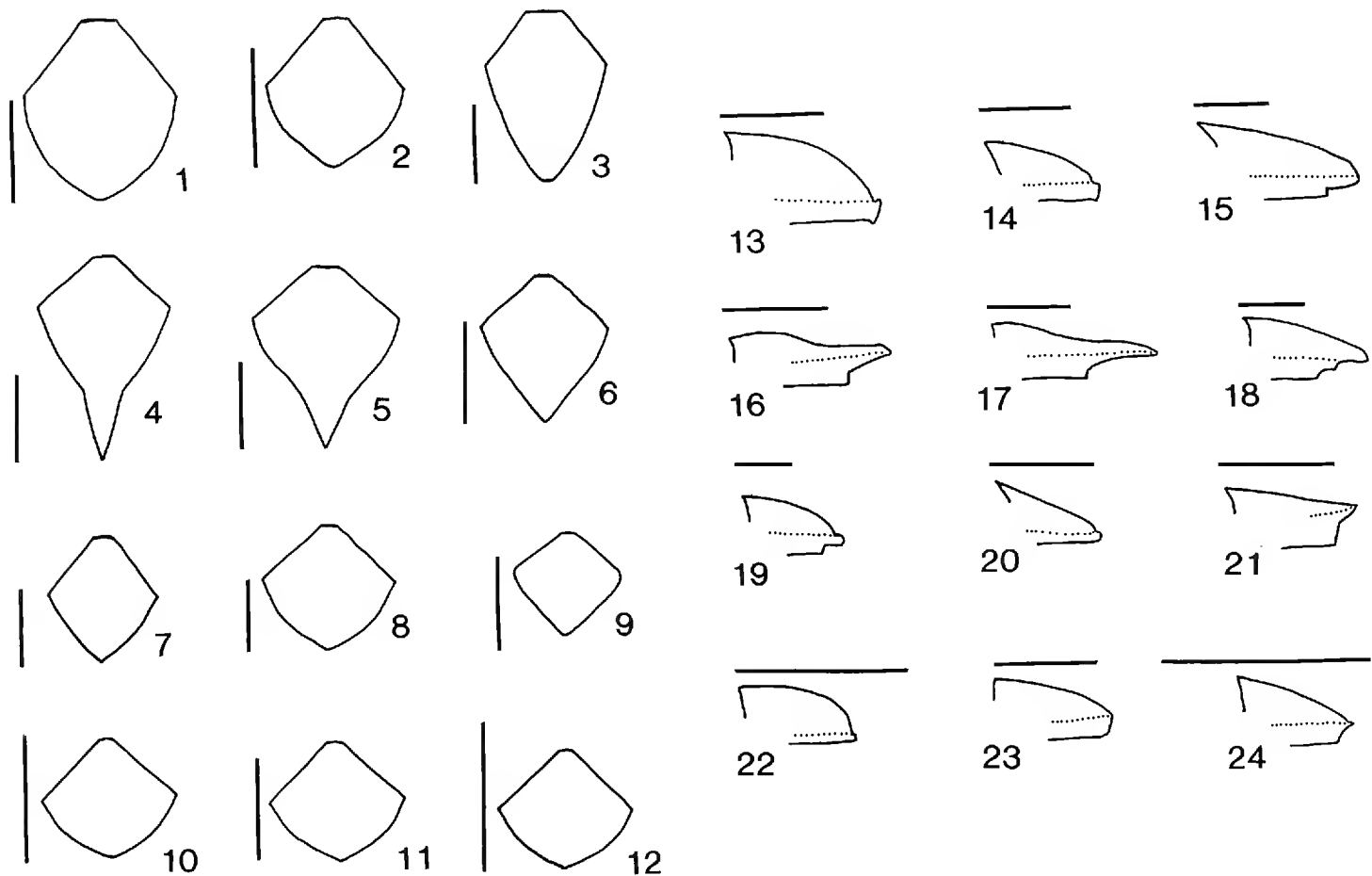
Notaspis formiciformis Walker, 1834: 38. Generic and male description.

Notaspidium formiciformis (Walker), Dalla Torre 1897: 87.

Notaspidium formiciformis (Walker), Narendran 1987: 10. Erroneous illustration of *N. giganteum* n. sp., male.

Types.—Holotype, male; data: WEST INDIES. “St. Vincent I., Lectotype, St. Vincent, *Notaspis formiciformis* Walker, B.M. TYPE HYM. 5.557.” Examined by author. Holotype resides in the British Museum (Natural History), London.

Redescription.—*Male* (holotype). *Length:* 2.2 mm. *Color:* dark metallic blue green with mesosoma dorsally metallic purple; tegula and apex of fore tibia testaceous; antenna dark brown. Middle legs and tarsi absent from holotype (but see female description). *Scrobe cavity:* deeply concave, coriaceous. *Preorbital carina:* prominent, broad, forming an arch just below anterior ocellus. *Scutellum:* long, subacuminate posteriorly in dorsal view (as in female, Fig. 3), dorsal margin slightly convex, posterior margin angled in lateral view (Fig. 61); punctures separated by $0.33 \times$ their diameter; sculpture coriaceous. *Metapleuron:* covered by about 15 oval punctures, sculpture in punctures rugose; septa between punctures $0.33\text{--}0.5 \times$ puncture diameter, integument polished. *Hind femora:* as in female (Fig. 51). *Propodeum:* apicolateral margin (dorsal view) with a rounded tooth (Fig. 39). *Gaster:* apex subacuminate, dorsal margin strongly convex (lateral view) (as in female, Fig. 27). *T1:* $0.75 \times$ length



Figures 1–24. *Notaspidium* spp., females. Scutellum in dorsal view (Figures 1–12); lateral view (Figures 13–24). Figures 1, 13. *N. giganteum* NEW SPECIES. Figures 2, 14. *N. villegasi* NEW SPECIES. Figures 3, 15. *N. formiciforme* (Walker). Figures 4, 17. *N. acutum* NEW SPECIES. Figures 5, 16. *N. burdicki* NEW SPECIES. Figures 6, 18. *N. truncatum* NEW SPECIES. Figures 7, 19. *N. brazilense* NEW SPECIES. Figures 8, 20. *N. hansonii* NEW SPECIES. Figures 9, 21. *N. lineatum* NEW SPECIES. Figures 10, 22. *N. boharti* NEW SPECIES. Figures 11, 23. *N. mexicanum* NEW SPECIES. Figures 12, 24. *N. minutum* NEW SPECIES. Scale lines 0.3 mm.

of gaster (dorsal view), dorsally with a strong, broad lateral and median carina (as in female, Fig. 39); sculpture rugose basally between lateral carina, longitudinally striated to apex of lateral carina, followed by a coriaceous band then minutely punctate along posterior margin, punctate laterally. *T2*: dorsally and sublaterally punctate, remainder polished. *T3–5*: basal one-half polished, apical one-half punctate. *T6*: punctate. *S1*: basally with a small tooth (as in female, Fig. 27).

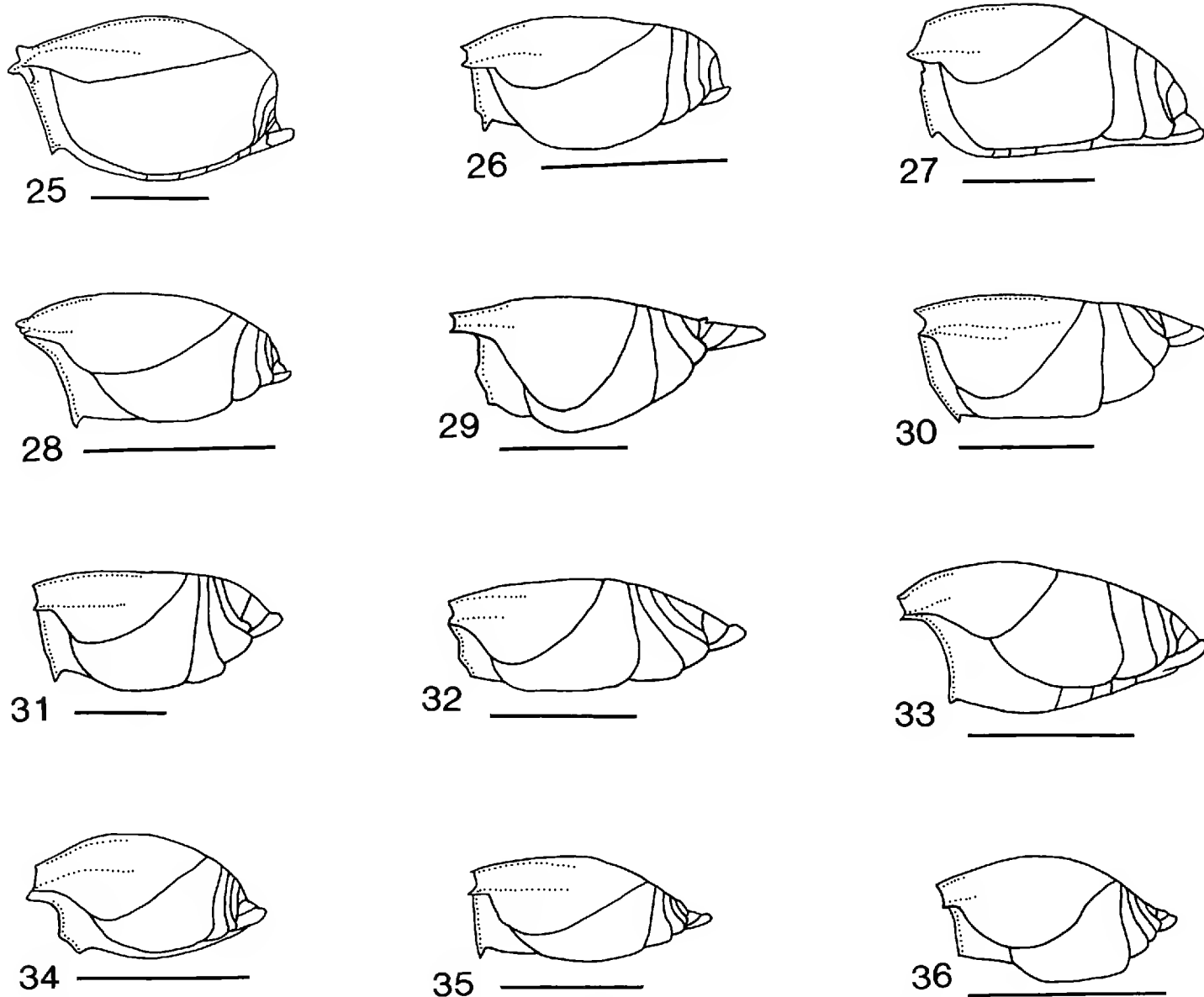
Female. (New description.) Length 3.2 mm. Like male except: mesosoma dorsally metallic green with apical one-half of mesoscutum violet; shape of scutellum (Fig. 15); metapleuron covered by 22 oval punctures, integument in punctures polished; *T1* $0.6 \times$ length of gaster; sculpture of *T1* dorsally, coriaceous between lateral carina, polished ventrad of lateral carinae, and punctate along posterior margin.

Diagnosis.—*Female*. This species can be distinguished from other species of *Notaspidium* by the presence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 3, 15), abdomen, especially the carinae of *T1* (Figs. 27, 39), and hind femur (Fig. 51). *Male*. The male can be distinguished by its arch-like preorbital carina, scutellar shape (Figs. 62–65) and carinae morphology of *T1* (Fig. 39).

Variation.—Unknown. The two female specimens examined are alike. The male is known only from the holotype.

Distribution.—Belize and the West Indies.

Material Examined.—Type, and two females with data: BELIZE. 0–25 m, Jul 1975, N.L.H. Krauss (BMNH, USNM).

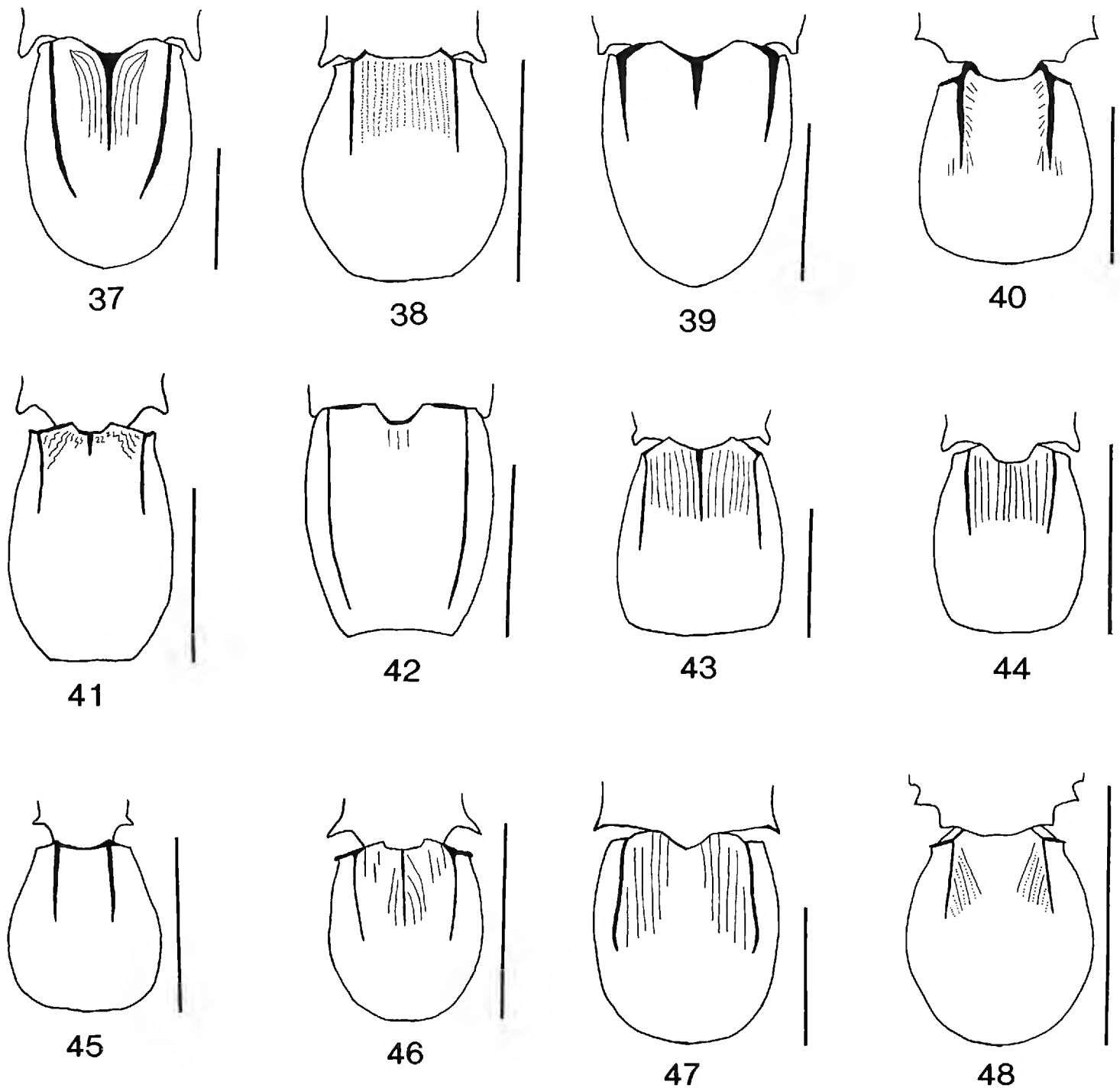


Figures 25–36. *Notaspidium* spp., females. Gaster in lateral view. Figure 25. *N. giganteum* NEW SPECIES. Figure 26. *N. villegasi* NEW SPECIES. Figure 27. *N. formiciforme* (Walker). Figure 28. *N. burdicki* NEW SPECIES. Figure 29. *N. acutum* NEW SPECIES. Figure 30. *N. truncatum* NEW SPECIES. Figure 31. *N. brazilense* NEW SPECIES. Figure 32. *N. hansonii* NEW SPECIES. Figure 33. *N. lineatum* NEW SPECIES. Figure 34. *N. boharti* NEW SPECIES. Figure 35. *N. mexicanum* NEW SPECIES. Figure 36. *N. minutum* NEW SPECIES. Scale lines 0.5 mm.

NOTASPIDIUM GIGANTEUM HALSTEAD, NEW SPECIES

(Figs. 1, 13, 25, 37, 49, 62–65)

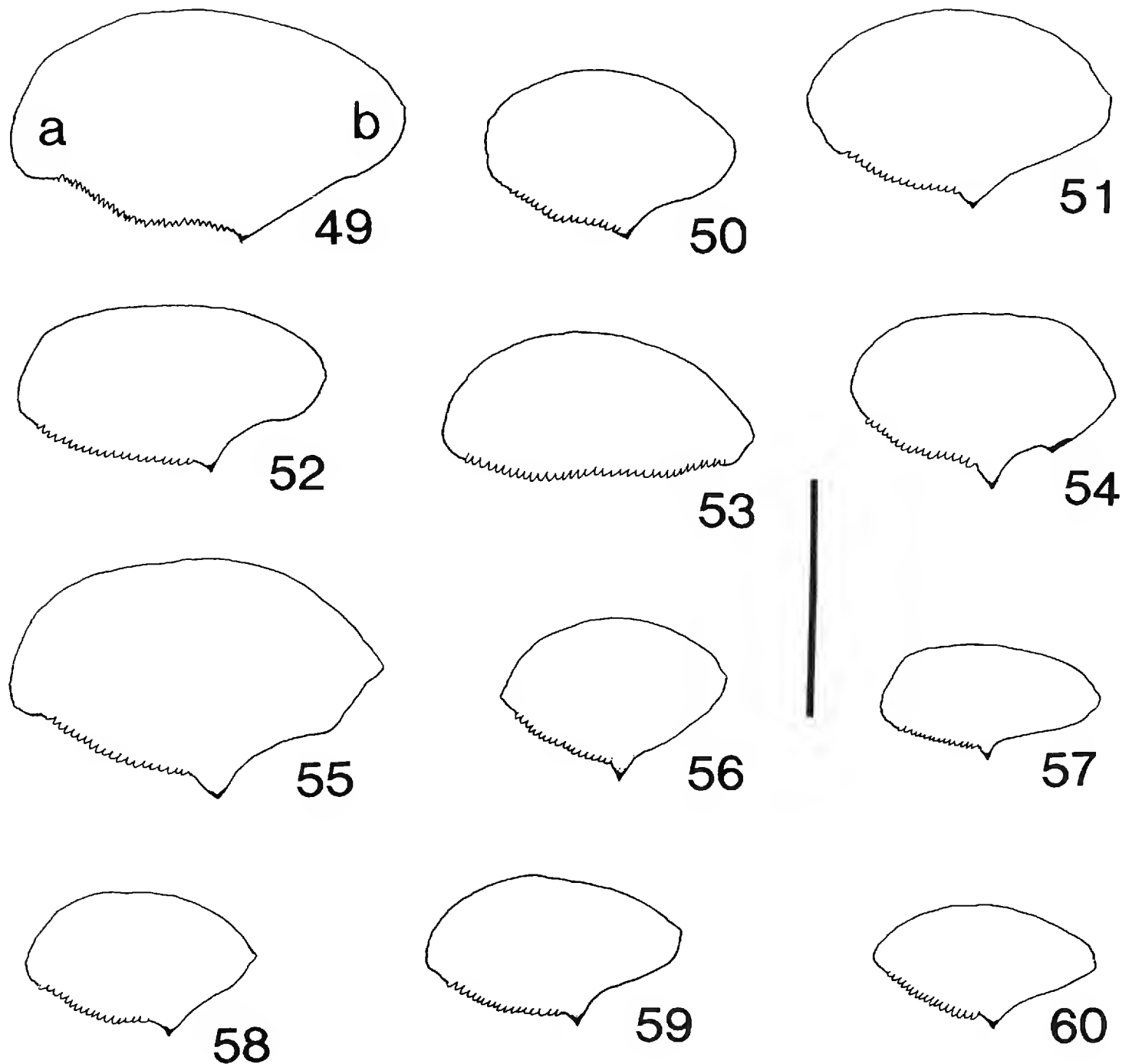
Types.—Holotype, female; allotype, male; data: MEXICO. *JALISCO*: Puerto Vallarta, 25 Jan 1984, G. E. Bohart. Holotype deposited in the Canadian National Collection, Ottawa (from USU). *Paratypes*: ARGENTINA. *JUJUY*: San Salvador de Jujuy, 21 Oct 1968, L. & C.W. O'Brien, 1 male, 1 female (AMNH). BRAZIL. "SP, Faz." Campininas, Mogi Gaucu, 1–8 Jan 1970, J. M. & B. A. Campbell, 1 male (USNM). COLOMBIA. 17 km S of Cali, 1000 m, 10 Apr 1971, Eberhard & Garcia, 1 male (USNM). COSTA RICA. C.A.T.I.E. (Centro Agronomico Tropical de Investigacion Y Ensenanza), 2 km SE of Turrialba, 7 July 1987, D. J. Burdick, 1 female (CNC, from CSUF). *GUANACASTE*: Guan. La Taborga For. Res., 9 km SW of Canas, 17–27 Feb 1987, W.L. Rubink, Malaise trap, 1 male, 1 female (USNM, from USU). ECUADOR. *NAPO*: Tena, 15 Feb 1986, A. Finnamore, 1 male (CNC). GUATEMALA. *ALTA VERAPAZ*: Cacao Trece Aguas, Apr 21, Schwartz & Barber, 1 female (USNM). HONDURAS. San Pedro Sula, Aug 1975, N.L.H. Krauss, 1 female (USNM). MEXICO. 1 male with same data



Figures 37–48. *Notaspidium* spp., females. Tergum 1 and apicolateral margin of propodeum in dorsal view. Figure 37. *N. giganteum* NEW SPECIES. Figure 38. *N. villegasi* NEW SPECIES. Figure 39. *N. formiciforme* (Walker). Figure 40. *N. burdicki* NEW SPECIES. Figure 41. *N. acutum* NEW SPECIES. Figure 42. *N. truncatum* NEW SPECIES. Figure 43. *N. brazilense* NEW SPECIES. Figure 44. *N. hansonii* NEW SPECIES. Figure 45. *N. lineatum* NEW SPECIES. Figure 46. *N. boharti* NEW SPECIES. Figure 47. *N. mexicanum* NEW SPECIES. Figure 48. *N. minutum* NEW SPECIES. Scale lines 0.5 mm.

and depository as holotype. *QUINTANA ROO*: 32 km N of Felipe Carrillo P., 17 Jul 1983, M. Kaulbars, 1 female (CNC). *YUCATAN*: 2 km E of Chichen Itza, 20 Jul 1983, 20 m, M. Kaulbars, 1 male (CNC). *PERU*. Rio Perene, Mar 29, C. H. T. Townsend, 1 male (USNM).

Description.—*Female* (holotype). *Length*: 3.7 mm. *Color*: dark metallic green with scape, pedicel, fore and mid trochanter and tibia, apex and base of mid femur, and tarsi testaceous; flagellum brown; scutellum centrally violet. *Scrobe cavity*: deeply concave, coriaceous. *Preorbital carina*: prominent, forming an arch just below anterior ocellus. *Scutellum*: rounded posteriorly in dorsal view (Fig. 1), dorsal margin convex and posterior margin truncate in lateral view (Fig. 13); punctures separated by their own diameter; sculpture coriaceous. *Metapleuron*: covered by about 25 oval punctures, sculpture in punctures coriaceous; septa between punctures $0.25 \times$ puncture diameter, integument polished. *Hind*



Figures 49–60. *Notaspidium* spp., females. Hind femur in lateral view. Base (b) of femur to right, apex (a) to left. Figure 49. *N. giganteum* NEW SPECIES. Figure 50. *N. villegasi* NEW SPECIES. Figure 51. *N. formiciforme* (Walker). Figure 52. *N. burdicki* NEW SPECIES. Figure 53. *N. acutum* NEW SPECIES. Figure 54. *N. truncatum* NEW SPECIES. Figure 55. *N. brazilense* NEW SPECIES. Figure 56. *N. hansonii* NEW SPECIES. Figure 57. *N. lineatum* NEW SPECIES. Figure 58. *N. boharti* NEW SPECIES. Figure 59. *N. mexicanum* NEW SPECIES. Figure 60. *N. minutum* NEW SPECIES. Scale lines 0.5 mm.

femur: as in Fig. 49. *Propodeum*: apicolateral margin (dorsal view) with a rounded tooth (Fig. 37); medially with a tear-drop shaped carina. *Gaster*: apex blunt, dorsal margin strongly convex (lateral view) (Fig. 25). T1 $0.8 \times$ length of gaster (dorsal view), dorsally with a strong lateral carina which curves medially near the apex of T1, with a shorter strong median carina and 8 weak longitudinal carinae (Fig. 37), sculpture coriaceous except for polished band along lateral carina. *Terga*: punctate to coriaceous. T3–5: not projecting posterior of T2. *S1*: basally with a small tooth (Fig. 25).

Male. Like the female except: scutellum in dorsal view acuminate posteriorly (as in Fig. 5), dorsal margin convex and posterior margin triangular in lateral view (Fig. 62), punctures separated by $0.33 \times$ (or less near apex) their diameter. T1 dorsally without longitudinal carinae.

Diagnosis.—*Female*. This species can be distinguished from other species of *Notaspidium* by the presence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 1, 13), abdomen, especially the carinae of T1

(Figs. 25, 37), and hind femur (Fig. 49). *Male*. The male can be distinguished by its arch-like preorbital carina, scutellar shape (Fig. 61) and lack of carinae on T1.

Variation.—*Female*. Several with scutellum less convex than illustrated by Fig. 13. Medial carina of T1 rarely weak, usually as prominent as lateral carina. Mesosoma dorsally sometimes with violet, gold-green, or silver iridescence. Tegula rarely blue. *Male*. Apex of the scutellum varies from the typical form (Fig. 62) to as illustrated by Figs. 63–65. Sculpture of propodeum between major carinae rugose to smooth. Sculpture in punctures on metapleuron rugose to smooth. Sculpture of mesopleural acetabulum coriaceous or coriaceous with weak transverse carinae.

A male and female from Saint Vincent Island are not designated as paratypes because their mesosomas are a different color and more robust, and the sculpture of their body fainter and less dense than the type material. Color of the mesosoma in dorsal view is: apical one-half of scapula, apical one-third of scutellum, and apical one-half of mesoscutum purple; axillae, tegulae, and base of scutellum blue; remainder gold-green. These specimens vary from the type materials as follows: scutellum more convex and punctures smaller and separated by 0.5 to 1.0× their diameter; mesosoma overall, with fewer punctures; typically coriaceous areas are faintly coriaceous or polished; preorbital carina below anterior ocellus not prominent; and male with apex of scutellum slimmer and more acute (Fig. 63). The shape of the gaster, sculpture of T1 and propodeum, and rest of body are like the type material.

Distribution.—Argentina, Brazil, Columbia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Peru, and West Indies.

Etymology.—Latin adjective describing the large body size.

Material Examined.—Types, and 1 male and 1 female from: WEST INDIES. Saint Vincent Island, H.H. Smith, #207 (USNM) (see Variation section).

NOTASPIDIUM VILLEGASI HALSTEAD, NEW SPECIES

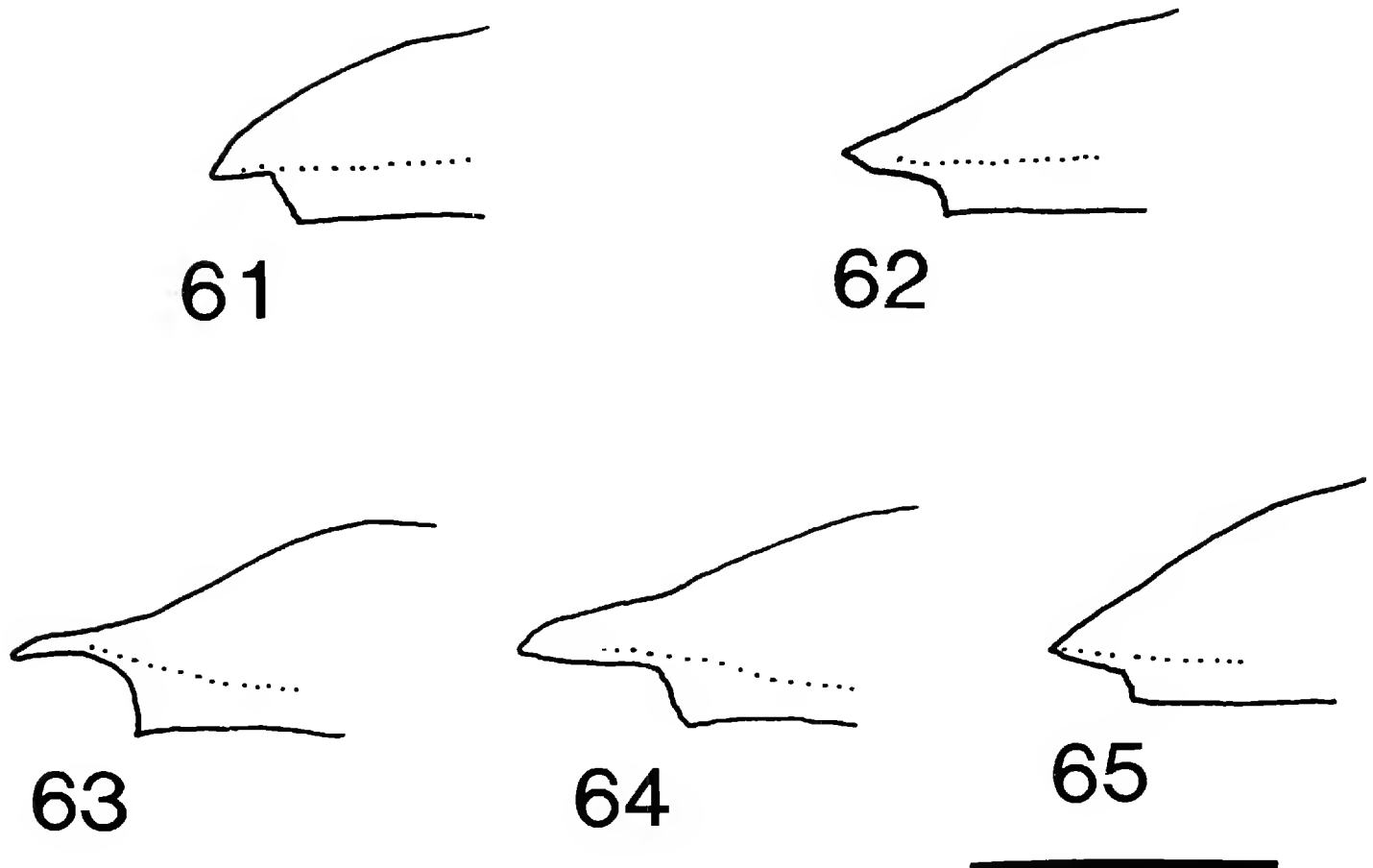
(Figs. 2, 14, 26, 38, 50)

Type.—Holotype, female; data: BRAZIL. *MATO GROSSO*: Sinop, Oct 1974, Malaise trap, M. Alvarenga. Holotype deposited in the Canadian National Collection.

Description.—*Female* (holotype). *Length*: 2.5 mm. *Color*: metallic green with flagellum brown; scape, pedicel, fore and mid legs (except coxa), and hind tarsus testaceous. *Scrobe cavity*: concave, coriaceous. *Preorbital carina*: weak, not arch-like below anterior ocellus. *Scutellum*: rounded posteriorly in dorsal view (Fig. 2), dorsal margin convex and posterior margin truncate in lateral view (Fig. 14); punctures separated by 0.25× their diameter; sculpture coriaceous. *Metapleuron*: covered by about 30 oval punctures, sculpture in punctures coriaceous; septa between punctures 0.16× puncture diameter, integument polished. *Hind femur*: as in Fig. 50. Apicolateral margin of propodeum (dorsal view) with a rounded tooth (Fig. 38). *Gaster*: apex blunt, dorsal margin convex (lateral view) (Fig. 26). *T1*: 0.6× length of gaster (dorsal view), dorsally with a strong lateral carina and 16 weak longitudinal carinae (Fig. 38), sculpture in carinate area coriaceous, basolateral area punctate, remainder polished. *T2*: basal one-half polished, apical one-half punctate. *T3–6*: coriaceous, and projecting slightly posterior of T2. *S1*: basally with a small tooth (Fig. 26).

Male. Unknown.

Diagnosis.—*Female*. This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique



Figures 61–65. *Notaspidium* spp., males. Scutellum in lateral view. Figure 61. *N. formiciforme* (Walker) (Holotype). Figures 62–65. *N. giganteum* NEW SPECIES. Figure 62. typical form. Figures 63–65. variation (Saint Vincent Island, West Indies; Mexico, and Ecuador, respectively). Scale line 0.5 mm.

morphology of its scutellum (Figs. 2, 14), abdomen, especially the carinae of T1 (Figs. 26, 38), and hind femur (Fig. 50).

Variation.—Unknown. Species known only from the type specimen.

Distribution.—Brazil.

Etymology.—A noun in the genitive case from a modern personal name. Named in honor of Baldomero Villegas, my mentor at the California Department of Food and Agriculture, Biological Control Services Program.

Material Examined.—This species is known only from the type specimen.

NOTASPIDIUM BURDICKI HALSTEAD, NEW SPECIES
(Figs. 5, 16, 28, 40, 52)

Types.—Holotype, female; data: BRAZIL. MATO GROSSO: Sinop, Oct 1976, Malaise trap, M. Alvarenga. Holotype deposited in the Canadian National Collection. *Paratypes:* BRAZIL. 1 female with same data and depository as holotype; Linhares, E. Santo, Sep 1972, M. Alvarenga, 1 female (CNC); Represa Rio Grande Guanabara Dec 1967, M. Alvarenga, 1 female (CNC).

Description.—*Female* (holotype). *Length:* 3.0 mm. *Color:* dark metallic green with scape, pedicel, tegula, fore and mid legs, hind trochanter, apex of hind tibia, and hind tarsi orange; flagellum light brown. *Scrobe cavity:* deeply concave, coriaceous. *Preorbital carina:* prominent basally, ending dorsally at $0.75 \times$ eye height. *Scutellum:* acuminate posteriorly in dorsal view (Fig. 5); dorsal margin with a concave area in center and posterior margin acuminate in lateral view (Fig. 16); punctures separated by $0.25 \times$ their diameter; sculpture coriaceous. *Metapleuron:* covered with about 35 oval punctures, sculpture in punctures coriaceous; septa between punctures $0.25 \times$ puncture diameter, sculpture rugose. *Hind femur:* as in Fig. 52. *Propodeum:* apicolateral margin (dorsal view) with a small acute tooth (Fig.

40). *Gaster*: apex subacuminate, dorsal margin convex (lateral view) (Fig. 28). *T1*: $0.8\times$ length of gaster (dorsal view), dorsally with a strong lateral carina (Fig. 40), integument polished except for rugose areas along carina. *Terga*: punctate to coriaceous. *T3-6*: projecting posterior of *T2*. *S1*: basally with a small tooth (Fig. 28).

Male. Unknown.

Diagnosis.—*Female*. This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 5, 16), abdomen, especially the carinae of *T1* (Figs. 28, 40), and hind femur (Fig. 52).

Variation.—Two paratypes with scutellum less pointed than Fig. 16 and apicolateral tooth of propodeum more acute than Fig. 40.

Distribution.—Brazil.

Etymology.—A noun in the genitive case from a modern personal name. Named in honor of Donald J. Burdick, my mentor at California State University, Fresno.

Material Examined.—This species is known only from the type specimens.

NOTASPIDIUM ACUTUM HALSTEAD, NEW SPECIES
(Figs. 4, 17, 29, 41, 53)

Types.—Holotype, female; data: BRAZIL. Linhares, E. Santo, Sep 1972, M. Alvarenga. Holotype deposited in the Canadian National Collection. *Paratypes*: BRAZIL. AMAZONAS: estirar de Equador, Rio Javari, Sep 1979, M. Alvarenga, 1 female (CNC). MATO GROSSO: Sinop, Feb 1976, O. Roppa, Malaise trap, 1 female (CNC). ECUADOR. NAPO: 12 km SW of Tena, 500 m, 8-11 Jul 1976, S. & J. Peck, 1 female (USNM).

Description.—*Female* (holotype). *Length*: 3.0 mm. *Color*: metallic green with gaster and hind coxa brown; antenna, tegula, fore and mid legs, hind trochanter, hind tarsi, and ovipositor sheath testaceous. *Scrobe cavity*: deeply concave, transversely striated. *Preorbital carina*: prominent, ending just below dorsal margin of eye. *Scutellum*: acuminate posteriorly in dorsal view (Fig. 4), dorsal margin with a concave area in center and posterior margin acuminate in lateral view (Fig. 17); punctures separated by $0.25\times$ their diameter; sculpture basomedially coriaceous, remainder polished. *Metapleuron*: covered with about 28 oval punctures, integument in punctures polished; septa between punctures $0.16\times$ puncture diameter, integument polished. *Hind femur*: as in Fig. 53. *Propodeum*: apicolateral margin (dorsal view) with a rounded tooth (Fig. 41). *Gaster*: apex acute, dorsal margin slightly convex (lateral view) (Fig. 29). *T1*: $0.6\times$ length of gaster (dorsal view), dorsally with a strong lateral and median carina, vague short sinuate carinae basally (Fig. 41), remainder of integument polished. *T2*: polished, with two transverse lines of sublateral punctures. *T3-5*: polished, with a transverse line of sublateral punctures. *T6*: coriaceous. *T3-6*: projecting posterior of *T2*. *S1*: basally without a small tooth (Fig. 29).

Male. Unknown.

Diagnosis.—*Female*. This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 4, 17), abdomen, especially the carinae of *T1* (Figs. 29, 41), and hind femur (Fig. 53).

Variation.—One paratype with dorsal margin of scutellum (lateral view) nearly straight.

Distribution.—Brazil and Ecuador.

Etymology.—Latin adjective describing the finger-like, posterior projecting scutellum.

Material Examined.—This species is known only from the type specimens.

NOTASPIDIUM TRUNCATUM HALSTEAD, NEW SPECIES

(Figs. 6, 18, 30, 42, 54)

Types.—Holotype, female; data: HONDURAS. San Pedro Sula, Aug 1975, N.L.H. Krauss. Holotype deposited in U.S. National Museum of Natural History. *Paratypes:* BRAZIL. SANTA CATHARINA: Nova Teutonia, 12 Aug 1941, Fritz Plaumann, ex. dead branch, 1 female (CNC). TRINIDAD. Curepa, 1 Nov 1977, Malaise trap, 1 female (CNC); Maracas, 1–9 Dec 1977, Malaise trap, 1 female (CNC).

Description.—*Female* (holotype). *Length:* 2.8 mm. *Color:* dark metallic green with scutellum and scapula violet; gaster, hind trochanter, and hind femur brown; antenna, tegula, fore and mid legs, hind tarsi and ovipositor sheath (except for black apex) testaceous. *Scrobe cavity:* deeply concave, sculpture coriaceous. *Preorbital carina:* prominent basally, ending dorsally at $0.75 \times$ eye height. *Scutellum:* subacuminate posteriorly in dorsal view (Fig. 6), dorsal margin slightly convex and posterior margin triangular in lateral view (Fig. 18); punctures on basal one-half separated by $0.5 \times$ their diameter, those on apical one-half by $0.25 \times$ their diameter; sculpture coriaceous. *Metapleuron:* covered with about 30 oval punctures, sculpture in punctures coriaceous; septa between punctures 0.25 to $0.33 \times$ puncture diameter, integument polished. *Hind femur:* as is Fig. 54, with an inner tooth near base. *Propodeum:* apicolateral margin (dorsal view) without a projecting tooth (Fig. 42). *Gaster:* apex acute, dorsal margin nearly straight (lateral view) (Fig. 30). *T1:* $0.66 \times$ length of gaster (dorsal view), basal and apical margin truncate, dorsally with a long strong lateral carina (Fig. 42). T1 (dorsal view) longitudinally striated, polished along posterior margin and laterally. *T2–6:* coriaceous. *T3–6:* projecting posterior of T2. *S1:* basally with a small tooth (Fig. 30).

Male. Unknown.

Diagnosis.—*Female.* This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 6, 18), abdomen, especially the carinae of T1 (Figs. 30, 42), and hind femur (Fig. 54).

Variation.—Unknown. Specimens examined are alike.

Distribution.—Brazil, Honduras, and West Indies.

Etymology.—Latin adjective describing the truncate base and apex of T1 (dorsal view).

Material Examined.—This species is known only from the type specimens.

NOTASPIDIUM BRAZILIENSE HALSTEAD, NEW SPECIES

(Figs. 7, 19, 31, 43, 55)

Types.—Holotype, female; data: BRAZIL. Nova Teutonia, 27, 11' S, 52, 23' W, 300–500 m, 17 Mar 1967, Fritz Plaumann. Holotype deposited in the Canadian National Collection. *Paratype:* 1 female with same data and depository as holotype but collected 1973.

Description.—*Female* (holotype). *Length:* 3.5 mm. *Color:* metallic green with apical one-half of T1, scutellum centrally, scapula posteriorly, and axilla anteriorly, violet; flagellum, fore tibia, and mid tibia brown; scape, pedicel, remainder of fore and mid legs, and hind tarsi testaceous. *Scrobe cavity:* concave, coriaceous. *Preorbital carina:* absent. *Scutellum:* subacuminate posteriorly in dorsal view (Fig. 7), dorsal margin convex and posterior margin with a small rounded projection in lateral view (Fig. 19); punctures on apical one-half $2.0 \times$ size on basal one-half, punctures basally separated by $2.0 \times$ their diameter, centrally $1.0 \times$ and apically by $0.25 \times$ their diameter; sculpture coriaceous. *Metapleuron:* covered with about 35 oval punctures, sculpture in punctures coriaceous; septa between punctures 0.2 to $0.25 \times$ puncture diameter, sculpture faintly coriaceous. *Hind femur:* as in Fig. 55. *Propodeum:* apicolateral margin (dorsal view) with a rounded tooth (Fig. 43). *Gaster:* apex subacuminate, dorsal margin slightly convex (lateral view) (Fig. 31). *T1:* $0.5 \times$ length of gaster (dorsal view), dorsally with a strong lateral and median carina, about 14 weak longitudinal carinae between lateral

carinae (Fig. 43), sculpture coriaceous except for polished area ventrad of lateral carinae and small punctate area sublaterally near posterior margin. *T2-6*: coriaceous. *T3-6*: projecting posterior of *T2*. *S1*: basally with a small tooth (Fig. 31).

Male. Unknown.

Diagnosis. —Female. This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 7, 19), abdomen, especially the carinae of *T1* (Figs. 31, 43), and hind femur (Fig. 55).

Variation. —Unknown. Specimens examined are alike.

Distribution. —Brazil.

Etymology. —Latinized noun describing the collection locality (Brazil) of the holotype.

Material Examined. —This species is known only from the type specimens.

NOTASPIDIUM HANSONI HALSTEAD, NEW SPECIES
(Figs. 8, 20, 32, 44, 56)

Types. —Holotype, female; data: MEXICO. NAYARIT: San Blas area, 16-21 Mar 1983, J. W. Hanson. Holotype deposited in the Canadian National Collection (from USU). Paratype: JAMAICA. Port Antonio (at quarantine from Philadelphia, Pennsylvania), 21 Mar 1922, ex. lepidopterous pupa, C.A. Davis, Phil. No. 471, 1 female (USNM).

Description. —Female (holotype). Length: 2.7 mm. Color: metallic green with tegula metallic blue; antenna, legs (except tarsi), T3-6 laterally, and ovipositor sheath brown; tarsi testaceous. Scrobe cavity: concave, coriaceous. Preorbital carina: absent. Scutellum: rounded posteriorly in dorsal view (Fig. 8), dorsal margin nearly straight and posterior margin with a small truncate projection in lateral view (Fig. 20); punctures separated by 1.0-2.0 × their diameter in central region, by 0.25-1.0 × in remainder; sculpture faintly coriaceous. Metapleuron: covered with about 25 oval punctures, integument in punctures polished; septa between punctures 0.2 to 0.33 × puncture diameter, integument polished. Hind femur: as in Fig. 56. Propodeum: apicolateral margin (dorsal view) with a rounded tooth (Fig. 44). Gaster: apex acute, dorsal margin slightly convex (lateral view) (Fig. 32). T1: 0.66 × length of gaster (dorsal view), dorsally with a strong lateral carina, and a weak median and 11 longitudinal carinae (Fig. 44), sculpture coriaceous centrally, polished band along posterior and lateral margins, and punctate sublaterally. T2-6: faintly coriaceous. T3-6: projecting posterior of T2. S1: basally without a small tooth (Fig. 32).

Male. Unknown.

Diagnosis. —Female. This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 8, 20), abdomen, especially the carinae of *T1* (Figs. 32, 44), and hind femur (Fig. 56).

Variation. —Paratype with dorsal margin of gaster (lateral view) nearly straight.

Distribution. —Mexico and Jamaica.

Etymology. —A noun in the genitive case from a modern personal name. Named in honor of Wilford Hanson, the collector.

Material Examined. —This species is known only from the type specimens.

NOTASPIDIUM LINEATUM HALSTEAD, NEW SPECIES
(Figs. 9, 21, 33, 45, 57)

Types. —Holotype, female; data: COSTA RICA. HEREDIA: Pto. Viejo, 50 m, rain forest, Feb 1980, W. Mason. Holotype deposited in the Canadian National Collection.

Description.—*Female* (holotype). *Length:* 3.0 mm. *Color:* dark metallic green with gaster and flagellum dark brown; scape, pedicel, tegula, fore and mid legs, hind trochanter, and hind tarsi testaceous; apex of fore and mid tibia cream-white. *Scrobe cavity:* deeply concave, coriaceous. *Preorbital carina:* absent. *Scutellum:* subacuminate posteriorly in dorsal view (Fig. 9), dorsal margin nearly straight and posterior margin obtuse in lateral view (Fig. 21); punctures separated by $0.25 \times$ their diameter; sculpture coriaceous. *Metapleuron:* covered with about 30 oval punctures, integument in punctures polished; septa between punctures $0.25 \times$ puncture diameter, sculpture rugose. *Hind femur:* as in Fig. 57. *Propodeum:* apicolateral margin (dorsal view) with a small acute tooth (Fig. 45). *Gaster:* apex subacuminate, dorsal margin convex (lateral view) (Fig. 33). *T1:* $0.5 \times$ length of gaster (dorsal view), dorsally with a strong lateral carina (Fig. 45), integument polished. *T2:* polished except for laterally on posterior one-half, remainder coriaceous. *T3–5:* with basal one-half polished, apical one-half coriaceous. *T6:* coriaceous. *T3–6:* projecting posterior of T2. *S1:* basally with a small tooth (Fig. 33).

Male. Unknown.

Diagnosis.—*Female.* This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 9, 21), abdomen, especially the carinae of T1 (Figs. 33, 45), and hind femur (Fig. 57).

Variation.—Unknown. Species known only from type specimen.

Distribution.—Costa Rica.

Etymology.—Latin adjective describing the linear or straight dorsal margin of the scutellum.

Material Examined.—This species is known only from the type specimen.

NOTASPIDIUM BOHARTI HALSTEAD, NEW SPECIES
(Figs. 10, 22, 34, 46, 58)

Types.—Holotype, female; data: MEXICO. CHIAPAS: Palenque, 10 Sep 1974, G. Bohart & W. Hanson. Holotype deposited in the Canadian National Collection (from USU).

Description.—*Female* (holotype). *Length:* 2.1 mm. *Color:* dark metallic green with flagellum brown; scape, pedicel, fore and mid legs, hind trochanter, and hind tarsi testaceous. *Scrobe cavity:* concave, coriaceous. *Preorbital carina:* absent. *Scutellum:* rounded posteriorly in dorsal view (Fig. 10), dorsal margin strongly convex and posterior margin rounded in lateral view (Fig. 22); punctures separated by 0.25 to $0.33 \times$ their diameter; sculpture coriaceous. *Metapleuron:* covered with about 32 oval punctures, integument in punctures polished; septa between punctures $0.2 \times$ puncture diameter, integument polished. *Hind femur:* as in Fig. 58. *Propodeum:* apicolateral margin (dorsal view) with a long acute tooth (Fig. 46). *Gaster:* apex subacuminate, dorsal margin convex (lateral view) (Fig. 34). *T1:* $0.75 \times$ length of gaster (dorsal view), dorsally with a strong lateral and median carina and five longitudinal carinae between lateral carinae (Fig. 46), integument polished. *T2:* laterally with posterior one-half coriaceous. *Terga:* remainder polished. *T3–6:* projecting posterior of T2. *S1:* basally without a small tooth (Fig. 34).

Male. Unknown.

Diagnosis.—*Female.* This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 10, 22), abdomen, especially the carinae of T1 (Figs. 34, 46), and hind femur (Fig. 58).

Variation.—Unknown. Species known only from type specimen.

Distribution.—Mexico.

Etymology.—A noun in the genitive case from a modern personal name. Named in honor of George Bohart, the collector.

Material Examined.—This species is known only from the type specimen.

NOTASPIDIUM MEXICANUM HALSTEAD, NEW SPECIES

(Figs. 11, 23, 35, 47, 59)

Types.—Holotype, female; data: MEXICO. *JALISCO*: “13 mi” N of Barra de Navidad, 13 Apr 1977, Davis & Hanson. Holotype deposited in the Canadian National Collection (from USU).

Description.—*Female* (holotype). *Length*: 2.3 mm. *Color*: metallic green with flagellum and fore tibia brown; scape, pedicel, first two flagellomeres, remainder of fore leg, mid leg (except coxa), hind trochanter, hind tarsi, and ovipositor sheath (except black apex) testaceous. *Scrobe cavity*: concave, coriaceous. *Preorbital carina*: absent. *Scutellum*: rounded posteriorly in dorsal view (Fig. 11), dorsal margin slightly convex and posterior margin truncate in lateral view (Fig. 23); punctures separated by $0.25\times$ their diameter; sculpture coriaceous. *Metapleuron*: covered with about 26 oval punctures, integument in punctures polished; septa between punctures $0.25\times$ puncture diameter, sculpture of ventral one-half coriaceous, remainder polished. *Hind femur*: as in Fig. 59. *Propodeum*: apicolateral margin (dorsal view) with a small acute tooth (Fig. 47). *Gaster*: apex acute, dorsal margin convex (lateral view) (Fig. 35). *T1*: $0.66\times$ length of gaster (dorsal view), dorsally with a strong lateral carina, and 12 weak longitudinal carinae (Fig. 47), sculpture in carinate area coriaceous, polished band along posterior and lateral margins, remainder punctate. *T2*: punctate. *T3–6*: faintly coriaceous, and projecting posterior of T2. *S1*: basally with a small tooth (Fig. 35).

Male. Unknown.

Diagnosis.—*Female*. This species can be distinguished from other species of *Notaspidium* by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 11, 23), abdomen, especially the carinae of T1 (Figs. 35, 47), and hind femur (Fig. 59).

Variation.—Unknown. Species known only from type specimen.

Distribution.—Mexico.

Etymology.—Latinized noun describing the collection locality (Mexico) of the holotype.

Material Examined.—This species is known only from the type specimen.

NOTASPIDIUM MINUTUM HALSTEAD, NEW SPECIES

(Figs. 12, 24, 36, 48, 60)

Types.—Holotype, female; data: MEXICO. *CHIAPAS*: Palenque, 10 Sep 1974, G. Bohart & W. Hanson. Holotype deposited in the U.S. National Museum of Natural History (from USU). *Paratype*: MEXICO. *JALISCO*: Puerto Vallarta, 25 Jan 1984, G.E. Bohart, 1 female (CNC, from USU).

Description.—*Female* (holotype). *Length*: 2.1 mm. *Color*: metallic green with flagellum, fore tibia, and mid tibia brown; scape, pedicel, remainder of fore and mid legs, and hind tarsi testaceous. *Scrobe cavity*: shallowly concave, coriaceous; preorbital carina absent. *Scutellum*: rounded posteriorly in dorsal view (Fig. 12), dorsal margin slightly convex and posterior margin obtuse in lateral view (Fig. 24); punctures separated by $0.16\times$ their diameter; sculpture coriaceous. *Metapleuron*: covered with about 20 oval punctures, sculpture in punctures forming asterisk-shaped ridges; septa between punctures $0.12\times$ puncture diameter, integument polished. *Hind femur*: as in Fig. 60. *Propodeum*: apicolateral margin (dorsal view) with a small triangular tooth (Fig. 48). *Gaster*: apex subacuminate, dorsal margin convex (lateral view) (Fig. 36). *T1*: $0.84\times$ length of gaster (dorsal view), dorsally with a strong lateral carina and a few weak medially angled carinae between lateral carina (Fig. 48), sculpture in carinate area rugose, laterally with a faintly punctate area, remainder polished. *T2*: punctate except for polished area along ventral and posterior margin. *T3–6*: polished (except for apical coriaceous band on T3), and projecting posterior of T2. *S1*: basally without a small tooth (Fig. 36).

Male. Unknown.

Diagnosis.—*Female*. This species can be distinguished from other species of

Notaspidium by the absence of an arch-like preorbital carina and the unique morphology of its scutellum (Figs. 12, 24), abdomen, especially the carinae of T1 (Figs. 36, 48), and hind femur (Fig. 60).

Variation.—Unknown. Specimens examined are alike.

Distribution.—Mexico.

Etymology.—Latin adjective describing the small body size.

Material Examined.—This species is known only from the type specimens.

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**PREDATION ON DOUGLAS-FIR TUSSOCK MOTH
(LEPIDOPTERA: LYMANTRIIDAE) AND
WHITE FIR SAWFLY (HYMENOPTERA: DIPRIONIDAE)
LARVAE BY CAPTIVE SPIDERS FROM
WHITE FIR IN CALIFORNIA**

S. L. SWEZEY,^{1,3} D. L. DAHLSTEN,¹ E. I. SCHLINGER,^{2,4} AND S. M. TAIT¹

¹Division of Biological Control and ²Department of Entomology,
University of California, Berkeley, California 94720

Abstract.—Eighteen spider species commonly collected on white fir (*Abies concolor* Gordon & Glendinning) in California were tested in a laboratory study to determine if they would feed on Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) and white fir sawfly larvae (*Neodiprion abietis* (Harris) complex). All spider species fed on first, second, or third instar tussock moth larvae. Seven species fed on the fourth and fifth instar sawfly larvae that were available for the study. Their capacity to feed on these prey indicates that spiders may be important predators of white fir defoliators.

Key Words.—Insecta, *Orgyia pseudotsugata*, *Neodiprion abietis*, Araneae, *Abies concolor*, predation

Spiders are abundant in forests and may be important in regulating insects of concern to forest managers. There are numerous records of spider predation on Douglas-fir tussock moth (DFTM), sawflies, and other forest insects (Dahlsten 1961; Coppel & Smythe 1963; Whitcomb & Tadic 1963; Jennings & Pase 1975, 1986; Fox & Griffith 1976; Wickman 1977; Fichter & Stephen 1984; Jennings & Crawford 1985; Sheehan & Dahlsten 1985; Mason & Paul 1988). Most of the literature is observational rather than experimental. Reichert & Lockley (1984) reviewed evidence on the importance of spiders as biological control agents, emphasizing that their effectiveness is greatest in systems with minimum disruption. Assessments of the role of spiders in forest defoliator population dynamics vary (Jennings & Crawford 1985, Morris 1972). Weseloh (1989) reviewed work on spider predation on Lymantriidae and concluded that effects, when quantified, were small. However, Mason & Torgersen (1983, 1987), Mason & Overton (1983), and Mason et al. (1983) suggest that predation by spiders may be important in larval DFTM disappearance, a key mortality factor. In view of spiders' presumed importance as DFTM predators, Moldenke et al. (1987) provide a key to common spiders on Douglas fir and true fir.

An earlier study by this laboratory (Dahlsten et al. 1977) found spiders abundant in the canopy of white fir, *Abies concolor* (Gordon & Glendinning), in association with the Douglas-fir tussock moth in California. In that study, 23 species of spiders in 10 families were associated with DFTM. A conservative estimate was calculated of at least one free-living spider per four early instar DFTM larvae. These spiders, thought the most likely spider predators of early instar larvae, were 37% of the

³ Current address: Department of Environmental Studies, University of California, Santa Cruz, California 95064.

⁴ Current address: 830 Coachman Place, Clayton, California 94517.

total spiders collected. Spiders were also counted in a study designed to develop a sampling program for DFTM larvae at low population levels (Dahlsten et al. 1985). Spiders were the most common arthropods collected from intensively sampled white fir trees; 52 species from 16 families were recorded.

To assess the possible importance of spiders in the natural enemy complex, this laboratory study tested the feeding capabilities of spiders associated with the DFTM and the white fir sawfly on white fir in central California. Eighteen species of spiders from eight families were tested.

MATERIALS AND METHODS

In July, 1975, the foliage of white firs on three sample plots in El Dorado Co., California (Iron Mountain, Baltic Ridge, and Plummer Ridge) was sampled for larval Douglas-fir tussock moth according to a midcrown sampling procedure described by Mason (1970). These plots were located in a west-slope Sierra mixed conifer forest dominated by white fir in association with several other coniferous species, including ponderosa pine, *Pinus ponderosa* Lawson, and incense cedar, *Calocedrus decurrens* (Torrey) Florin. Dahlsten et al. (1977) sampled tussock moth on these same plots from 1971–1973.

Over a period of 30 days, in three repeat sampling periods, 674 live spiders suitable for the feeding study were collected from the midcrown samples of 240 white firs. The spiders were assigned preliminary identification and placed individually into 20-dram vials stoppered with moist cotton. The vials were transported to the laboratory of the U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station (PSW) in Berkeley, California.

Immediately upon receipt of the live spiders at PSW, a sawfly or DFTM larva was introduced into each vial. The cotton plug was remoistened to prevent desiccation of spider or larva. Late instar (fourth and fifth) larvae of *N. abietis* were obtained from the midcrown field samples, while first through fourth instar DFTM larvae were obtained from laboratory populations at PSW. The larval instar offered each spider was based on the size of the spider. Most spiders collected were immatures, and due to their small size could presumably feed effectively only on first and second instar tussock moth larvae, which range from 2–10 mm in length. Penultimate instar or mature tussock moth larvae were assumed to be too large for capture by most spiders available, except for some larger adult Philodromidae and Thomisidae species. Similarly, the fourth and fifth instar larvae of *N. abietis* were too large for many spider species. In all, 563 DFTM trials and 111 sawfly trials were performed.

Spider behavior was observed for one hour immediately after introduction of the larva, and thereafter for two hours every 24 hours for seven days. Capture and feeding behavior, web and retreat construction, other spider activity, and mortality were noted. Evidence of feeding was either direct observation of capture and feeding on the introduced larva; or desiccated, rolled or otherwise deformed larval wastes in webs or retreats. Enlarged spider abdomens following suspected feeding were corroborating evidence. All spiders were preserved for subsequent identification.

RESULTS AND CONCLUSIONS

All spider species, 18 species in eight families, fed on first, second, and/or third instar DFTM larvae (Table 1). Previous observations indicated that spiders were

most capable of feeding on first and second instar larvae. However, this is not strongly evident in Table 1. Due to the sporadic availability of field collected spiders, total numbers of third instar trials were small and are difficult to compare by spider species with the larger first and second instar trials. Overall, predation rate was about the same on first and second instars ($n = 486$) as on third and fourth instars ($n = 77$); about 35% of spiders fed on each group. Of the four free-living spider species with more than 40 trials, *Xysticus locuples* Keyserling and *Metaphidippus* sp. had lower rates of predation on older instars, but the rates are based on only nine and three late instar larvae respectively. For the two frequently collected web-spinners, *Pityophantes* sp. fed on first and second instars more than on third instars, and Linyphiidae sp. more on first than on second instars. These rates are based on trials with only 15 and four later instar larvae.

In the field free-living spiders may be more important predators than web-spinners for this wingless prey, although both DFTM and sawfly larvae drop from foliage during dispersal or to escape from natural enemies. In this study predation rates on DFTM larvae were similar, 38% and 33% respectively for free living and web spinning spiders. This is not surprising because all prey was placed close to spiders in a confined space.

Seven spider species in four families, of the 16 species in eight families tested, fed on fourth or fifth instar *N. abietis* complex (Table 2). Overall, only 16% of the spiders fed on the larvae, compared to 35% for DFTM. Because conditions for feeding tests with the two prey species differed (both sawfly larvae and the spiders confined with them were larger and older than in the DFTM trials), the difference in feeding rates cannot be attributed to prey species without further testing. Free-living spiders fed on the sawfly larvae in 11% of the trials ($n = 71$), whereas web-spinners fed on 25% of the offered prey ($n = 40$). Again, this difference under artificial conditions does not necessarily reflect predation rates in the field.

Free-living forms such as *Apollophanes margareta* (Lowrie & Gertsch), *Philodromus rufus* Walckenaer, and *P. spectabilis* Keyserling (Philodromidae), *Xysticus locuples* and *Misumenops lepidus* (Thorell) (Thomisidae), and *Metaphidippus* spp. (Salticidae), often immediately attacked larvae and fed through the head capsule or just behind the head on either the dorsal or ventral surface, largely avoiding the dorsal tussocks. The urticating hairs of *O. pseudotsugata* apparently did not deter feeding. One large adult female *X. locuples* attacked and consumed a large (20–25 mm) fourth instar *O. pseudotsugata* larva (Table 1). *Metaphidippus* spp. often captured *O. pseudotsugata* larvae and carried them into web retreats previously constructed in the vial. One female *Philodromus rufus*, having laid eggs in the vial prior to the introduction of prey, immediately took the introduced tussock moth larva and consumed it while remaining in a protective position over the clutch. Jennings & Pase (1975) observed similar behavior of a female oxyopid feeding on *Ips pini* (Say).

Our observations of successful salticid feedings are consistent with Turnbull's (1956) laboratory and field observations with the spruce budworm. He observed that spiders were not repelled by the "violent thrashing and oral exudation of a sticky, brown, evil-smelling liquid" of first through third instar spruce budworm larvae (sawfly larvae also exude a repellent fluid). However, he found that fourth and fifth instar larvae often did repel spiders. Our results with thomisids differ from Turnbull's. In his study, thomisids did not capture spruce budworms in the laboratory or the field.

Table 1. Spider taxa and feeding on *Orgyia pseudotsugata* larvae. Spiders collected from *Abies concolor* on Iron Mountain, Baltic Ridge, and Plummer Ridge, El Dorado County, California, July 1975. M = male. F = female.

	Larval instar	Total trials	Feeding	M	F	I.U. ^a	Non-feeding	Dead	% of sample feeding
Free-living spiders									
Philodromidae									
<i>Apollophanes margareta</i> Lowrie & Gertsch	1st	28	8	0	0	8	13	7	28.6
	2nd	15	10	0	0	10	5	0	66.6
	3rd	16	9	0	0	9	7	0	56.3
	4th	<u>1</u>	<u>1</u>	<u>0</u>	<u>0</u>	<u>1</u>	<u>0</u>	<u>0</u>	<u>100.0</u>
	Total	60	28	0	0	28	25	7	46.7
<i>Philodromus rufus</i> Walckenaer	1st	22	7	0	6	1	13	2	31.8
	2nd	21	8	1	6	1	13	0	38.1
	3rd	<u>13</u>	<u>4</u>	<u>0</u>	<u>3</u>	<u>1</u>	<u>9</u>	<u>0</u>	<u>30.8</u>
	Total	56	19	1	15	3	35	2	33.9
<i>Philodromus spectabilis</i> Keyserling	3rd	3	2	0	1	1	1	0	66.6
<i>Philodromus speciosus</i> Gertsch	2nd	2	2	0	0	2	0	0	100.0
Thomisidae									
<i>Xysticus locuples</i> Keyserling	1st	20	11	0	0	11	9	0	55.0
	2nd	14	3	0	0	3	11	0	21.4
	3rd	8	1	0	0	1	7	0	12.5
	4th	<u>1</u>	<u>1</u>	<u>0</u>	<u>1</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>100.0</u>
	Total	43	16	0	1	15	27	0	37.2
<i>Misumenops lepidus</i> (Thorell)	1st	2	2	1	0	1	0	0	100.0
	3rd	<u>1</u>	<u>1</u>	<u>0</u>	<u>1</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>100.0</u>
	Total	3	3	1	1	1	0	0	100.0
Salticidae									
<i>Metaphidippus</i> sp.	1st	78	25	1	0	24	37	16	32.0
	2nd	17	5	0	1	4	12	0	29.4
	3rd	<u>3</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>3</u>	<u>0</u>	<u>00.0</u>
	Total	98	30	1	1	28	52	16	30.6
<i>Metaphidippus harfordi</i> (Peckham)	1st	5	2	0	0	2	3	0	40.0
	2nd	2	2	0	1	1	0	0	100.0
	3rd	<u>3</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>3</u>	<u>0</u>	<u>00.0</u>
	Total	10	4	0	1	3	6	0	40.0
Anyphaenidae									
<i>Anyphaena pacifica</i> (Banks)	1st	7	4	0	0	4	3	0	57.1
	3rd	<u>2</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>2</u>	<u>0</u>	<u>00.0</u>
	Total	9	4	0	0	4	5	0	44.4
Web-building spiders									
Linyphiidae									
<i>Pityohyphantes</i> sp.	1st	47	19	0	0	19	28	0	40.4
	2nd	3	1	0	0	1	2	0	33.3
	3rd	<u>15</u>	<u>1</u>	<u>1</u>	<u>0</u>	<u>0</u>	<u>14</u>	<u>0</u>	<u>6.6</u>
	Total	65	21	1	0	20	44	0	32.3

Table 1. Continued.

	Larval instar	Total trials	Feeding	M	F	I.U. ^a	Non-feeding	Dead	% of sample feeding
Linyphiidae sp.	1st	109	31	14	0	17	77	1	28.4
	2nd	45	5	1	0	4	38	2	11.1
	3rd	4	4	0	0	4	0	0	100.0
	Total	158	40	15	0	25	115	3	25.3
<i>Prolinyphia</i> sp.	3rd	3	3	1	1	1	0	0	100.0
Araneidae									
<i>Araniella displicata</i> (Hentz)	1st	14	4	0	0	4	10	0	28.6
	2nd	3	0	0	0	0	3	0	00.0
	3rd	2	0	0	0	0	2	0	00.0
	Total	19	4	0	0	4	15	0	21.0
<i>Araneus</i> sp. 1	1st	10	6	0	0	6	3	1	60.0
	2nd	2	2	0	0	2	0	0	100.0
	Total	12	8	0	0	8	3	1	66.6
<i>Araneus</i> sp. 2	1st	5	4	0	0	4	0	0	80.0
Dictynidae									
Dictynidae sp. 1	1st	5	5	0	0	5	0	0	100.0
Theridiidae									
<i>Theridion neomexicanum</i> Banks	1st	1	1	1	0	0	0	0	100.0
	2nd	2	2	0	2	0	0	0	100.0
	Total	3	3	1	2	0	0	0	100.0
Agelenidae									
Agelenidae sp. 1	1st	3	2	0	0	2	0	1	66.6
	2nd	4	1	0	0	1	3	0	25.0
	3rd	2	0	0	0	0	2	0	00.0
	Total	9	3	0	0	3	5	1	33.3
Total sample size		563	199						34.8

^a Immature, sex undetermined.

Web-building forms such as *Araniella displicata* (Hentz), *Araneus* spp., Agelenidae, *Anyphaena pacifica* (Banks), and Linyphiidae spun webs in the vials, and spun additional webbing around entangled larvae before consuming them. Web-building spiders most often fed upon captured larvae through the head capsule or ventrally, midway along the length of the larva. These laboratory observations are again consistent with Turnbull's (1956) field observations of spiders and the spruce budworm. Many of the genera and species used in this study were also used in Turnbull's study.

The results of these feeding trials may have been complicated by factors such as differing feeding by spiders in the field prior to collection, differences in size and maturity of the spiders fed different larval instars (e.g., adult males may not feed), onset of molting, and small size of the feeding environment (in a confined space, spiders may accept food they would not eat in the field). However, the results do indicate the ability of these species to feed on the defoliators. In a

Table 2. Spider taxa and feeding on *Neodiprion abietis* complex larvae. Spiders collected from *Abies concolor* on Iron Mountain, Baltic Ridge, and Plummer Ridge, El Dorado County, California, July 1975. M = male. F = female.

	Larval instar	Total trials	Feeding	M	F	I.U. ^a	Non-feeding	Dead	% of sample feeding
Free-living spiders									
Philodromidae									
<i>Apollophanes margareta</i>	4/5	24	3	0	0	3	20	1	12.5
<i>Philodromus rufus</i>	4/5	19	1	0	1	0	15	3	5.3
Thomisidae									
<i>Xysticus locuples</i>	4/5	11	3	0	1	2	8	0	27.3
<i>Misumenops lepidus</i>	4/5	2	0	0	0	0	1	1	00.0
Salticidae									
<i>Metaphidippus</i> sp. 1	4/5	10	1	0	0	1	8	1	10.0
Anyphaenidae									
<i>Anyphaena pacifica</i>	4/5	5	0	0	0	0	4	1	00.0
Web-building spiders									
Linyphiidae									
<i>Pityohyphantes</i> sp.	4/5	10	0	0	0	0	7	3	00.0
<i>Prolinyphia</i> sp.	4/5	3	0	0	0	0	2	1	00.0
Linyphiidae sp. 1	4/5	2	0	0	0	0	2	0	00.0
Araneidae									
<i>Araniella displicata</i>	4/5	5	2	0	2	0	3	0	40.0
<i>Araneus</i> sp. 1	4/5	2	1	0	0	1	1	0	50.0
<i>Araneus</i> sp. 2	4/5	4	0	0	0	0	4	0	00.0
Dictynidae									
Dictynidae sp. 1	4/5	2	0	0	0	0	1	1	00.0
Theridiidae									
<i>Theridion neomexicanum</i>	4/5	9	7	0	4	3	1	1	77.8
<i>Dipoena</i> sp.	4/5	2	0	0	0	0	1	1	00.0
Agelenidae									
Agelenidae sp. 1	4/5	<u>1</u>	<u>0</u>	0	0	0	1	0	<u>00.0</u>
Total sample size		111	18						16.2

^a Immature, sex undetermined.

limited 1976 field trial, predation also occurred when free-living spiders were caged with DFTM larvae on white fir branches (Dahlsten et al. 1978).

This laboratory study is a preliminary step in determining the role of spiders in the DFTM and white fir sawfly complex on white fir. Further research should examine predation in the field, not only on larvae but also on tussock moth egg masses just prior to eclosion. Such studies should match spiders of different age classes with defoliator instars that they actually encounter in the field. Free-living forms such as Thomisidae and Salticidae species are especially amenable to field studies on caged foliage. The effect of spiders on other natural enemies of DFTM and sawflies should also be studied, to help determine the net effect of spider predation on the defoliators. Finally, although spiders are difficult and costly to

raise in mass because of their cannibalistic nature, efforts should be made in order to evaluate experimental augmentation of forest spider populations.

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INDUCTION OF *ASCOSPHAERA*
(ASCOMYCETES: ASCOSPHAERALES) INFECTIONS IN
FIELD POPULATIONS OF
OSMIA LIGNARIA PROPINQUA CRESSON
(HYMENOPTERA: MEGACHILIDAE)

R. W. RUST¹ AND P. F. TORCHIO²

¹Biology Department, University of Nevada, Reno, Nevada 89557

²U.S. Department of Agriculture, Agricultural Research Service,
Bee Biology & Systematics Laboratory,
Utah State University, Logan, Utah 84322-5310

Abstract. — Offspring of field populations of *Osmia lignaria propinqua* Cresson were contaminated by forcing females to emerge through larval cadavers filled with chalk brood spores. Infection rates of subsequent larvae varied from 0 to 54% suggesting a varietal or biotype difference in the pathogenicity of *Ascospaera torchioi* Youssef & McManus on *O. l. propinqua*. Differences were found in infection rates for bees from Reno, Nevada, and between bees from Reno and Logan, Utah. Chalk brood infection rates did not vary significantly by season or by cell construction sequence of nests.

Key Words. — Insecta, chalk brood, mycosis, disease, bees

Studies on the biology and pathogenicity of *Ascospaera* spp. infecting the blue orchard bee, *Osmia lignaria propinqua* Cresson, have shown that six species of *Ascospaera* will produce mycosis (Youssef et al. 1985). Developmental temperatures of the host affected rates of infection, with low temperatures increasing the mycosis. The number of spores ingested by feeding larvae also increased the prevalence of chalk brood (Rust & Torchio in press).

Ascospaera spores, the infective agent of chalk brood syndrome, develop within densely packed spore cysts immediately below or on the surface of larval species cadavers (Stephen et al. 1981, Vandenberg & Stephen 1982, McManus & Youssef 1984, Youssef et al. 1985). Ingested spores germinate within the foregut of host bee larva and resultant hyphae penetrate the gut wall before the host larva dies (Vandenberg & Stephen 1983, McManus & Youssef 1984). As adult bees emerge from natal nests containing sibs killed by *Ascospaera*, spores are dispersed on individuals as they move past or chew through these larval cadavers (Stephen & Undurraga 1978, Vandenberg et al. 1980, Stephen et al. 1981, Vandenberg & Stephen 1983).

Emerging alfalfa leafcutting bees, *Megachile rotundata* (Fabr.), can each carry more than 100 million *Ascospaera aggregata* Skou spores, with the spore load depending on the number of larval cadavers contacted during emergence (Vandenberg et al. 1980). Stephen et al. (1981) found that spore loads carried by individual *M. rotundata* declined from several million at emergence to several thousand after three weeks of activities under field conditions. They also showed that spore counts in nesting domiciles increased as the season progressed.

Our field study was designed to determine infection rates of *O. l. propinqua* offspring whose mothers were forced to emerge from nests containing known

numbers of larval cadavers infected with *Ascosphaera torchioi* Youssef & McManus (Youssef & McManus in press), using larval cadavers obtained from Logan, Utah and Reno, Nevada. Rust & Torchio (in press) obtained spore loads of 1.0 to 6.0 billion from *O. l. propinqua* larval cadavers infected with *A. torchioi*. We thus hypothesize that the first emerging female to contact a larval cadaver will be more heavily contaminated than subsequent individuals crawling through the same cell during emergence. As a result, the first female to emerge from a nest contaminated with *Ascosphaera* spores should infect more offspring than subsequent females emerging from the same nest. Chalk brood infections also should be greater in larvae produced early in the nesting season by contaminated females than in larvae produced late in the season. In addition, larvae produced by uncontaminated females that reutilize contaminated nests should also have higher prevalence of *Ascosphaera* infection than larvae produced by uncontaminated females using new, clean nests.

MATERIALS AND METHODS

1988 Study.—Nest traps of *O. l. propinqua* from Reno were x-rayed to determine nest-cell occupancy. Nests containing *Ascosphaera* infected larval cadavers were carefully dissected and the cell contents were removed. Cell partitions and nest plugs were left undisturbed. Thirteen larval cadavers were weighed to 0.1 mg and placed in the outer-most cells of 10 infected nests (seven with one cadaver each and three with two cadavers each). Twenty-five adult *O. l. propinqua* females were weighed, individually color coded, returned to their cocoons, and placed in inner cells of the 10 infected nests (one in one nest, two in three nests, and three in six nests). Ten additional cadaver-free nests were assembled with each containing five male *O. l. propinqua* as mates for the emerging females. A second population of 25 color coded females and 50 males assembled into 10 male and 10 female cadaver-free nests, was also prepared as controls.

The two populations were placed in the field on 1 May 1988 approximately 500 m apart and adjacent to Sagehen Creek, 15 km N of Truckee, California. Both were provided with clean nest traps (19 mm × 19 mm × 150 mm pine blocks drilled with 5–9 mm diameter holes to a depth of 130 mm). Nests were examined every other day for nesting, and active nests were coded for identification of marked females and dates of activity. Completed nests were returned to the laboratory on 2 Jul 1988. Nests were x-rayed and dissected during Nov to determine offspring production and survival or mortality. Ambient temperature ranges were recorded at the site.

1889 Study.—Nest traps of *O. l. propinqua* from Logan and Reno were prepared in a similar manner as described above; 26 contaminated nests were assembled, each with one *Ascosphaera* larval cadaver in the outer cell: Thirteen of these nests contained *Ascosphaera* cadavers recorded from Logan and the remaining 13 cadavers originated from Reno. Two female *O. l. propinqua* from Logan were placed in the inner cells of each nest. Twenty additional nests were prepared each with five males bees from Logan. The 13 *Ascosphaera* nests from Logan and 10 male nests were placed in a mixed fruit orchard in Logan on 8 Apr 1989 along with clean nest materials as described above. The 13 *Ascosphaera* nests from Reno and 10 male nests were placed in a mixed fruit orchard in Reno on 28 Feb 1989 along with clean nest materials. Nests were examined daily at both sites for nesting

Table 1. Experimental design, nesting results, and infection rates for *Ascosphaera torchioi* Youssef & McManus on field populations of *Osmia lignaria propinqua* Cresson.

Nest treatment		Number of nests	Bee source	Cadaver source	Experimental location	Number of nests	Number of cells	Number of larvae infected	Percentage
Bees	Cadavers								
1988 Study									
3	1	3	Reno	Reno	Truckee	25	80	7	8.75
3	2	3	Reno	Reno	Truckee				
2	1	2	Reno	Reno	Truckee				
2	2	1	Reno	Reno	Truckee				
1	1	1	Reno	Reno	Truckee				
Control ^a	2	5	Reno	—	Truckee	4	10	2	20.00
Control	3	5	Reno	—	Truckee	35	114	0	0.00
1989 Reno Study									
2	1	13	Logan	Reno	Reno	22	132	72	54.50
2	1	13	Reno	Reno	Reno	— ^b	— ^b	— ^b	— ^b
Control ^c			Reno	—	Reno	16	84	18	21.40
1989 Logan Study									
2	1	13	Logan	Logan	Logan	16	103	15	14.50
2	1	13	Reno	Logan	Logan	— ^b	— ^b	— ^b	— ^b
Control ^c			Logan	—	Logan	18	117	11	9.40

^a—Female nesting at treatment site.

^b—No nesting, females died over winter.

^c—Natural.

activity and active nests were coded for identification of marked females and dates of activity. Nests produced by unmarked females were used as field controls at both sites. Temperature and humidity were recorded at both sites. Nests were returned to the laboratory in Jul, x-rayed and dissected in Nov to determine offspring production and mortality.

The reciprocal test using Reno *O. l. propinqua* was prepared and the nests and bees were placed in the field. The Reno bees suffered severe overwintering mortality and only a few individuals emerged. One female began nesting but produced no offspring (RWR, unpublished data).

Chi-square test for goodness of fit and Student's *t*-test for comparing two population means were used. *Osmia l. propinqua* chalk brood cadavers representative of those used in this study are deposited at the USDA ARS Bee Biology and Systematics Laboratory, Logan, Utah.

RESULTS

1988 Study.—Table 1 shows the experimental results. Ten of the 25 spore-contaminated *O. l. propinqua* females nested at the contaminated site (none nested at the control site). One control female nested at the *Ascosphaera* site, and these 11 females together produced 29 nests and 90 cells; averaging 3.1 ± 2.8 (range, 1–7) cells per nest. These females were exposed to 0–7.4 billion spores, and nine cells (10.0%) were infected with *Ascosphaera*. Mean *Ascosphaera* cells per nest was 0.3 ± 0.6 (0–2). Seventy-one cells in the remaining 22 nests had no chalk brood deaths.

Thirteen of the control females nested at the control site where 35 nests and

114 cells were produced; averaging 3.2 ± 2.1 (1–7) cells per nest. None of those 114 cells contained *Ascosphaera*, and no *Ascosphaera* infected larvae have been recovered from *O. l. propinqua* reared from the Sagehen Creek area during the three previous years of nest trapping (RWR, unpublished data). No differences were found in the mean cells per nest between contaminated and clean bees ($t = 0.23$, $df = 62$, $P = 0.82$).

Five contaminated females each produced one or more cells with chalk brood offspring, but the remaining five contaminated females produced chalk brood-free offspring. The one control female nesting at the contaminated site produced 10 cells in four nests of which two larvae were infected with chalk brood.

There was no difference in the occurrence of chalk brood in cells produced during first, middle, or last parts of the nesting season from that expected based on the number of cells completed during those intervals ($\chi^2 = 2.403$, $df = 2$, $0.50 > P > 0.25$). Also, there was no difference in the position of chalk brood cells within a nest when compared to the number of first, second, etc. constructed cells in a nest ($\chi^2 = 3.887$, $df = 5$, $0.75 > P > 0.50$).

1989 Logan Study.—Logan bees released through Logan *Ascosphaera* cadavers produced 16 nests with 103 cells, averaging 6.4 ± 1.5 (2–9) cells per nest. Fifteen (14.5%) chalk brood cadavers were recovered, or 0.9 ± 0.9 (0–3) cadavers per nest.

Eighteen nests and 117 cells were produced by clean Logan bees averaging 6.5 ± 1.9 (2–9). Eleven (9.4%) offspring were infected with *Ascosphaera* or 0.6 ± 1.1 (0–4) cells per nest. No clean or contaminated bees nested in the contaminated nests.

The Logan bees released in Logan showed no differences between mean number of *Ascosphaera* deaths or average number of cells in any of the treatments (*Ascosphaera* deaths—first to second emerging bees: $t = 1.69$, $df = 14$, $P = 0.11$; *Ascosphaera* to clean bees: $t = 0.86$, $df = 32$, $P = 0.40$; cells per nest—*Ascosphaera* to clean bees: $t = 0.10$, $df = 32$, $P = 0.92$; first to second emerging bees: $t = 2.0$, $df = 14$, $P = 0.066$). In addition, no differences were found in frequency of *Ascosphaera* infection during the first, middle, or later periods of the nesting season from that expected based on the number of cells constructed during the same intervals (*Ascosphaera* bees: $\chi^2 = 0.045$, $df = 2$, $P > 0.95$; *Ascosphaera* bees emerging first: $\chi^2 = 0.061$, $df = 2$, $P > 0.95$; *Ascosphaera* bees emerging second: $\chi^2 = 0.49$, $df = 2$, $0.90 > P > 0.75$; clean bees: $\chi^2 = 2.45$, $df = 2$, $0.50 > P > 0.25$). There was, however, one significant difference in the position of *Ascosphaera* cells within a nest compared to the number of first, second, etc. constructed cells in a nest: contaminated bees that emerged first produced more first (1, 2) and last (6, 7) constructed cells having *Ascosphaera* infected offspring than expected ($\chi^2 = 14.0$, $df = 6$, $0.05 > P > 0.025$).

1989 Reno Study.—Twenty-two nests with 132 cells were produced in Reno by Logan bees emerging through Reno *Ascosphaera* cadavers. Of these, 72 *Ascosphaera* cadavers (54.5%) were recovered with 3.4 ± 2.2 (1–8) cells per nest. Bees emerging first produced 11 nests and 63 cells with 47.6% (30) *Ascosphaera* mortality with 2.7 ± 2.1 (1–5) *Ascosphaera* cells per nest. Bees emerging second produced 10 nests and 69 cells from which 42 *Ascosphaera* larval cadavers were recovered (60.8%) with 4.2 ± 2.1 (1–8) chalk brood deaths per nest. There was, however, no difference in the mean number of *Ascosphaera* cells per nest produced by bees emerging first or second ($t = 1.59$, $df = 19$, $P = 0.13$).

Clean bees at Reno produced 16 nests and 84 cells with 5.2 ± 2.2 (2–8) cells per nest. Of these 18 *Ascospheera* larval cadavers were found (21.4%) with an average of 1.1 ± 1.0 (0–3) per nest. Six nests with 24 cells were free of chalk brood.

There were no differences in frequency between contaminated and clean bees in the seasonal distribution of Reno *Ascospheera* mortality, cell production, or cell distribution of *Ascospheera* (seasonal distribution—*Ascospheera* bees: $\chi^2 = 3.00$, $df = 4$, $0.75 > P > 0.50$; *Ascospheera* bees emerging first: $\chi^2 = 6.33$, $df = 4$, $0.25 > P > 0.10$; *Ascospheera* bees emerging second: $\chi^2 = 3.38$, $df = 4$, $0.50 > P > 0.25$; clean bees: $\chi^2 = 2.77$, $df = 4$, $0.75 > P > 0.50$; cell sequence—*Ascospheera* bees: $\chi^2 = 1.78$, $df = 7$, $P > 0.95$; *Ascospheera* bees emerging first: $\chi^2 = 1.86$, $df = 7$, $P > 0.95$; *Ascospheera* bees emerging second: $\chi^2 = 2.13$, $df = 7$, $P > 0.95$; clean bees: $\chi^2 = 3.62$, $df = 7$, $0.90 > P > 0.75$).

Ascospheera mortality increased whenever nesting populations were exposed to the Reno chalk brood spores. These differences were highly significant with Reno *Ascospheera* killing more than three times as many offspring ($t = 4.19$, $df = 35$, $P = 0.0002$). There was a highly significant difference in the average *Ascospheera* cells between the Reno *Ascospheera* bees and clean bees ($t = 3.83$, $df = 35$, $P = 0.0005$). There was no difference in the cells constructed per nest between the two populations ($t = 1.45$, $df = 35$, $P = 0.15$). There was no difference in the average number of cells constructed per nest between Logan and Reno bee populations ($t = 0.25$, $df = 35$, $P = 0.80$).

Logan bees began nesting on 15 Apr and continued to nest for 27 days. During this period, the average hours of adult activity, based on temperatures $\geq 15.7^\circ\text{C}$ (Torchio 1985) was 3.7 ± 2.6 (0–7) h per day. Bees in Reno began nesting on 22 Mar and continued for 30 days with an average of 5.0 ± 4.0 (0–10) working h per day $\geq 15.7^\circ\text{C}$. The hours available to adults for nesting were not different between the sites ($t = 1.35$, $df = 55$, $P = 0.18$). The average hours per day $\geq 21^\circ\text{C}$ for the first 60 days of larval development (Rust & Torchio in press) was not different between Logan and Reno (Logan 2.6 ± 3.3 (0–10); Reno 2.6 ± 3.1 (0–9); $t = 0.14$, $df = 118$, $P = 0.89$). Rust and Torchio (in press) found that larvae reared at 21°C required more than twice the time to complete their development to the fifth instar when compared to larvae reared at 29°C (5–6 versus 12–14 days). Also, the highest *Ascospheera* infection rate was obtained when larvae were reared at 21°C . Larvae reared below 21°C have a decreased survival rate.

DISCUSSION

Three unexpected sets of results were obtained from these experiments. First, neither clean or contaminated females utilized nests from which they emerged. We could not, therefore, test the effect of these nests as a source of *Ascospheera* contamination. However, contaminated nests were visited by known clean females (1988 Study) that then nested in clean holes in which 20% *Ascospheera* mortality was measured (two of 10 cells) that accounted for 22% of the total *Ascospheera* mortality at the site. If the wild, native bees were in fact free of *Ascospheera* spores before searching for suitable nest holes, then some of these bees became contaminated while exploring the cavities from which the experimentally contaminated bees had emerged.

Second, our prediction that females emerging first through a larval cadaver

should infect more of their offspring but at a decreasing rate was not generally supported by the data except for one nest cell sequence (1989 Logan). Although there were more first constructed cells with chalk brood in the Logan nests, there were almost equal numbers of chalk brood cadavers in last constructed cells and fewer than expected cadavers in middle cells. Thus, there does not seem to be a seasonal decline in infectivity potential even though spore load has been shown to decline with time in the alfalfa leafcutting bee (Stephen et al. 1980). Spore loads obtained by emerging bees can be sufficiently high to contaminate cells at the same frequency throughout the nesting periods.

Third, there was an unexpected significant difference in the infection rates between Logan and Reno *A. torchioi* spores. Reno *A. torchioi* spores infected almost four times (3.7) as many offspring as did Logan *A. torchioi* spores. Yet, spore loads, numbers of spores per cadaver, nesting periods, temperatures during nesting and larval development, average number of cells constructed per nest, and number of nesting females were similar for both bee populations. These results suggest that there may be a difference in the infectivity potential of spores from each location. Perhaps Reno spores germinate more readily, or hyphae penetrate the gut wall more rapidly, or rapid mycelial growth assures increased host mortality. Future studies on comparative pathogenicity are required to determine potential varietal differences in *A. torchioi* in nests of *O. l. propinqua*.

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**A REVIEW OF THE INTRODUCED LYGAEIDAE OF THE
PACIFIC NORTHWEST, INCLUDING THE NEWLY
DISCOVERED *PLINTHISUS BREVIPENNIS* (LATREILLE)
(HETEROPTERA: LYGAEIDAE)**

ADAM ASQUITH¹ AND JOHN D. LATTIN

Systematic Entomology Laboratory, Department of Entomology,
Oregon State University, Corvallis, Oregon 97330

Abstract. — The Palearctic lygaeid *Plinthisus brevipennis* (Latreille) is reported from North America for the first time. The status¹ of three other adventive species in the Pacific Northwest *Stygnocoris rusticus* (Fallen), *Stygnocoris sabulosus* (Schilling), and *Megalonotus sabulicola* (Thomson) are reviewed. Dorsal habitus illustrations and distribution maps are provided for all species.

Key Words. — Insecta, Heteroptera, Lygaeidae, *Stygnocoris*, *Megalonotus*, *Plinthisus*, introduced species

The accidental introduction, establishment and dispersal of insects is a dynamic problem of contemporary biogeography (Elton 1958). In a review of insect introductions into North America, Sailer (1983) noted that 66% of all introduced species come from the western Palearctic; in contrast, the Southern Hemisphere has contributed relatively few (Lattin & Oman 1983). Here we discuss the establishment and spread of four species of ground inhabiting seed bugs (Heteroptera: Lygaeidae) that have been introduced into the Pacific Northwest from the Palearctic. One of these species, *Plinthisus brevipennis* (Latreille), is reported from North America for the first time.

Abbreviations used for depositories of the material examined are: Oregon State University (OSU); University of British Columbia (UBC); Canadian National Collection (CNC).

PLINTHISUS BREVIPENNIS (LATREILLE)

Morphological Characteristics. — *Male* (Figs. 1–2): relatively large species, total length 2.45–3.00 mm; elongate oval in outline; general coloration dark brown to black; antenna red-brown, distal ends of each segment lighter; rostrum red-yellow, basal segment fuscous; femora red-brown; tibiae and tarsi light red-yellow, ventral surfaces fuscous to black; lateral margin of pronotum occasionally yellow-red. Pronotum quadrate, length 0.82–0.95 mm, width 0.82–1.00 mm, anterior corners of pronotum produced forward, lateral margins weakly sinuate, posterior margin straight or weakly concave; anterior lobe of pronotum smooth, posterior lobe shallowly punctate, dorsal surface almost glabrous, with short, pale, inclined setae; hemelytra (brachypterous form) reaching just anterior of fourth visible abdominal tergite, dorsal surface with short, pale setae arising from shallow, linearly arranged punctures.

Female. — slightly larger than male, total length 2.98–3.20 mm; pronotum length 0.83–0.93 mm, pronotum width 1.03–1.15 mm; posterior pronotal lobe without punctures.

Diagnosis. — *Plinthisus brevipennis* is easily distinguished from the three native western species by its large size. *Plinthisus longisetosus* Barber, *P. martini* Van

¹ Present address: College of Tropical Agriculture, University of Hawaii, Kauai Branch Station, 7370-A Kuamoo Road, Kapaa, Hawaii 96746.

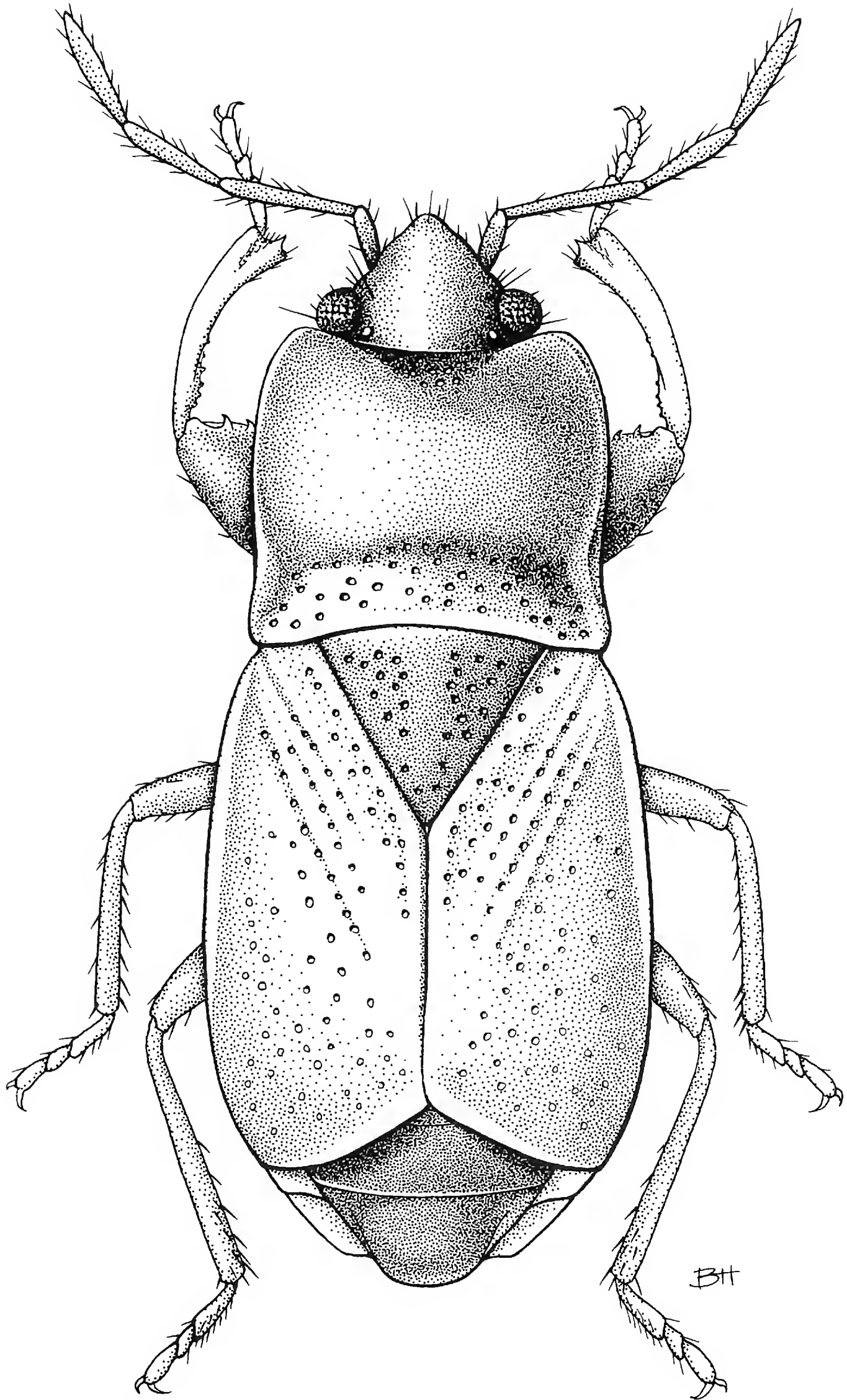


Figure 1. *Plinthisus brevipennis* (Latreille). Dorsal habitus of adult male. Brachypterous form.

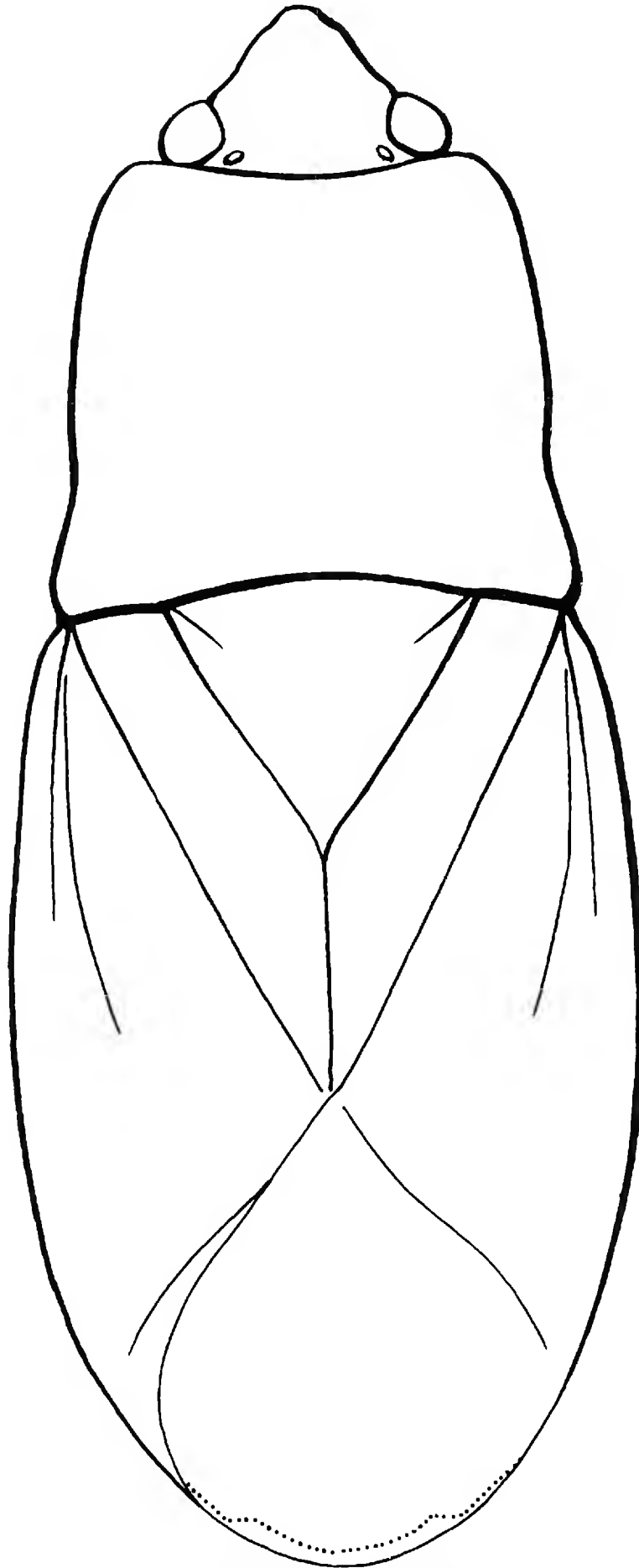


Figure 2. *Plinthisus brevipennis* (Latreille). Dorsal habitus of adult male. Macropterous form.

Duzee, and *P. pallidus* Barber are all less than 2.0 mm total length. In *Plinthisus indentatus* Barber and *P. americanus* Van Duzee the pronotum is much more convex, both transversely and longitudinally, than that of *P. brevipennis*. The two former species and *P. compactus* (Uhler) also have long erect setae on the pronotum and hemelytra, and the posterior lobe of the pronotum is punctate in females. *Plinthisus brevipennis* also has much thicker fore femora. The maximum

width of the fore femur in *brevipennis* is equal to, or greater than, the width of vertex, whereas in native North American *Plinthisus* this measurement is less than the width of the vertex.

Discussion.—*Plinthisus brevipennis* (Latreille) (Latreille 1807) is widely distributed in the western Palaearctic, occurring in England and Norway, throughout Europe, east to the western U.S.S.R., south to Turkestan, Israel and North Africa (Slater 1964). This species inhabits sandy areas, such as littoral sand hills and sand pits in England (Butler 1923), and is often found under dead leaves and at the roots of low plants. Carayon (1949) found it common in the bases of grass clumps on littoral dunes and under heather in pine forests in France.

In June, 1988, a single adult specimen of *P. brevipennis* was collected from roadside vegetation in Benton Co., Oregon. In April, 1989, several individuals were collected from a rodent burrow in moss under matted grass. Additional specimens were extracted from the base of grass clumps collected in two other localities in Benton Co., Oregon. Two specimens were also found in litter samples from a clearcut forest area near Seattle, Washington, in April, 1989. The only other specimen we have seen was also collected near Seattle, Washington, in 1964.

We (JDL) have made extensive collections of ground-inhabiting Heteroptera, with special emphasis on the Lygaeidae, in western Oregon from the late 1950s to the mid-1960s. The map in Fig. 7 shows numerous collecting sites for another introduced lygaeid, *Megalonotus sabulicola* (Thomson) (see below), which reflects this collecting activity. We believe the failure to collect specimens of *P. brevipennis* during that collecting period indicates its absence, at least from the Willamette Valley of Oregon. This suggests that *P. brevipennis* is a relatively recent introduction into the Pacific Northwest, rather than a species that has gone undetected.

In England, *P. brevipennis* overwinters as an adult and oviposition occurs in late May or June with nymphs maturing in late July or early August (Southwood & Leston 1959). Guerin & Peneau (1905) found adults under moss in the winter, and Halbert (1935) reported adults and nymphs collected from moss in July. Brachypterous (Fig. 1) and macropterous (Fig. 2) forms occur in both sexes and Butler (1923) reported that although the macropterous form is usually rare, it occasionally occurs in large numbers. In one collection of 55 individuals from Benton Co., Oregon, we found both male and female macropters, but the brachypterous forms were much more numerous (Male ratio, 22 brachypterous : 3 macropterous; Female ratio, 25 brachypterous : 6 macropterous). Southwood & Leston (1959) stated that macropters fly readily, and we collected one individual by sweeping roadside grasses. The occasional high frequency of macroptery may contribute to its dispersal in the Pacific Northwest.

Plinthisus, containing approximately 75 species worldwide, is currently the only genus in the tribe Plinthisini. It is unique in the Rhyparochrominae in that the intersegmental conjunctivum is present between sterna IV and V of the female (Slater et al. 1962). Based on these unusual characters, including the unique structure of the phallus, it has been suggested as deserving subfamilial status (Putshkov 1958, Sweet 1967). Currently, there are six species described from North America (Ashlock & Slater 1988), *P. americanus* (Van Duzee) from New England, and the others from the western U.S., although there may be several undescribed species from western North America (Sweet 1964b, Ashlock 1977, J. A. Slater, personal communication).

Material Examined.—USA. WASHINGTON. KING Co.: Carnation, 14 May 1964, O. Milne (OSU). MASON Co.: Matlock, 23 Apr 1989, ex clearcut litter sample, A. Moldenke (OSU). OREGON. BENTON Co.: Alsea Falls St Pk, 22 Jun 1988, A. Asquith. Corvallis, 8 Apr 1989, ex moss in grass clump, A. Asquith (OSU); 1.6 km (1 mi) S of Corvallis, 16 Apr 1989, ex grass clump, A. Asquith (OSU); Finley Wildlife Refuge, 16 Apr 1989, ex grass clump, A. Asquith (OSU).

STYGNOCORIS RUSTICUS (FALLEN)

Stygnocoris rusticus (Fallen) (Fig. 3) is a widespread, western Palaearctic species found throughout Europe, the Mediterranean, central Asia, to Sinkiang province of northwestern China (Hsiao et al. 1981). Although the extent of its distribution in northeastern Asia is unclear, it was not reported from eastern Siberia by Kerzhner (1988). Horvath (1908) and Heidemann (1908) both reported *Stygnocoris rusticus* from North America in 1908, with Heidemann's specimens collected in New York. Gibson (1917) recorded it from Truro, Nova Scotia (along with *S. sabulosus* (Schilling) from the same locality) and Van Duzee (1917) reported *S. rusticus* from Quebec. Barber (1918) discussed both species and gave additional records. Downes (1924) recorded *S. rusticus* from Vernon, British Columbia based upon specimens he collected in 1919. Barber (1928) provided data on both *S. rusticus* and *S. sabulosus* from a site in the Adirondacks.

Sweet (1964b, 1967) provided a thorough treatment of the biology and life history of this species, including abdominal morphology, male and female genitalia, egg, hind wing venation, illustration of the fifth instar nymph, as well as a review of earlier records. A detailed bibliography of the species can be found in the catalogue by Slater (1964), and Wheeler (1983) recently reviewed the distribution and history of *S. rusticus* in eastern North America.

Stygnocoris rusticus is a commonly collected lygaeid in British Columbia, but not so in Oregon and Washington, especially when compared with *S. sabulosus* (Schilling) (see below). Downes (1924) reported its capture in 1919 at Vernon, British Columbia and Barber (1948) reported it from Dukabush, Washington (approximately 24 km (15 mi) south of Quilcene, Jefferson Co.) based on specimens collected by the late Herbert Ruckes. Besides these records, we have seen only three additional specimens from the state of Washington: a brachypterous female, a macropterous female and a brachypterous male (see material examined). Southwood & Leston (1959) stated that *S. rusticus* is usually brachypterous, and that it normally overwinters in the egg stage, although some adults may persist until spring.

Its occurrence in the Pacific Northwest is far more restricted than in the eastern U.S. (Fig. 4). This may be because forested mountains, high moisture gradients, and patterns of agricultural development in the west present potential dispersal problems for less vagile species. *Stygnocoris rusticus*, like other introduced species, is probably synanthropic, and may be restricted to relatively disturbed areas. The collection site at Niles Lake in northeastern Washington clearly showed signs of past disturbance; it was apparently an old saw mill and has the remains of concrete foundations.

Material Examined.—CANADA. BRITISH COLUMBIA. Celistia, 11 Sep 1954, W. Downes (UBC); Cultus Lake, 2 Sep 1959, G. G. E. Scudder (UBC); Enderby, 22 Aug 1920, W. Downes (UBC); Erickson, 2 Jul 1982, G. G. E. Scudder (UBC); Galiano Isl., Spanish Hills, 31 Aug 1983, G. G. E. Scudder (UBC); Green Timbers, 16 Aug 1938, R. Longmore (UBC); Hope, 28 Aug 1961, G. G. E. Scudder (UBC); Kelowna, 8 Aug 1926, W. Downes (UBC); Langley, 24 Aug 1954, W. Downes (UBC); Merritt,

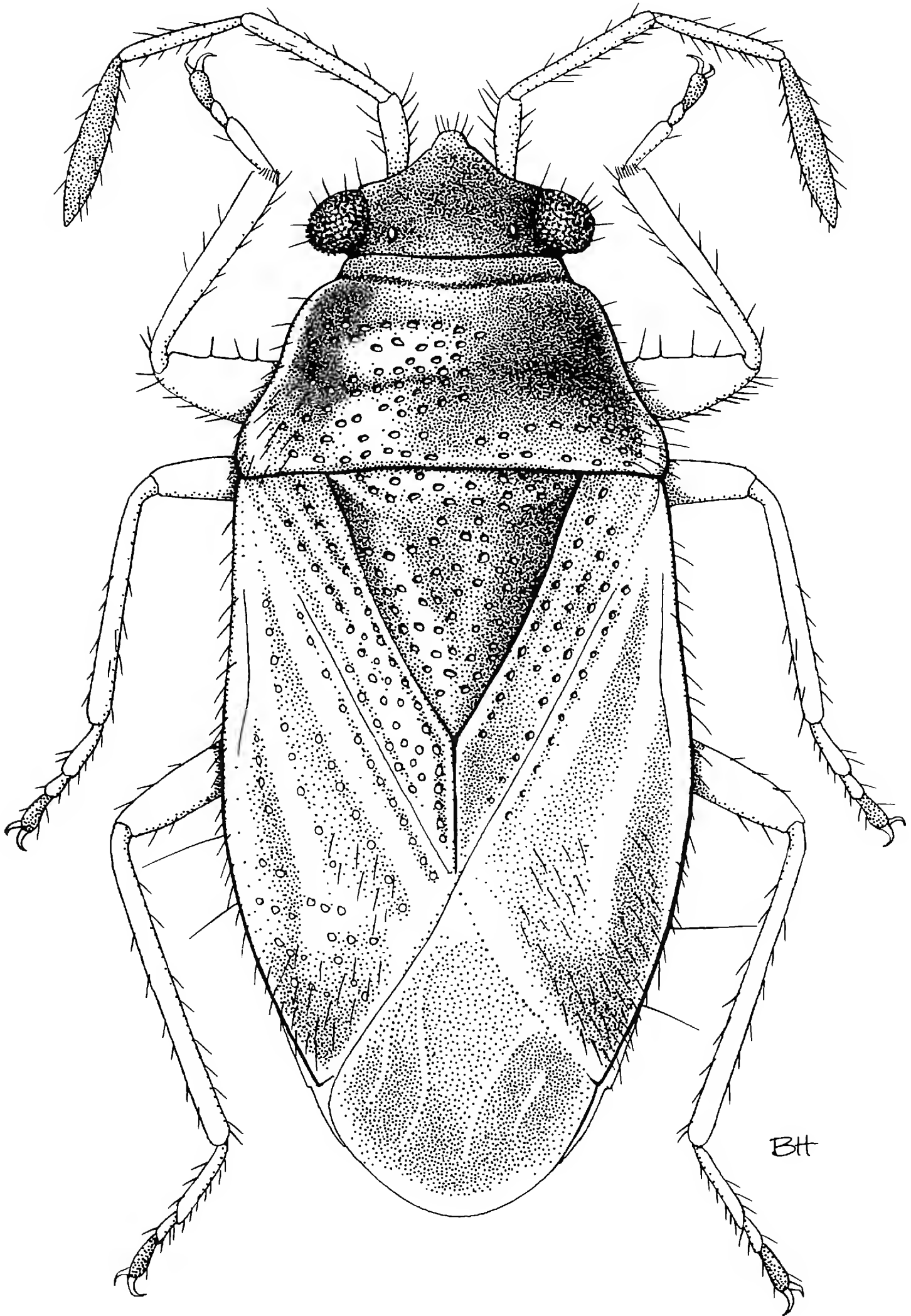


Figure 3. *Stygnocoris rusticus* (Fallen). Dorsal habitus of adult male.

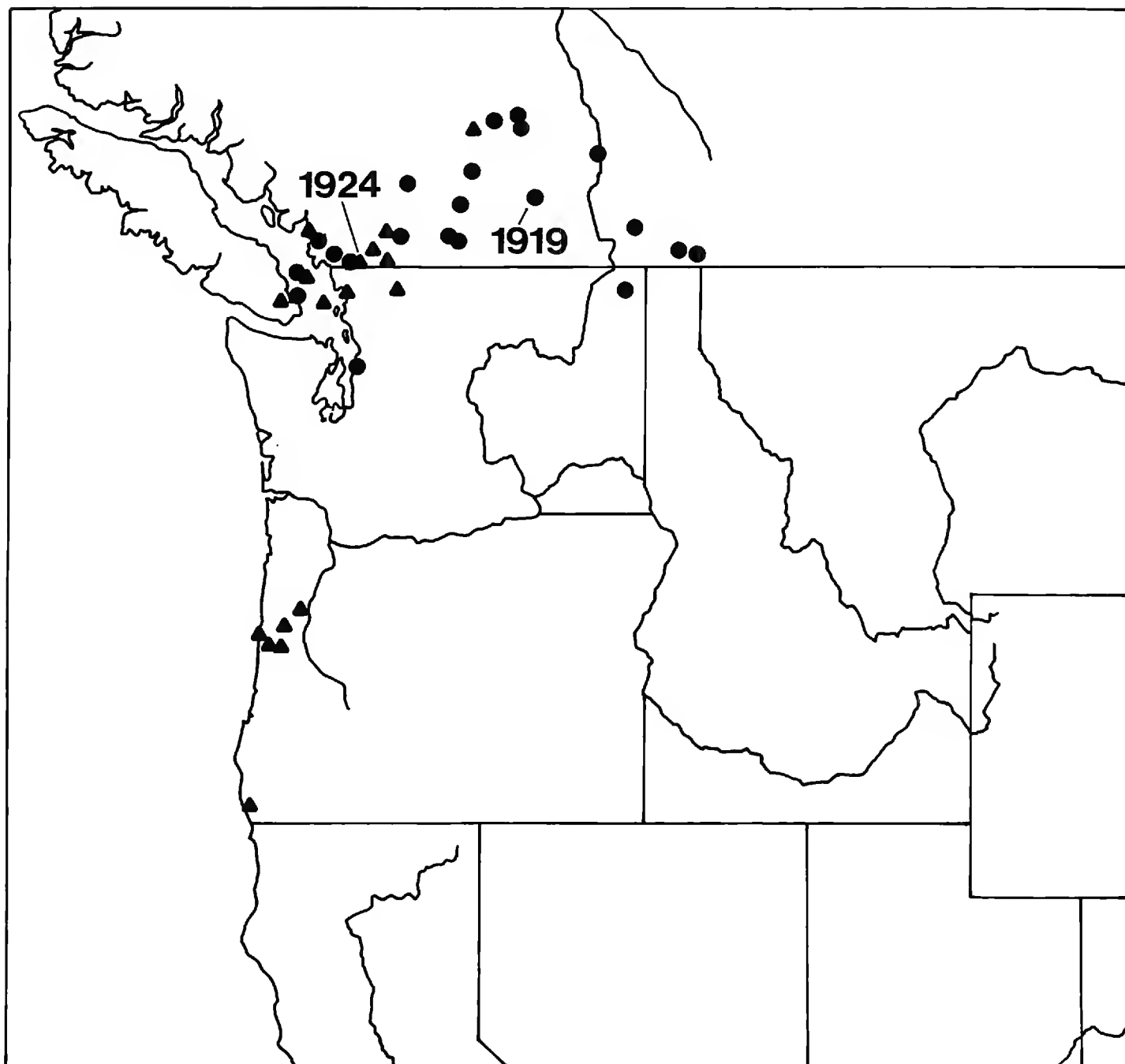


Figure 4. Distributions of *Stygnocoris rusticus* (circles) and *S. sabulosus* (triangles) in western North America.

12 Aug 1948, C. L. Neilson & D. Finlayson (UBC); Nakusp, 25 Aug 1989, G. G. E. Scudder (UBC); Nelson, 26 Aug 1953, M. H. Hatch (OSU). Penticton, 25 Aug 1924, W. Downes (UBC); Royal Oak, 19 Sep 1949, W. Downes (UBC); Saanich, 28 Jul 1954, W. Downes (UBC); Salmon Arm, 6 Oct 1934, H. B. Leech (CNC); Sandspit, Moresby Isl., Queen Charlotte Islands, 25 Aug 1984, G. G. E. Scudder (UBC); Sidney, 31 Aug 1949, W of Downes (UBC); Steelhead, Sep 1933, H. B. Leech (UBC); Summerland, 1 Oct 1932, A. N. Gartrall (CNC); Vancouver, 9 Aug 1929, W. Downes (UBC); Vernon, 22 Sep 1923, D. G. Gillespie (CNC); Yahk, 29 Aug 1989, G. G. E. Scudder (UBC). USA. WASHINGTON. KING Co.: Bothell, 20 Jul 1939 (OSU). PEND ORIELLE Co.: Niles Lake 1350 m (4500 ft), 9.6 km (6 mi) SW of Tiger, 9 Sep 1958, J. D. Lattin, on ground (OSU).

STYGNOCORIS SABULOSUS (SCHILLING)

Stygnocoris sabulosus (Schilling) (Fig. 5) was first reported from North America by Gibson (1917) [as *Stygnocoris pedestris* (Fallen)], based upon specimens collected in 1923 at Truro, Nova Scotia. Barber (1918) recorded several localities from New York and Cape Breton Island, Nova Scotia, and Barber (1928) provided the numerical data of a collection from New York. It was then reported from Quebec (Moore 1950), Newfoundland (Lindberg 1958), Connecticut, Maine, Massachusetts and New Hampshire (Sweet 1964a, b; Slater 1964).

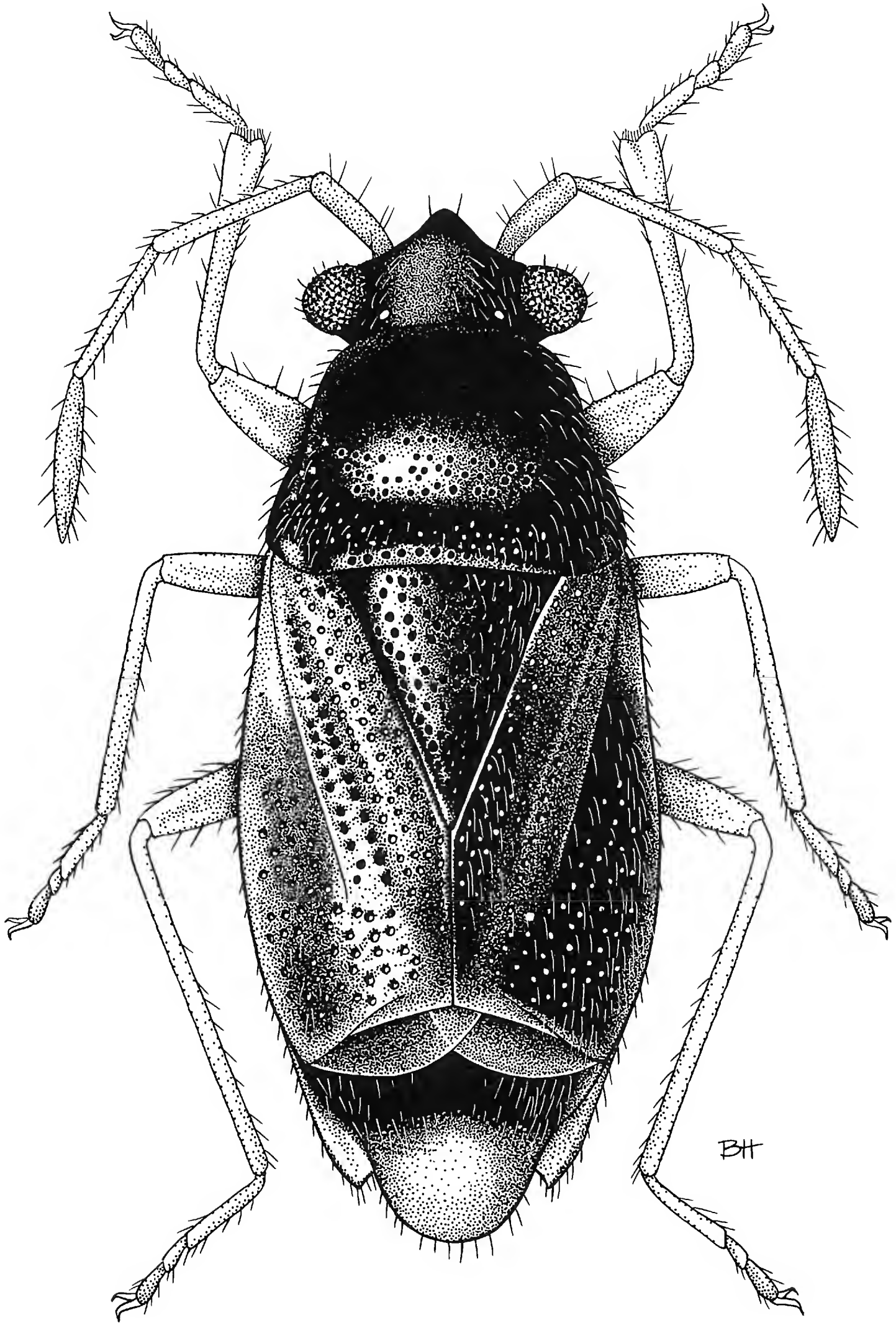


Figure 5. *Stygnocoris sabulosus* (Schilling). Dorsal habitus of adult male.

In 1961, Scudder reported *Stygnocoris sabulosus* [as *S. pedestris*] from British Columbia. The earliest collection in the west dates from 1924, taken at Agassiz, British Columbia. Ashlock & Slater (1988) added an Oregon record but did not include the records of Sweet (1964b). We have examined specimens from southwestern British Columbia and western Washington and Oregon (Fig. 4) with most records either from the coast or the Willamette-Puget lowlands. In Britain, this species is always fully winged (Southwood & Leston 1959), and indeed, all specimens we examined were macropterous. This suggests that this species is probably more vagile than its congener *S. rusticus* (see above).

Material Examined.—CANADA. BRITISH COLUMBIA. Agassiz, 14 Sep 1924, R. Glendenning (CNC); Chilliwack, 14 Oct 1938, J. K. Jacob (CNC); Cultus Lake, 21 Oct 1938, J. K. Jacob (CNC); Cultus Lake, 2 Sep 1959, G. G. E. Scudder (UBC); Galiano Isl, north end, 18 Aug 1982, 11 Oct 1987, G. G. E. Scudder (UBC); Hope, 28 Aug 1961, 20 Sep 1962, G. G. E. Scudder (UBC); Jack Lake, 1 Sep 1953 (CNC); Kamloops, Lac de Bois, 14 Aug 1988, G. G. E. Scudder (UBC); Lions Bay, Squamish Road, 16 Oct 1960, G. J. Spencer (UBC); Malahat, 20 Sep 1950, W of Downes (UBC); Vancouver Island, Shawnigan Lake, 4.8 km (3 mi) SW of Cobble Hill, gravel pit, 10 Sep 1960, J. D. Lattin coll. (OSU). USA. OREGON. BENTON Co.: N Fork, Alsea River, 8 km (5 mi) NE of Alsea, 5 Oct 1970, moss on cedar log, J. D. Lattin (OSU); Corvallis, 10 Sep 1967, in dry sawdust under *Cotoneaster*, J. D. Lattin (OSU); Mary's Peak 22.4 km (14 mi) W of Corvallis, 8 Sep 1971, Summit Meadow campground, 1080 m (3600 ft), J. D. Lattin (OSU); 23 Jul 1977, ex *Corylus*, J. D. Lattin (OSU). CURRY Co.: Brookings, 21 Aug 1977, J. D. Lattin, under Sitka spruce (OSU). LINCOLN Co.: Canal Creek, 16 km (10 mi) ESE of Waldport, 8–15 Aug 1968, J. D. Lattin (OSU); 3.4 km (2.5 mi) N of Waldport, 23 Jul 1970, P. Oman (OSU). WASHINGTON. SAN JUAN Co.: Orcus Island, Crescent Lake, Moran St Pk, 4 Sep 1960, ex grass clumps along lake, J. D. Lattin (OSU). WHATCOM Co.: Bellingham, 8 Aug 1976 (OSU); Mt Baker Nat'l For, R9E-T39N-Sec17, 7 Sep 1979, ex *Tsuga mertensiana*, G. M. Stonedahl (OSU).

MEGALONOTUS SABULICOLA (THOMSON)

This species (Fig. 6), known from North America for more than 60 years, was first reported by Van Duzee (1928) when he described *Rhyparochromus chiragra* “var. *californicus*.” Although much of the literature on this species is cited under *Megalonotus chiragra* (Fabr.), ultimately, the correct name was determined to be *Megalonotus sabulicola* (Thomson) (Scudder 1961, Southwood 1963, Ashlock 1977).

Megalonotus sabulicola is widespread in western Europe, North Africa, the Middle East and the western U.S.S.R. (Slater 1964, Wheeler 1989). Southwood & Leston (1959) provided a brief summary of its habits and Scudder (1961) and Southwood (1963) clarified the status of *M. sabulicola* as a species distinct from *M. chiragra*.

Slater & Sweet (1958) recorded *M. sabulicola* from eastern North America for the first time, based upon specimens they collected in 1957 in Connecticut. Sweet (1964a, b) gave an excellent account of the history, biology and ecology of this species in New England, including a discussion of “a cryptic form” of brachyptery, with only slightly reduced forewings and short hind wings. Wheeler (1989) recently provided information on the present distribution of this species in the eastern U.S. as well as a discussion of habits and host plant preferences including its potential as a biological control for spotted knapweed (*Centaurea maculosa* Lamarck). Williams (1947) recorded *M. sabulicola* as prey for a species of *Diploplectron* (Hymenoptera: Sphecidae) in California.

Scudder (1960, 1961) provided detailed records for British Columbia (earliest

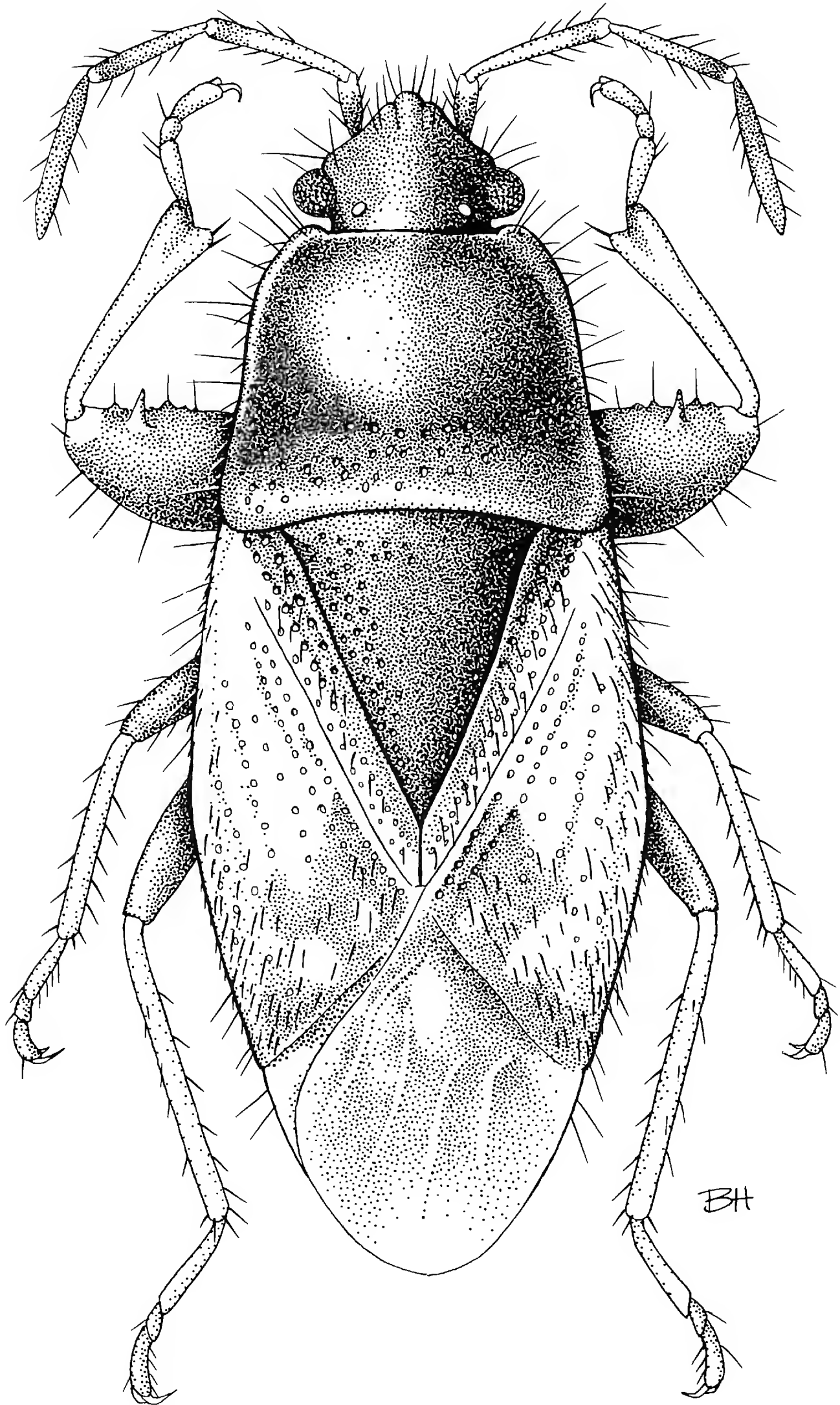


Figure 6. *Megalonotus sabulicola* (Thomas). Dorsal habitus of adult male.

collection record is now West Vancouver, 1926) and included a record for Seattle, Washington (no date). Ashlock (1977) gave a thorough discussion of *M. sabulicola*, emphasizing dispersal and earliest dates of collection in different parts of western North America. He also provided the first records from Idaho and Utah (Ashlock 1977). *Megalonotus sabulicola* is now a rather common species in the Pacific Northwest in disturbed areas and is widespread in western North America, from southern British Columbia to southern California (Fig. 7).

DISCUSSION

The four species discussed above are presently the only members of the Lygaeidae considered adventive in the Pacific Northwest. Although we have attempted to be exhaustive in our review of the pertinent information for these species, numerous questions remain unanswered or are at least equivocal. The distributions of these species are still imperfectly known and extrapolation from historical records is tenuous; therefore, we cannot be certain that they are all truly nonnative. Consider, for example, that *Stygnocoris sabulosus* is predominately western Palaearctic in natural distribution (Slater 1964), thus its records from far eastern U.S.S.R. by Kerzhner (1988) are of special interest. All Siberian records are clustered just north of Vladivostok and on the Kurile Islands. Whether these represent introductions or relictual populations is unclear. This also suggests that *S. sabulosus* is also natural to the Pacific Northwest. The four arguments for its adventive status are: (1) the rather late date of collection (1950); (2) the absence of any other species of Stygnocorini in North America, except the introduced *S. rusticus*; (3) its absence from the area of Eastern Beringia; and (4) its preponderance in disturbed habitats.

The status of some *M. sabulicola* localities is also unclear. One Palaearctic record of considerable interest is that of Kerzhner (1988), where he reported *M. sabulicola* from two regions of far eastern U.S.S.R., the Amur River region and the area immediately north of, and including, Vladivostok. The Amur River region is known for relictual populations, whereas Vladivostok is a busy seaport at about the same latitude as Portland, Oregon. Because there is an enormous discontinuity between these two regions and the European portion of U.S.S.R., it would be interesting to know if the date of collection of the Siberian material is also relatively recent, and whether other synanthropic taxa are known from these localities.

We can only speculate how these ground inhabiting species became established in North America. Sweet (1964b) suggested that *Stygnocoris rusticus* was introduced into North America with discharged ship ballast. Wheeler (1983) felt that the species had been introduced into eastern North America well after the ballast period (Lindroth 1957) and suggested that a more likely mode of introduction was imported nursery stock. The collection of this species in 1919 in the interior of British Columbia by Downes (1924) is particularly interesting and may corroborate the ballast hypothesis in the Pacific Northwest at least. Movement of nursery stock is possible as well, however, because there is a strong representation of the British flora in southern British Columbia.

Although Slater & Sweet (1958) believed that ballast was a possible vehicle for the introduction of *Megalonotus sabulicola* into western North America, they believed that it was more likely to have been introduced into eastern North America by plant introductions. The late discovery of this species in the eastern

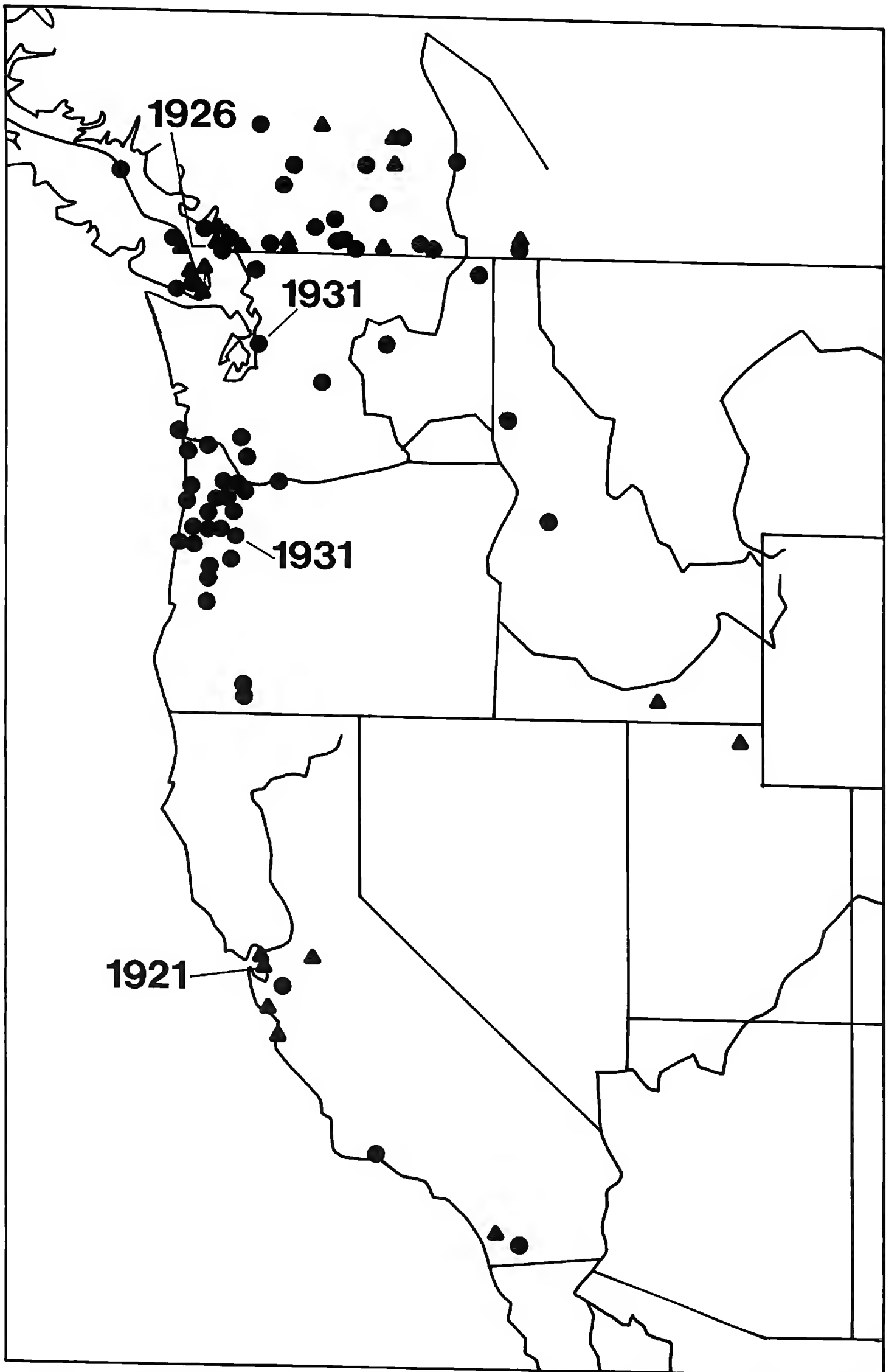


Figure 7. Distribution of *Megalonotus sabulicola* in western North America. Circles represent specimens examined; triangles represent literature records.

U.S. (1957) was probably past the ballast period for the east coast (Sailer 1983). Although the use of ballast continued much longer along the west coast (Lindroth 1957; Scudder 1958, 1960, 1961; Lattin 1966), the very recent discovery of *Plinththisus brevipennis* (earliest collection record is 1964) also suggests a post-ballast entry time.

Comparing the distributions of these species with other groups might also be enlightening. It is interesting, for example, that the localities for *Stygnocoris rusticus* in southeastern British Columbia and northeastern Washington are mirrored by the introduced carabid beetle, *Pristonychus terricola* Herbst. This beetle is known only from Creston, in southeastern British Columbia (Spence & Spence 1988), a locale very close to the collections of *S. rusticus*. Spence & Spence (1988), in their work on the introduced ground beetles of western Canada, considered Creston to be one of the four centers of carabid introduction in British Columbia. More intensive collecting around likely areas of introduction and continued periodic monitoring will increase our understanding of these adventive species and provide the opportunity for more accurate data should future introductions occur.

ACKNOWLEDGMENT

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**UROCTONITES, A NEW GENUS OF SCORPION FROM
WESTERN NORTH AMERICA
(SCORPIONES: VAEJOVIDAE)**

STANLEY C. WILLIAMS AND WARREN E. SAVARY¹

Department of Biology, San Francisco State University,
San Francisco, California 94132

Abstract.—A new genus of scorpion, *Uroctonites* Williams & Savary NEW GENUS, and a species, *Uroctonites giulianii* Williams & Savary NEW SPECIES, are named and described. The new species is found in the Inyo Mountains, White Mountains, and eastern Sierra Nevada of California, at elevations of 1370 to 3080 m. Three previously named species, *Vaejovis huachuca* (Gertsch & Soleglad), *Vaejovis montereus* (Gertsch & Soleglad), and *Vaejovis sequoia* (Gertsch & Soleglad), are assigned to *Uroctonites*. *Uroctonites* is known only from California and Arizona in the western United States of America.

Key Words.—Arachnida, Scorpiones, Vaejovidae, *Uroctonites*, systematics

In 1972, Gertsch and Soleglad revised the scorpion genus *Uroctonus* Thorell, which prior to 1972 included the single species *Uroctonus mordax* Thorell. They named 13 new species of *Uroctonus*, and concluded that *Uroctonus* was related to *Vaejovis*, with most characters assigned to *Uroctonus* intergrading with those of *Vaejovis*. No single character defined *Uroctonus*, so assignment of taxa to *Uroctonus* required an inconsistently applied combination of characters. The inexactness of generic definitions prompted subsequent workers to consider a number of the new *Uroctonus* species to belong to *Vaejovis* rather than to *Uroctonus* (Stahnke 1974; Williams 1976, 1980).

Our interest in the phylogenetic relationships among the *Uroctonus*-like scorpions was renewed by the collection of a series of scorpions from the Inyo Mountains of California during the mid 1970s. We conclude that these specimens represent an undescribed species that has a morphological similarity to *Uroctonus mordax*, but lacks a number of diagnostic characters uniquely shared by *U. mordax*, *Uroctonus franckei* Williams, and *Uroctonus grahami* Gertsch & Soleglad. They share with *Vaejovis huachuca* (*Uroctonus huachuca* Gertsch & Soleglad), *Vaejovis montereus* (*Uroctonus montereus* Gertsch & Soleglad), and *Vaejovis sequoia* (*Uroctonus sequoia* Gertsch & Soleglad) a unique arrangement of spiniform setae on the soles of the telotarsi, a character not found among other vaejovids. We, therefore, propose that *V. huachuca*, *V. montereus*, *V. sequoia*, and the new species be assigned to a new genus. This new genus and the new species are named and described in this paper.

MATERIALS AND METHODS

Measurements cited are standard ones used in scorpion systematics, as defined by Williams (1980), unless otherwise noted. Color descriptions are as defined in Maerz and Paul (1930). Where morphometric data are characterized, means \pm

¹ Current address: Food and Drug Administration, 50 United Nations Plaza, San Francisco, California 94102.

one standard deviation, and sample size (n) are given. Trichobothrial notations conform to those of Gertsch and Soleglad (1972). In describing the keels of the pedipalp palm, the palm is viewed in natural orientation, as held by a resting scorpion. In this orientation, three keels are apparent on the dorsal surface. The middle keel is called the dorsal, the more lateral one is the retrodorsal, and the more medial one is called prodorsal. When the palm is viewed ventrally, three keels are apparent on the ventral surface. The middle keel (which may be obscure or absent) is called the ventral, the more lateral one is called the retroventral, and the more medial one is called the proventral keel. Between the prodorsal and proventral keels is an interior keel, the prolateral. Between the retrodorsal and retroventral keels is an exterior keel, the retrolateral. When morphometric measurements are taken from the palm, however, the palm is oriented differently with the fingers held in the vertical plane, and at right angles to this plane, the horizontal plane defines the axis for width measurements.

Specimens cited are deposited in the entomology collection of the California Academy of Sciences (CAS) in San Francisco unless otherwise indicated. Alternatively, they are in the University of California, Riverside (UCR); Essig Museum of Entomology, University of California, Berkeley (UCB); or the American Museum of Natural History, New York (AMNH).

TAXONOMY

Uroctonites Williams & Savary, NEW GENUS

Table 1, Figs. 1, 3–5, 7, 9–12, 13, 15–18

Uroctonus (in part): Gertsch & Soleglad 1972: 553, 557, 559, 561, 564–565 (key), 573–575, 589–592, Figs. 10, 36, 37, 64–67, 116–118, Tables 2, 5, 8; Stahnke 1974: 129, 130.

Vejoavis (in part): Stahnke 1974: 119 (key), 130, 132–136, Table 1.

Vaejoavis (in part): Williams 1976: 2, Table 1.

Type Species. — *Uroctonites giulianii* Williams & Savary, NEW SPECIES.

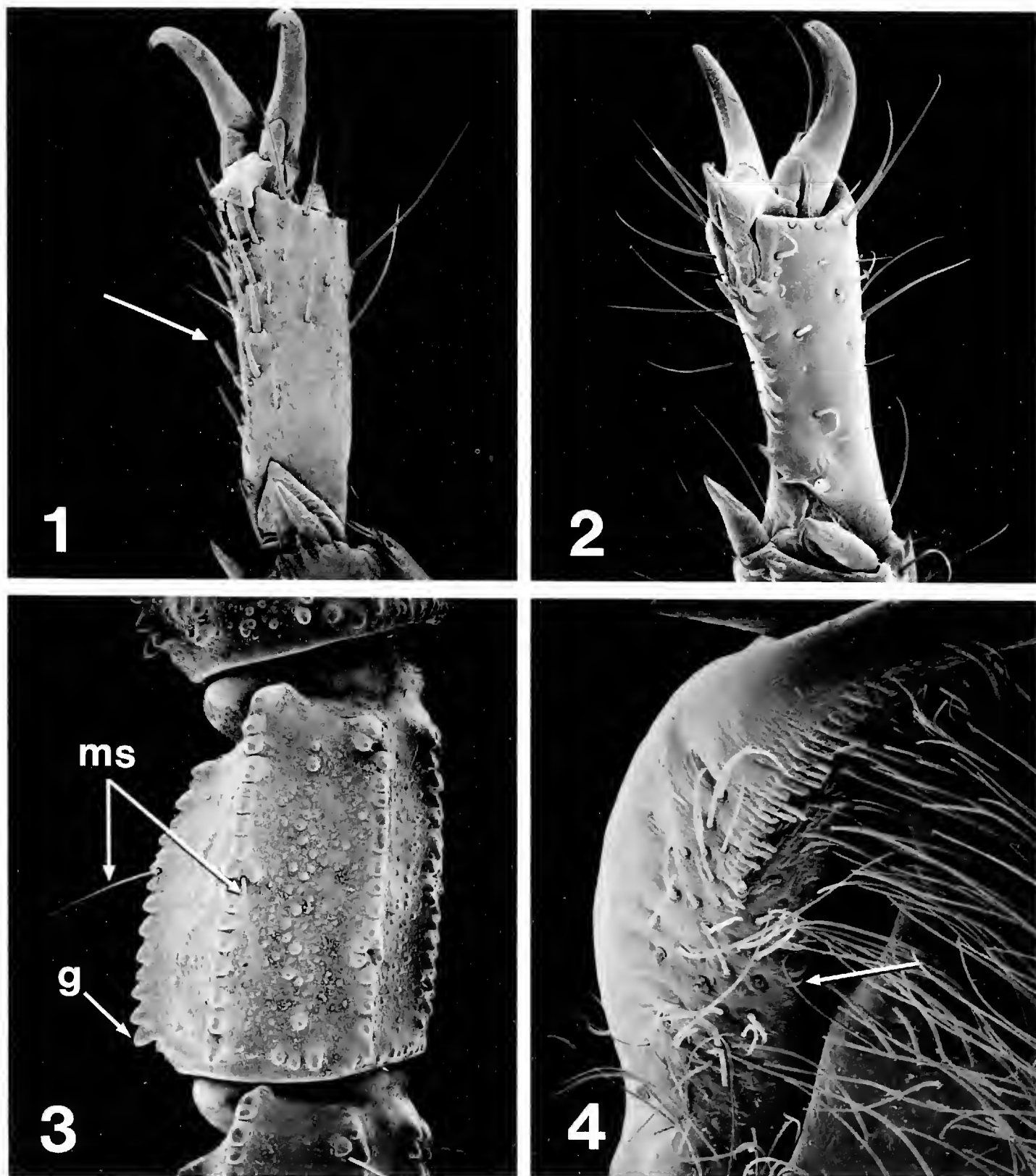
Description. — Prosoma: carapace frontal margin more or less bilobed; median ocelli relatively small, inconspicuous, on low tubercule; lateral ocelli two to three per group; sternum pentagonal, with deep posterior median depression. Mesosoma: terga I–VI lacking median and submedian keels, tergum VII with two pairs lateral keels, these not terminating in enlarged posterior denticle; sterna I–VI smooth, lacking keels; stigma small (carapace length/stigma length = 15–20), oval, length 2.0–3.0 × width; sternum VII lacking lateral keels; males with conspicuous genital papillae; hemispermatophore with lamellar hook basal, not adnate to lamella (Figs. 9–12), sclerotized mating plug reduced or absent. Pectine small, 7–12 teeth per comb; anterior lamella of three elongate sclerites, middle lamella with elongate basal sclerite and three to six subcircular sclerites; fulcra large, subtriangular, similar to adjacent middle lamellar sclerites in size or larger. Metasoma with dorsal, dorsolateral, ventral, and ventrolateral keels I–IV well developed and granular, dorsal and dorsolateral keels with angular termination, terminal denticle similar to adjacent denticles in elongation (Fig. 3); ventromedian keels paired on I–IV, on V single, not branched at terminus (Fig. 7). Chelicera with ventral margin of movable finger smooth to weakly crenulate (Fig. 4), superior tine of movable finger with one or two subdistal teeth, fixed finger with ventral surface lacking denticles. Pedipalp chela with palm swollen obliquely towards prodorsal keel, keels coarsely granular, intercarinal spaces granular dorsally, fixed finger with trichobothrium id near finger origin, trichobothrium eb2 slightly distal to finger origin, trichobothria pair eb1/eb2 not widely separated from trichobothria pair est/et (Fig. 13), supernumerary denticles six on fixed finger, six to seven on movable finger (Figs. 13, 15, 16), primary row denticles in five to six subrows on fixed finger, six subrows on movable finger; proventral keel of pedipalp chela terminating medially at movable finger base. Brachial trichobothria: two dorsals, 14 retrolaterals, two

Table 1. Measurements (in mm) of *Uroctonites giulianii* Williams & Savary NEW SPECIES, holotype and allotype. Abbreviations: aw = anterior width, d = depth, ditd = distal internal trichobothrium distance, ff = fixed finger, fmd = frontal margin distance, l = length, mf = movable finger, mw = median width, p-row = primary row denticles of chela, w = width.

Variables	Holotype (female)	Allotype (male)
Total length	36	35
Prosoma, carapace, (l/w)	4.2/3.8	3.9/3.2
Diad (l/w/fmd)	0.16/0.42/1.7	0.13/0.45/1.5
Sternum (l/aw/mw)	1.1/1.2/1.3	1.0/1.1/1.1
Metasoma, length	14.2	14.4
Segment I (l/w/d)	1.9/2.3/1.8	2.1/2.2/1.7
Segment II (l/w/d)	2.2/2.2/1.7	2.3/2.1/1.6
Segment III (l/w/d)	2.3/2.1/1.7	2.4/2.0/1.6
Segment IV (l/w/d)	3.0/2.0/1.6	2.9/1.8/1.6
Segment V (l/w/d)	4.8/2.0/1.6	4.7/1.7/1.5
Telson, length	4.7	4.6
Vesicle (l/w/d)	3.4/2.2/1.7	3.2/2.0/1.6
Aculeus (l)	1.4	1.4
Pedipalp, humerus (l/w)	3.8/1.3	3.4/1.2
Brachium (l/w)	3.9/1.3	3.4/1.4
Chela (l)	7.2	6.2
Palm (l/w/d)	4.4/2.3/3.2	3.9/2.3/3.2
Movable finger (l)	3.7	3.3
Fixed finger (l/ditd)	2.7/2.5	2.3/2.2
Supernumerary denticles (ff/mf)	6/6	6/6
Fixed finger p-row denticles	8-12-13-13-13-18	9-10-12-12-13-21
Movable finger p-row denticles	4-11-13-16-14-27	2-10-13-14-14-23
Pectine teeth (left/right)	7/8	8/8
Leg IV, patella (l/d)	3.4/0.95	2.9/0.9
Stigma III (l/w)	0.2/0.1	0.2/0.1

ventrals (Fig. 5), one prolateral. Humeral trichobothria: one dorsal, one retrolateral, no ventral, one prolateral. Legs with single ventromedian row of short spinules on telotarsus, this flanked pro- and retrolaterally by row of stout spiniform setae (Fig. 1).

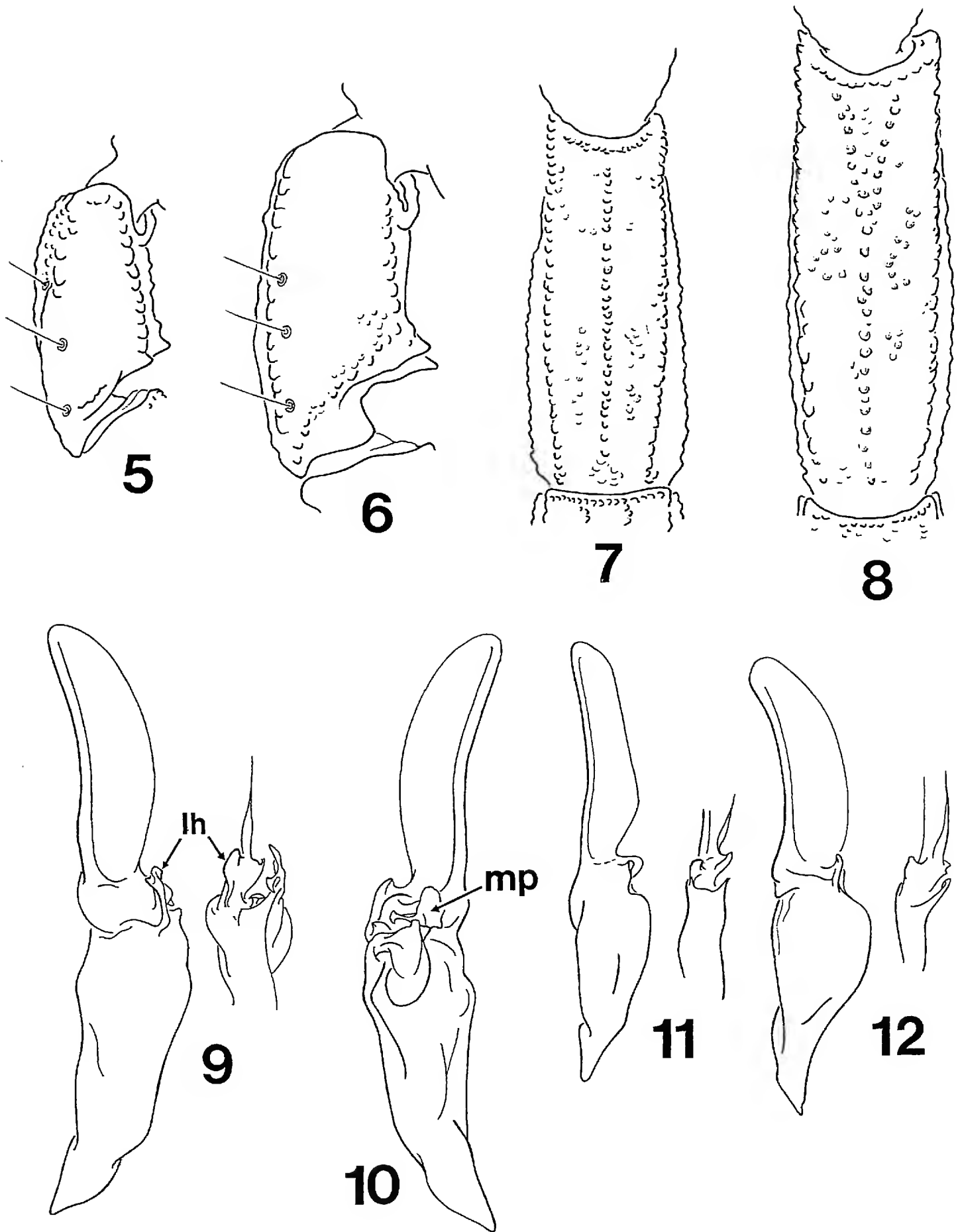
Diagnosis. — Members of this genus are distinguished from other vaejovids by the presence of a row of stout spiniform setae on each side of the ventromedian row of telotarsal spinulae (Fig. 1). Such spiniform setae are lacking in other vaejovids (Fig. 2). Members of *Uroctonites* are further distinguished from other vaejovids except *Uroctonus mordax*, *Uroctonus franckei*, *Uroctonus grahami*, and *Vaejovis lindsayi* by the absence of prolateral keels on the pedipalp brachium and by the reduction or loss of the sclerotized mating plug of the spermatophore (Fig. 10). They are further distinguished from members of *Uroctonus* by the lack of distinct denticles on the ventral margin of the movable finger of the chelicera (Fig. 4), by the presence of only two trichobothria on the ventral surface of the pedipalp brachium (Fig. 5), by the relative proximity of trichobothrial pairs et/est and eb1/eb2 (Fig. 13), and by the linear termination of the ventromedian keel of the fifth metasomal segment (Fig. 7). Members of *Uroctonus* bear denticles on the ventral margin of the movable finger of the chelicera, have three trichobothria on the ventral surface of the pedipalp brachium (Fig. 6), have trichobothrial pairs



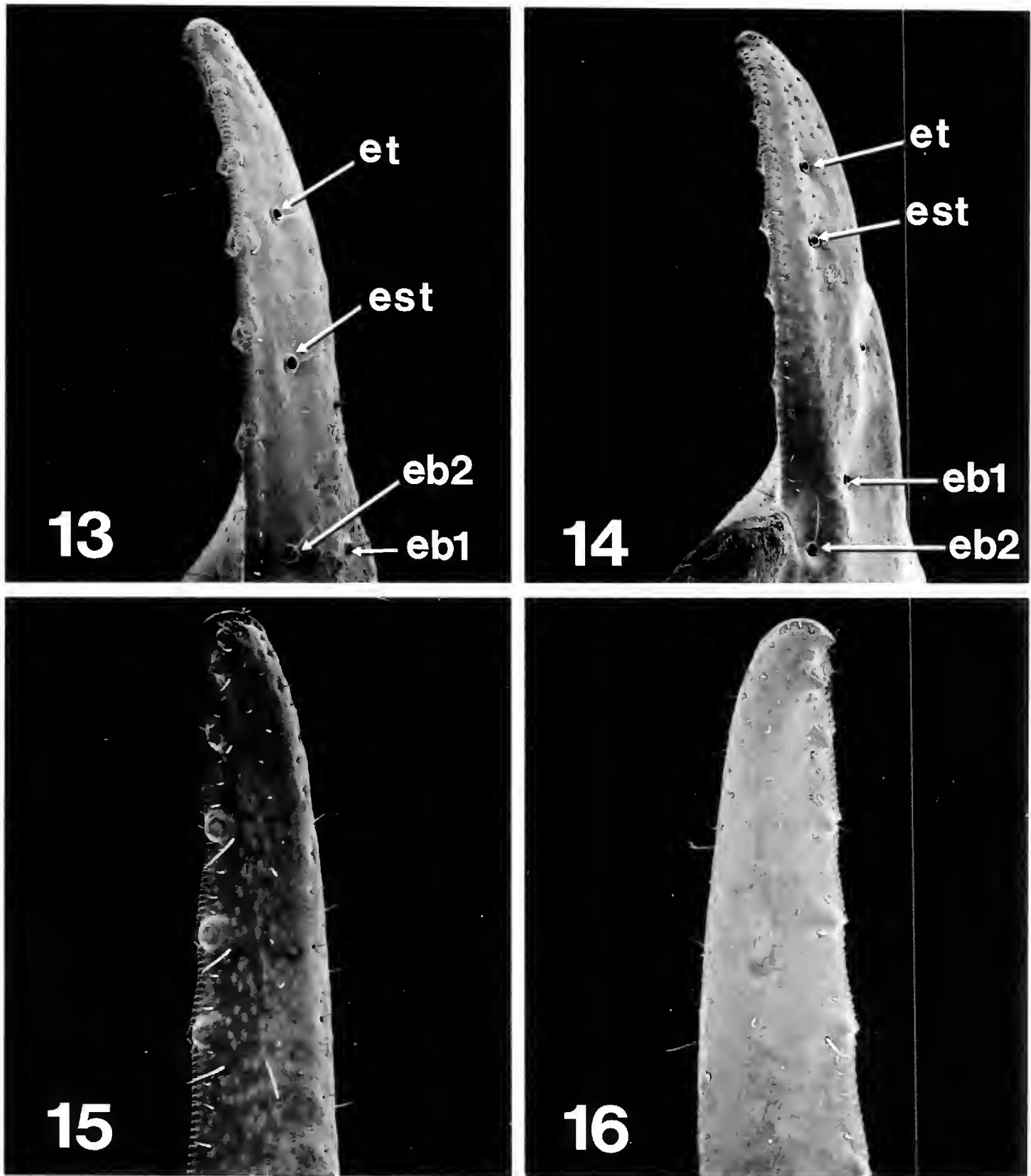
Figures 1–4. Morphological characters of *Uroctonus* and *Uroctonites*. Figure 1. *Uroctonites giulianii*, right telotarsus III, ventral aspect, showing arrangement of spiniform setae. Figure 2. *Uroctonus mordax*, right telotarsus III, ventral aspect, note lack of ventral rows of spiniform setae. Figure 3. *Uroctonites giulianii*, metasomal segment III, right lateral view, showing relative size of granules of dorsal and dorsolateral keels, note distal terminal granules (g) are similar to adjacent in size; macrosetae (ms) associated with dorsal and dorsolateral keels of metasoma III are shown. Figure 4. *Uroctonites giulianii*, right chelicera, ventral view, showing weak crenulations on the ventral margin of the movable finger. Illustrations in Figs. 1–4 are based on the following specimens: *Uroctonites giulianii*, adult male paratype from Waucoba Canyon, Inyo Mountains, Inyo County, California; *Uroctonus mordax*, adult male from Mount Diablo, Contra Costa County, California.

et/est and eb1/eb2 widely separated (Fig. 14), and have a Y-shaped caudal divergence of the ventromedian keel of the fifth metasomal segment (Fig. 8).

Taxa included in Uroctonites.—*Uroctonites montereus* (Gertsch & Soleglad, 1972); *Uroctonites sequoia* (Gertsch & Soleglad, 1972), *Uroctonites huachuca*



Figures 5–12. Morphological characters of *Uroctonites* and *Uroctonus* species. Figure 5. *Uroctonites montereus*, right pedipalp brachium, ventral aspect, showing characteristic two ventral trichobothria. Figure 6. *Uroctonus mordax*, right pedipalp brachium, ventral aspect, showing characteristic three ventral trichobothria. Figure 7. *Uroctonites montereus*, metasomal segment V, ventral aspect, showing linear termination of ventromedian keel caudally. Figure 8. *Uroctonus mordax* metasomal segment V, ventral aspect, showing “Y”-shaped divergence of ventromedian keel caudally. Figure 9. *Uroctonites montereus*, right hemispermatothore, external view, lamellar hook (lh) is indicated. Figure 10. *Uroctonites montereus*, right hemispermatothore, internal view, sclerotized mating plug indicated (mp). Figure 11. *Uroctonites giulianii*, right hemispermatothore, external view. Figure 12. *Uroctonites huachuca*, right hemispermatothore, external view. Illustrations in Figs. 5–12 are based on the following specimens: *Uroctonites giulianii*, adult male, paratype from Waucoba Canyon, Inyo Mountains, Inyo County, California; *Uroctonites montereus*, adult male, from Monterey, Monterey County, California; *Uroctonites huachuca*, male, Huachuca Mountains, Cochise County, Arizona.

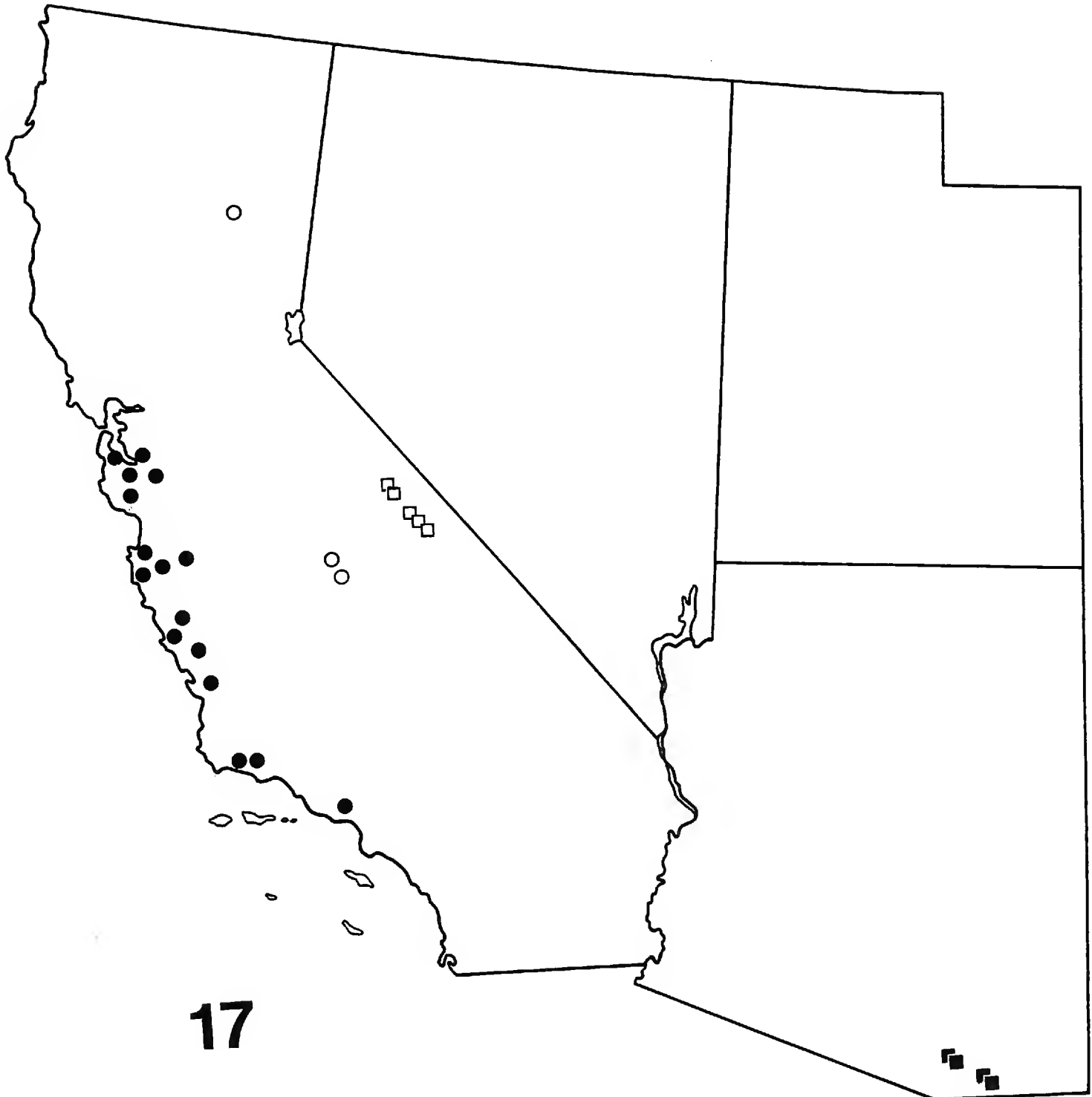


Figures 13–16. Morphological characters of *Uroctonus* and *Uroctonites* species. Figure 13. *Uroctonites giulianii*, pedipalp fixed finger, retrolateral aspect, showing presence of six supernumerary granules; positions of trichobothria et, est, eb1, and eb2 are indicated. Figure 14. *Uroctonus mordax*, pedipalp fixed finger, retrolateral aspect, showing presence of seven supernumerary granules and wide separation of trichobothria pairs et/est and eb1/eb2. Figure 15. *Uroctonites giulianii*, pedipalp movable finger, prolateral aspect, showing presence of six supernumerary granules. Figure 16. *Uroctonites montereus*, pedipalp movable finger, prolateral aspect, showing presence of seven supernumerary granules. Figures 13–16 are based on the same specimens as cited for Figs. 1–4.

(Gertsch & Soleglad, 1972); *Uroctonites giulianii* Williams & Savary, NEW SPECIES.

Distribution.—Southern Arizona to coastal California (Fig. 17).

Remarks.—The name *Uroctonites* combines the name *Uroctonus* with the suffix “-ites,” which suggests relationship with *Uroctonus*. Members of this genus are



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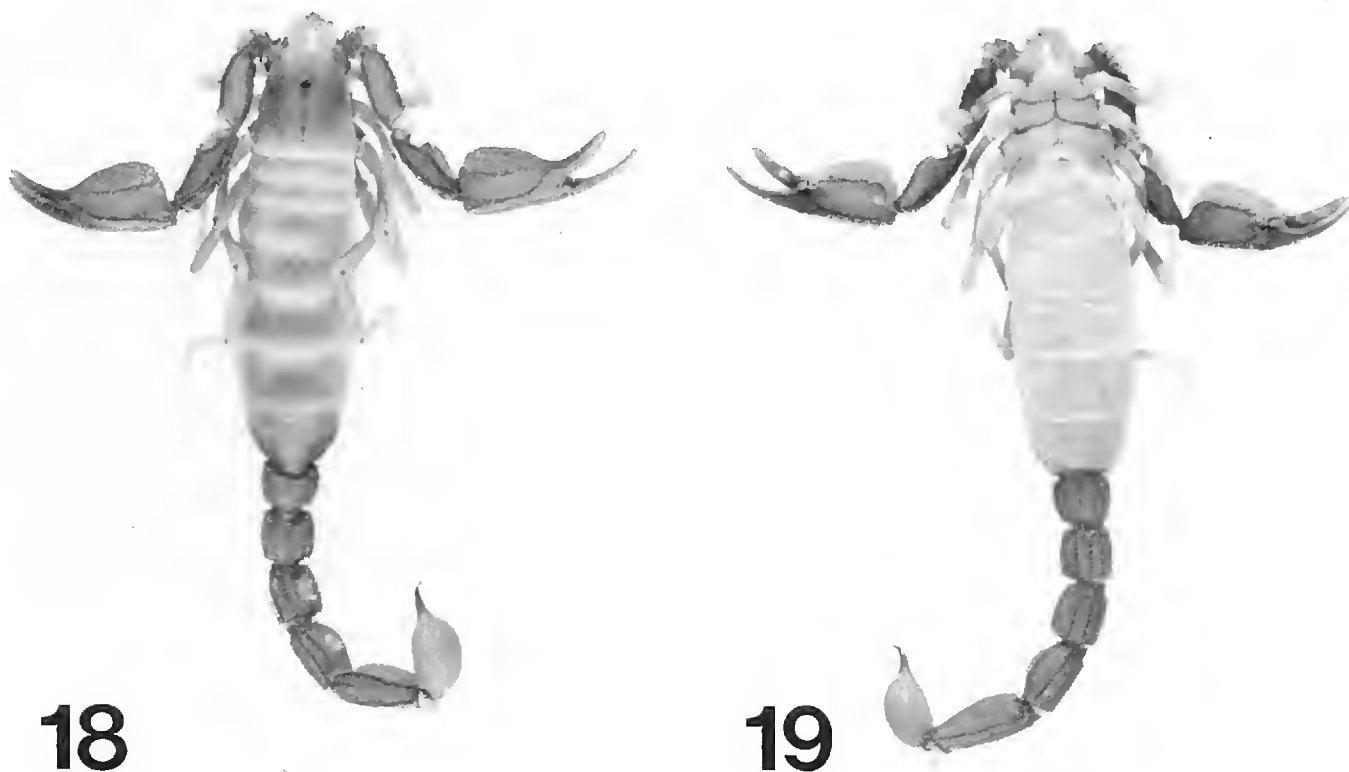
Figure 17. Distribution of *Uroctonites montereus* (solid circles), *Uroctonites sequoia* (open circles), *Uroctonites huachuca* (solid squares), and *Uroctonites giulianii* new species (open squares).

found on exposed rock surfaces and talus slopes and under rocks in xeric, montane, cave, and coastal environments. Their occurrence as geographically isolated species with restricted ranges suggests they are relicts of a previously more broadly distributed lineage. Of the four known species, all appear to reside in small, isolated populations, except for the more broadly distributed *U. montereus*.

Uroctonites giulianii Williams & Savary, NEW SPECIES

Table 1, Figs. 1, 3, 4, 11, 13, 15–19

Types.—Holotype, female, deposited in the California Academy of Sciences (CAS Type No. 16436), data: USA. CALIFORNIA. *INYO Co.*: White Mountains, Inyo National Forest, Ancient Bristlecone Pine Forest, 1.1 km (0.7 mi) S of Schulman Grove, el. 3080 m, 4 Sep 1988, S. C. Williams, V. F. Lee. Allotype, male, deposited in the California Academy of Sciences (CAS Type No. 16436), data: USA. CALIFORNIA. *INYO Co.*: Inyo Mountains, Lead Canyon, el. 1951



Figures 18–19. *Uroctonites giulianii* Williams & Savary, NEW SPECIES, paratype, female, from Addie Canyon, Inyo Mountains, Inyo County, California.

m, 18 May 1976, D. Giuliani. Paratypes: USA. CALIFORNIA. *INYO Co.*: (Inyo Mountains): Addie Canyon, el. 2160 m, 5 Aug 1975, D. Giuliani, 1 female; Addie Canyon, el. 2130 m, 20 May 1976, D. Giuliani, 2 females, 3 juveniles; Addie Canyon, el. 2130 m, 8 May 1974, L. LaPre, S. Mifras, 1 female (UCR); Beveridge Canyon, el. 2000 m, 4 Jul 1975, D. Giuliani, 2 males, 1 juvenile; Beveridge Canyon, el. 2900 m, Jul 1975, D. Giuliani, 1 male; Lead Canyon, el. 1950 m, 18 May 1976, D. Giuliani, 1 male, 2 females, 1 juvenile; Lead Canyon, el. 1980 m, under rock, 11 Apr 1974, L. LaPre, M. Eells, 1 juvenile male (UCR); ridge N of Lead Canyon, el. 2134 m, Dec 1980, D. Howell, 1 female; 11.3 km (7 mi) N and 4.8 km (3 mi) E of Lone Pine, el. 1829 m, 14 Apr 1989, D. Giuliani, 1 male; Waucoba Canyon, el. 1980-2290 m, 9 Jun 1976, D. Giuliani, 2 males, 1 juvenile; Willow Creek, el. 1370 m, 16 Sep 1976, D. Giuliani, 3 females; White Mountains: 0.2 km (0.1 mi) NE of Batchelder Spring, 8.8 km (5.5 mi) N of and 8.8 km (5.5 mi) E of Big Pine, el. 1860 m, 28 Aug 1984 to 11 Jun 1985, D. Giuliani, alcohol/antifreeze pitfall, 1 male; The Narrows, 16.1 km (10 mi) NE of junction of state Highways 395 and 168 on Highway 168, el. 2100 m, 13 Aug 1988, W. E. Savary, R. Jackson, 1 male; 0.2 km (0.1 mi) NE of Batchelder Spring, 8.8 km (5.5 mi) N of and 8.8 km (5.5 mi) E of Big Pine, el. 1860 m, 1 Oct 1985 to 28 Jun 1986, D. Giuliani, alcohol/antifreeze pitfall, 1 male; Ancient Bristlecone Pine Forest, 1.1 km (0.7 mi) S of Schulman Grove, el. 3080 m, 4 Sep 1988, S. C. Williams, V. F. Lee, female; 1.8 km (1.2 mi) S of Schulman Grove, el. 2930 m, 4 Sep 1988, S. C. Williams, V. F. Lee, 3 females, 1 juvenile; (Sierra Nevada): Shannon Canyon, 4.8 km (3 mi) N and 8.0 km (5 mi) W Big Pine, el. 2042 m, 9 Jun 1988, D. Giuliani, 1 male. *MONO Co.*: White Mountains, Marble Canyon, 16.1 km (10 mi) NNE of Big Pine, el. 2041 m, 9 Jun 1988, D. Giuliani, 1 male.

Description.—Female (Holotype). Coloration: dorsum of carapace, metasoma, and pedipalps moderate burnt umber, carapace with slight brown marbling, mesosoma slightly lighter, keels of pedipalps and metasoma contrastingly darker brown than background cuticle; walking legs slightly paler than mesosoma, more yellow; vesicle slightly yellow; pedipalp palms amber brown, keels and fingers contrastingly darker brown; venter white-yellow, similar to legs; pectines slightly white. Prosoma: anterior carapace margin deeply bilobed, with three pairs of frontal setae; carapace lacking distinct keels, finely granular, granules homogeneous, posterior median groove deep; median ocelli small, on low, inconspicuous ocular tubercle, ocelli separated by more than 1.2 ocellar diameters; three lateral ocelli per group; sternum pentagonal, with broad posterior median depression, four pairs of sternal macrosetae. Mesosoma: terga I–VI lacking keels, finely granular, granules homogeneous; tergum VII lacking median keel, with two pairs of serrated lateral keels that do not terminate in an enlarged posterior denticle; sterna I–VI smooth, lacking keels; stigma small, oval, length to width ratio 2.1, sternum VII with about 12 irregular posterior granules; 10 pairs of genital macrosetae, variable in length; Pectine: Three sclerites in marginal lamella, one proximal angular sclerite plus three irregular sclerites in middle lamella, large subtriangular fulcra, with fulcra similar to or slightly larger than adjacent sclerites of middle lamella, most fulcra lacking macrosetae, distal tooth laterally swollen, $2.0\times$ wider than adjacent teeth. Metasoma: dorsal and dorsolateral keels I–IV coarsely granular, with angular termination, terminal denticle similar to adjacent ones in size (Fig. 3); ventral and ventrolateral keels raised, coarsely granular, homogeneously developed on I–IV, ventromedian V single, not branched at terminus, dorsal keels with 0-1-1-1 pairs of macrosetae on segments I–IV, dorsolateral keels with 0-1-1-1 pairs of macrosetae on segments I–IV. Telson: vesicle smooth, lustrous, seven to eight pairs of macrosetae ventrally, Chelicerae: ventral margin of movable finger with three to four crenulations (Fig. 4), ventral surface of fixed finger lacking denticles; movable finger with two subdistal teeth on dorsal tine. Pedipalps: palm swollen obliquely, with heavy granular keels. Ventral surface of palm broad and flat; internal surface of fingers with narrow space proximally between fingers when chela closed; dorsal, prodorsal, and retrodorsal keels distinct and coarsely granular, ventral keel obsolete to obscure; retrolateral, prolateral, retroventral, and proventral keels distinct and broadly granular; proventral keel terminating medially at movable finger base; palm swollen toward prodorsal keel. Brachial macrosetae: two dorsals, five retrolaterals, one ventral, four prolaterals. Humeral macrosetae: three dorsals, nine retrolaterals, four ventrals, four prolaterals. Leg III: telotarsi each with 15–17 fine spinules in single ventromedian row, this row flanked by a prolateral and retrolateral row of three to five stout spiniform macrosetae (Fig. 1).

Male.—(Allotype). Similar to female (holotype) in color and structure except: smaller body size; large genital papillae present; metasoma slightly more slender; dorsal keel with 0-0-1-1 pairs of macrosetae; pedipalp palm more swollen.

Variation.—Paratypes similar to holotype and allotype in size, color, and structure with following exceptions: total length 20–36 mm in males, 27–40 mm in females; pectine tooth counts eight to nine in males, seven to eight in females; one female with one subdistal tooth on dorsal tine of each movable cheliceral finger, one female with one subdistal tooth on one side and two on the other side; smaller individuals lighter in coloration than larger ones; several specimens light tan in general coloration. Several specimens with lateral ocelli reduced to two per group.

Diagnosis.—Characters that distinguish *U. giulianii* are: total length up to 40 mm; base color of body burnt umber to light tan, keels of metasoma and pedipalps often contrastingly darker than surrounding cuticle; median ocelli small, ratio of carapace width to diameter of diad 6.6–9.4 ($\bar{x} = 8.0 \pm 0.7$, $n = 14$); chelicera with several small crenulations on ventral margin of movable finger (Fig. 4), superior tine of movable finger with two (rarely with one) subdistal teeth; pedipalp palm swollen obliquely toward prodorsal keel, ratio of chela length to palm width 2.7–3.4 ($\bar{x} = 3.0 \pm 0.2$, $n = 14$), ratio of palm width to depth 0.7–0.8 ($\bar{x} = 0.8 \pm 0.04$, $n = 14$); fixed finger of chela with trichobothrium on palm near finger origin, supernumerary denticles six on fixed and movable fingers (Figs. 13, 15), primary row denticles divided into six linear subrows on fixed and movable fingers; pectine teeth eight to nine in males, seven to eight in females.

This species is related to *U. huachuca* in structure and coloration, but differs

as follows: metasoma with dorsal keel macrosetal formula 0-0-1-1 or 0-1-1-1 on segments I-IV (not 0-0-0-0 or 0-0-0-1); aculeus shorter, ratio of vesicle length to aculeus length greater than 1.9 ($\bar{x} = 2.2 \pm 0.1$, $n = 14$).

Distribution.—White Mountains, Inyo Mountains, and eastern Sierra Nevada of California from 1370–3080 m elevation (Fig. 17).

Remarks.—Variable in coloration, adult size, and morphology. This and *Paruroctonus boreus* (Girard) are the only scorpions known to inhabit the Ancient Bristlecone Pine Forest. These two species are found at elevations higher than any other scorpion in North America. In the bristlecone pine forest, the environmental conditions probably restrict normal foraging and growing conditions to no more than three to four months of the year. The concurrence of light tan forms and a distinctly melanic form suggests a life cycle that may be longer than one year. It has been collected under rocks and from exposed rocky surfaces at night by ultraviolet detection. This species is named after Derham Giuliani, a resident of Big Pine, California, in recognition of his significant collections of desert scorpions and contributions to our knowledge of desert biology.

Material Examined.—See types.

Uroctonites montereus (Gertsch & Soleglad), NEW COMBINATION
Figs. 5, 7, 9, 16, 17

Uroctonus montereus Gertsch & Soleglad 1972: 565, 583, 589–591.

Vejovis montereus (Gertsch & Soleglad): Stahnke 1974: 130, 136, Table 1.

Vaejovis montereus (Gertsch & Soleglad): Williams 1976: 2.

Types.—Holotype, female, deposited in the American Museum of Natural History, data: USA. CALIFORNIA. MONTEREY Co.: Hastings Natural History Reservation, Red Hill, 3 Feb 1951, J. Linsdale.

Diagnosis.—Characters that distinguish *U. montereus* are: total length up to 40 mm; base color of body dark fuscous brown to light tan, keels of metasoma and pedipalps often contrastingly darker than surrounding cuticle; frontal margin of carapace deeply bilobed, median ocelli small, ratio of carapace width to diameter of diad 6.0–8.3 ($\bar{x} = 7.0 \pm 0.6$, $n = 30$); chelicera lacking crenulations on ventral margin of movable finger, superior tine of movable finger with one (rarely two) subdistal tooth; pedipalps with palm swollen obliquely toward prodorsal keel, ratio of chela length to palm width 2.6–3.1 ($\bar{x} = 2.9 \pm 0.1$, $n = 30$), ratio of palm width to depth 0.6–0.8 ($\bar{x} = 0.7 \pm 0.05$, $n = 30$); supernumerary denticles six on fixed finger, seven on movable finger (Fig. 16), primary row denticles in six subrows on fixed and movable fingers; telotarsi with single row of fine spinulae ventrally, this flanked pro- and retrolaterally by a row of four stout spiniform setae; pectine teeth 10–12 in males, 8–10 in females.

This species is related to *U. sequoia* in structure, but differs in having primary row denticles of fixed pedipalp finger divided into six (not five) subrows.

Distribution.—California: Alameda and San Mateo counties—south to Los Angeles County, from sea level to 700 m elevation (Fig. 17).

Remarks.—This is the most broadly distributed and frequently encountered member of the genus, but it is never locally abundant. It can be encountered throughout the year by turning rocks and other ground surface debris. Females with associated litters were recorded from the Monterey area from July and

December. Litters ranged in size from 21–50 offspring ($\bar{x} = 34 \pm 11$, $n = 5$). One specimen in the CAS collection has a Sedona, Coconino County, Arizona locality label but is probably incorrectly labeled because there is no other evidence that this species ranges east of coastal California.

Material Examined.—USA. CALIFORNIA. ALAMEDA Co.: approx. 1.6 km (1 mi) S of Niles district, Fremont, Kimber Farms Chicken Ranch, open, grassy, SW facing hillside along roadcut, el. 76 m, 11 Jan 1970, J. Hjelle, T. Glimme, F. Koehler, F. Salazar, 1 male. LOS ANGELES Co.: Canoga Park, el. 500 m, 7 Apr 1969, P. McLynn, 1 female. MONTEREY Co.: Monterey (all collected by R. Johnson): 28 Jan 1963, 1 male, 25 Feb 1963, 1 female, 18 Mar 1963, 1 female, 22 Mar 1966, 1 male, 1 juvenile, 30 Apr 1965, 1 female, 22 May 1961, under chalk rock, 1 female, 27 May 1963, 1 male, 2 females, 30 May 1970, 1 female with 32 offspring, 1 female with 21 offspring, 1 female with 38 offspring (labeled “eggs 7/21/1970”), 17 Jun 1963, 2 females, 26 Jun 1967, 3 males, 2 females, 2 juveniles, 2 Aug 1963, 3 males, 3 females, 2 juveniles, 2 Aug 1963, 1 female with 50 offspring, 5 Aug 1963, 2 males, 4 females, 16 Aug 1970, 3 females, 1 juvenile, 26 Oct 1962, beneath chalk rock, 1 male, 8 Nov 1970, 1 female; 15 Nov 1962, 1 female, 19 Nov 1962, 1 female, 21 Nov 1962, 1 female, 24 Dec 1969, 1 female with 31 offspring; approx. 1.6 km (1 mi) S of Monterey, 2 Apr 1972, R. Johnson, 1 male, 1 female; woods near Monterey Peninsula College, approximately 1.6 km (1 mi) from Monterey, 30 Apr 1965, R. Johnson, 1 male, 4 females; 1.6 km (2 mi) from Monterey, R. Johnson, 24 Feb 1961, under rock, 1 female, 10 Jul 1961, 1 female, 22 May 1961, under chalk rock, 1 female; Palo Colorado Canyon: 19 Jul 1963, R. Johnson, 1 female; 22 Jul 1963, R. Johnson, male; 30 Jul 1963, R. Johnson, 1 male, 1 juvenile; Pena Blanca Lake, 30 May 1971, G. Bowden, 1 female; La Gloria Rd., 16.1 km (10 mi) from Gonzales, 22 Jun 1963, R. Johnson, 1 male; Hastings Natural History Reserve nr Jamesburg, 16 Mar 1957, J. Powell, 1 female (UCB). SAN BENITO Co.: La Gloria Rd, 13 May 1963, R. Johnson, 1 male. SAN LUIS OBISPO Co.: 3.7 km (2.3 mi) NE of San Luis Obispo along Stenner Creek Road, 15 Jul 1974, R. Haradon, V. Lee, W. Savary, 1 male; 19.3 km (12 mi) W of State Highway 101 on State Highway 46, el. 400 m, 13 Feb 1987, T. Briggs, V. Lee, 1 female; 3.9 km (2.4 mi) NW of road to Hearst San Simeon State Historical Monument on State Highway 1, el. 60 m, 13 Feb 1987, T. Briggs, V. Lee, 1 female; 2.9 km (1.8 mi) NW of San Luis Obispo on Stenner Creek Road on underside of serpentine rock in grassland, 26 Feb 1967, V. Lee, 1 juvenile. SAN MATEO Co.: Crystal Springs Lake, under stones, 18 Oct 1920, C. Duncan, 1 female, 1 male; 1.3 km (0.75 mi) N of Crystal Springs Dam on County Road 14, under rock near spring, 26 Feb 1966, K. Hom, 3 males, 1 female, 2 juveniles; Edgewood County Park, along Serpentine Trail, el. 210 m, 2 Jan 1987, T. Briggs, V. Lee, D. Ubick; Jasper Ridge (date and collector unknown), 1 male. SANTA BARBARA Co.: About 3.2 km (2 mi) N of Gaviota Beach State Park, 26 Dec 1966, T. S. Briggs, 1 female; E of San Marcos Pass, el. 680 m, 16 Jun 1956, Coll. PBS [probably P. S. Bartholomew], 1 female. SANTA CLARA Co.: Montebello Ridge, short grass on gravel, 25 Jun 1965, D. Kavanaugh, 1 male; Alum Rock Park, 12 Sep 1977, J. Hjelle, J. Ramsey, 1 male. SANTA CRUZ Co.: Castle Rock, 17 Jul 1971, G. Burden, 1 male.

Uroctonites huachuca (Gertsch & Soleglad), NEW COMBINATION

Figs. 12, 17

Uroctonus huachuca Gertsch & Soleglad 1972: 565, 573–576.

Uroctonus? *huachuca* Stahnke 1974: 130.

Type.—Holotype, female, deposited in the American Museum of Natural History, data: USA. ARIZONA. SANTA CRUZ Co.: Santa Rita Mountains, Madera Canyon, 7 Jun 1952, W. J. Gertsch.

Diagnosis.—This species is related to *U. giulianii* in structure and coloration, but differs as follows: metasoma with dorsal keel macrosetal formula 0-0-0-0 or 0-0-0-1 (not 0-0-1-1 or 0-1-1-1) on segments I–IV; aculeus longer, ratio of vesicle length to aculeus length less than 1.9 ($\bar{x} = 1.7 \pm 0.1$, $n = 8$).

Distribution.—Santa Rita and Huachuca Mountains of Arizona, from 1600–2440 m elevation (Fig. 17).

Remarks.—*Uroctonites huachuca* is found in limestone cave and surface environments, but no evidence of unique cave adaptations is apparent. Observations by Bill Peachey, an Arizona speleologist, suggest a permanent population inhabits Hidden Cave in Santa Cruz County, Arizona. This is the first cave record for this species.

Material Examined.—USA. ARIZONA. COCHISE Co.: Huachuca Mountains, Reef Road terminus, el. 2439 m, 20 Aug 1967, 2 females, 3 juveniles; Huachuca Mountains, Carr Canyon, 16 Aug 1969, R. Haradon, 2 females. SANTA CRUZ Co.: Santa Rita Mountains, Gardner Canyon, Hidden Cave, el. 1616 m, 24 Jun 1988, W. E. Savary, T. S. Briggs, D. Ubick, W. Rauscher, in dark zone, 2 males, 2 juveniles.

Uroctonites sequoia (Gertsch & Soleglad), NEW COMBINATION

Fig. 17

Uroctonus sequoia Gertsch & Soleglad 1972: 565, 590–592.

Vejovis sequoia (Gertsch & Soleglad): Stahnke 1974: 130, 136.

Vaejovis sequoia (Gertsch & Soleglad): Williams 1976: 2.

Type.—Holotype, female, deposited in the American Museum of Natural History, data: USA. CALIFORNIA. TULARE Co.: Sequoia National Park, Clough Cave, under rocks in Ladder Room, 14 May 1966, T. S. Briggs.

Diagnosis.—This species is related to *U. montereus*, but has primary-row denticles of fixed pedipalp finger divided into five (not six) subrows.

Distribution.—Sierra Nevada of California from Plumas and Tulare counties from elevations of 900–1500 m (Fig. 17).

Remarks.—This is one of the rarest species of scorpion in California, being known only from seven specimens, of which only four are adults. A young male specimen from Clough Cave, listed by Gertsch & Soleglad (1972) has three small lateral eyes on each side of the carapace, as do the three specimens from near Hammond. A single juvenile female from near Quincy has two eyes on the left side of the carapace and three on the right.

Material Examined.—USA. CALIFORNIA: PLUMAS Co.: Soda Springs Cave area, 16.1 km (10 mi) N of Quincy, 5 Sep 1961, W. J. Gertsch, W. Ivie, 1 juvenile (AMNH). TULARE Co.: 19.3 km (12 mi) NE of Hammond, 21 Mar 1941, S. & D. Mulaik, 2 males, 1 female (AMNH); Sequoia National Park, Clough Cave, 26 Nov 1965, V. Lee, 1 juvenile male.

Key to Species of *Uroctonites*

1. Movable cheliceral finger with dorsal tine bearing one (rarely two) subdistal tooth; seven supernumerary denticles on pedipalp movable finger. (Fig. 16) 2
- Movable cheliceral finger with dorsal tine bearing two (rarely one) subdistal teeth; six supernumerary denticles on pedipalp movable finger. (Fig. 15) 3
- 2(1). Pedipalp fixed finger with primary row denticles in five subrows. (Sierra Nevada, California) *U. sequoia*
- Pedipalp fixed finger with primary row denticles in six subrows. (coastal central and southern California) *U. montereus*
- 3(1). Metasoma with dorsal keel macrosetal formula 0-0-0-0 or 0-0-0-1 on segments I–IV; aculeus elongate, ratio of vesicle length to aculeus length less than 1.9. (southern Arizona) *U. huachuca*

- Metasoma with dorsal keel macrosetal formula 0-0-1-1 or 0-1-1-1 on segments I–IV; aculeus short, ratio of vesicle length to aculeus length greater than 1.9. (Inyo Mountains, White Mountains and Sierra Nevada of southeastern California) *U. guilianii*

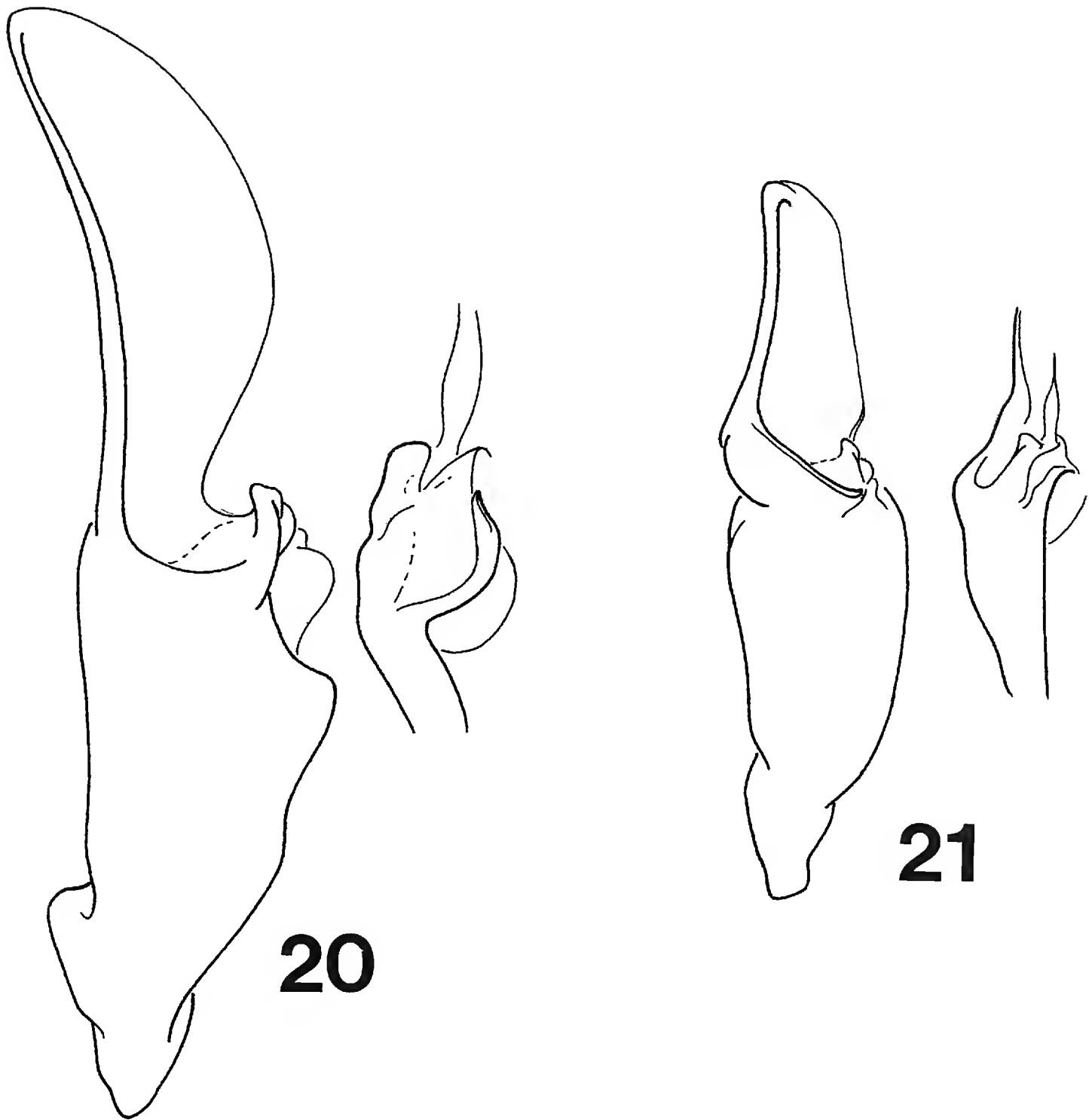
DISCUSSION AND CONCLUSIONS

Phylogenetic Relationships.—Our hypothesis of common ancestry for *Uroctonites*, *Uroctonus*, and *Vaejovis lindsayi* is supported by their shared absence of prolateral keels on the pedipalp brachium, the suppression of the ventral keel on the pedipalp chela, and by the reduction or loss of the sclerotized mating plug of the spermatophore. These character states are regarded as synapomorphies. *Vaejovis lindsayi* lacks the additional synapomorphies that currently define *Uroctonus* or *Uroctonites* and, thus, should not be assigned to either of these genera at this time. Transfer of *V. lindsayi* to its own monotypic genus is a possible solution for systematic placement, but this would appear to erect a genus defined solely on plesiomorphic character states. We, therefore, prefer to treat this enigmatic relic as an “incertae sedis” within the *Uroctonus/Uroctonites* lineage.

We conclude that the genus *Uroctonus* is currently composed of only three species: *U. mordax*, *U. franckei* and *U. grahami*. We also conclude that *Uroctonites* is currently composed of only four species: *U. guilianii*, *U. huachuca*, *U. montereus*, and *U. sequoia*. We further conclude that the remaining species that have previously been associated with *Uroctonus* belong to a subgroup of *Vaejovis* that we refer to as the *minimus* group. Placement into the *minimus* group is done largely on the basis of spermatophore characters (Figs. 22–29). The *minimus* subgroup includes the following taxa: *Vaejovis andreas*, *Vaejovis angelenus*, *Vaejovis apacheanus*, *Vaejovis bogerti*, *Vaejovis chicano*, *Vaejovis glimmei*, *Vaejovis iviei*, *Vaejovis minimus*, *Vaejovis montcazieri*, *Vaejovis rufulus*, and *Vaejovis williamsi*. Members of this group share with *Serradigitus*, *Syntropis* and other *Vaejovis* subgroups, spermatophores that have elevated lamellar hooks that are adnate to the lamella (Figs. 22–29). The shared possession of this character state is regarded as synapomorphic, and contrasts with the basal positioning of the lamellar hooks in species of *Uroctonites* and *Uroctonus* and in *Vaejovis lindsayi* (Figs. 9–12, 20–21). A second synapomorphy, the longitudinal orientation of the larvae on the dorsum of the female following parturition, supports this association of the *minimus* group with *Serradigitus*, *Syntropis*, and other *Vaejovis* (Savary, unpublished data).

Suppression of the ventral keel of the pedipalp chela and reduction (but never the complete loss) of the prolateral keels of the pedipalp brachium occur in the *minimus* group. This reduced keel configuration would tend to suggest a similarity between the *minimus* group members of *Vaejovis*, and *Uroctonus* but this similarity appears homoplastic.

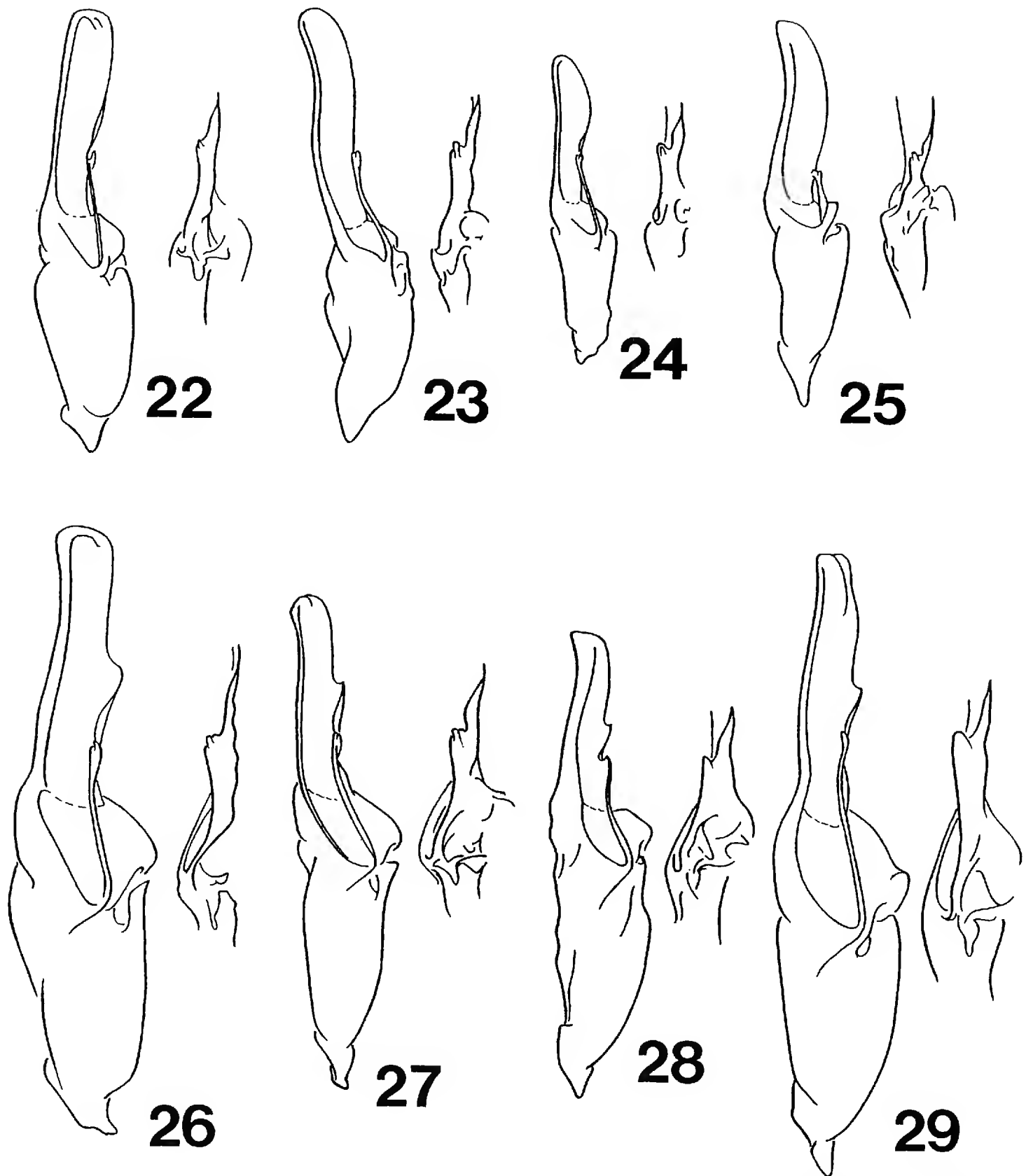
Distribution Patterns.—The members of *Uroctonites* are distributed as two species pairs, which are separated from one another by the intervening crest of the Sierra Nevada. To the west of the Sierra Nevada crest the sister species *U. montereus* and *U. sequoia* occur. Both have a single subdistal tooth (rarely two) on the dorsal tine of the movable cheliceral finger (a synapomorphy) and seven supernumerary denticles on the movable finger of the pedipalp (a symplesiomorphy). The ventral series of trichobothria on the pedipalp chela is compressed in



Figures 20–21. Right hemispermatophores of *Uroctonus* and *Vaejovis lindsayi*, figured from external view. Figure 20. *Uroctonus mordax mordax* from Mount Diablo, Contra Costa County, California. Figure 21. *Vaejovis lindsayi* from La Laguna, Sierra de la Laguna, Baja California Sur, Mexico.

these two species, with the distance between trichobothria Vt and Vst usually equaling less than two-thirds the distance between Vb and Vsb. The San Joaquin Valley, which lies between the known ranges of these two species, and a possible association of *U. sequoia* with caves and limestone outcrops, suggest that both geographical and ecological isolation have played a role in their speciation.

The sister species *U. giulianii* and *U. huachuca* are distributed to the east of the Sierra Nevada crest. Both have two subdistal teeth (rarely one) on the dorsal tine of the movable cheliceral finger (a symplesiomorphy) and have six supernumerary denticles on the movable finger of the pedipalp (a synapomorphy). The ventral series of trichobothria on the pedipalp chela is not as compressed in these species as it is in the western species pair, and the distance between chelal trichobothria Vt and Vst usually equals more than two-thirds the distance between



Figures 22–29. Representative hemispermatothores of the *minimus* group of *Vaejovis*. The external view of the right hemispermatothore is figured. Figure 22. *Vaejovis minimus minimus* from San Clemente Island, California. Figure 23. *Vaejovis rufulus* from Punta Banda, Baja California Norte, Mexico. Figure 24. *Vaejovis andreas* from Mount Palomar, San Diego County, California. Figure 25. *Vaejovis montcazieri* from Mission San Borja, Baja California Norte, Mexico. Figure 26. *Vaejovis bogerti* from Whitewater Canyon, Riverside County, California. Figure 27. *Vaejovis angeleus* from the Santa Monica Mountains, Los Angeles County, California. Figure 28. *Vaejovis iviei* from Mountain Millhouse, Napa County California. Figure 29. *Vaejovis glimmei* from Intersection of Cache and Davis Creeks, Lake County California.

Vb and Vsb. These two species appear to be montane relicts, with *U. giulianii* now restricted to the Inyo Mountains, White Mountains and eastern Sierra Nevada of California, and *U. huachuca* restricted to the Huachuca Mountains and Santa Rita Mountains of Arizona.

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BEHAVIORAL INTERACTIONS AMONG FORMICID SPECIES IN THE ANT MOSAIC OF AN ORGANIC PEAR ORCHARD

G. S. PAULSON AND R. D. AKRE

Department of Entomology, Washington State University,
Pullman, Washington 99164-6432

Abstract.—Structure of the ant mosaic of an organic pear orchard was studied. Based on behavior, colony dispersion, and colony size species inhabiting the pear orchard were categorized as follows: *Leptothorax muscorum* (Nylander), *Tapinoma sessile* (Say), and *Myrmica incompleta* Provancher were submissive species; *Lasius pallitarsis* (Provancher) were encounterers; the top level of the competitive hierarchy in the orchard was occupied by *Formica neoclara* Emery, a polygynous species, which has formed high density nests throughout the orchard. *Camponotus modoc* Wheller could not be categorized. Structure of the ant mosaic was very stable. Field surveys and pitfall traps showed that foraging territories of the ant species did not change over four years. There was considerable overlap in the spatial territories of the ant species. All six species foraged in pear trees and collected psylla honeydew, and all but *C. modoc* also were predators of pear psylla. However, they differed in their reliance on these food sources. Niches of each species were further differentiated by interspecific aggression and temporal mechanisms, especially ambient temperature and circadian cycles of behavior, which facilitated the coexistence of dominant and subdominant species.

Key Words.—Insecta, Formicidae, population structure, competition, ant interaction

In permanent habitats, such as forests and orchards, ants form a three-dimensional patchwork of nonoverlapping, foraging territories referred to as an ant mosaic. The distribution of each ant species within the mosaic is delineated by the availability of nesting material, nesting site preference, vegetation, abiotic requirements, availability of preferred food sources, and the intensity of intercolonial aggression (Savolainen & Vepsalainen 1988, Vepsalainen & Pisarski 1982, Jackson 1984, Leston 1973, Majer 1972).

Each mosaic is considered stable and able to withstand minor perturbations due to the elasticity of its components. However, major ecological changes will alter the structure of the mosaic. Disturbances associated with agroecosystems are examples of major changes that affect the ant mosaic. Common cultivation practices and the extensive use of pesticides simplify and destabilize the mosaic, often preventing beneficial ants from becoming permanently established (Altieri & Schmidt 1984, Leston 1973). For this reason, predation by ants in short term crops is insignificant unless the crop is grown next to a permanent habitat (Risch & Carroll 1982). In long term crops, such as in orchards, pesticide applications are almost entirely responsible for the breakdown of the ant mosaic. If the ant mosaic can be stabilized in an orchard, predatory ants can significantly contribute to the control of arthropod pests. Integrated pest management programs, incorporating modified spray schedules designed to conserve ant populations, have resulted in successful control of insect pests on cocoa and coffee plantations (Majer 1972, Leston 1973). Ants also contribute to the management of lepidopteran pests in coconuts (Way & Cammell 1989).

temperature readings of the soil (using a 15 cm probe), canopy, and ant trails were recorded with a telethermometer.

Pitfall traps were used in 1987–1989 to monitor ground activity of ants. Traps were constructed from 12 oz plastic cups. Approximately 20 ml of diluted anti-freeze (1:5 antifreeze : water) were poured into the cups, which were then buried up to their rim in the orchard. Pitfalls were collected after 24 h, and the contents examined under a dissecting microscope in the laboratory. Ants in the traps were counted and identified to species. Pitfall traps were rotated throughout the study area with 40–60 traps placed during each 24 h period. In three years 865 traps were examined.

Laboratory studies of inter- and intraspecific trail following behavior were carried out in the following manner. Two colonies of each ant species found in the orchard, except *L. muscorum*, were maintained in the laboratory. One colony of each species pair was given unrestricted access to food (honey and dead insects), which was removed 24 hours prior to testing. In the second colony, ants could obtain food only by climbing to the end of balsa wood sticks (5 × 10 × 20 mm long) inserted into the nesting material (approximately 45 degrees). In this way, foraging trails, established on the sticks, could be freely moved between colonies. A balsa stick was taken from a colony using a pair of forceps and, using caution to avoid agitating the ants, placed into a colony without sticks. The elapsed times were recorded, from the time of placement of the stick, until an ant located the food and a new foraging trail was established. Behavior of the ants in response to the trail (stick) was also observed. All possible intra- and interspecific combinations (25) were tested and replicated five times. Combinations were carried out in a random order with a new stick used for each test. Observations of *C. modoc*, a nocturnal forager, were carried out in simulated night conditions by using red lights.

RESULTS AND DISCUSSION

Structure of the pear orchard ant mosaic was very stable. During the four years of this study field surveys and pitfall traps showed that foraging territories of the six ant species did not change. Even removal of a large portion of the mature trees had little effect on the mosaic, possibly because sprouting pear tree stumps proved to be a suitable replacement for lost trees. There was considerable overlap in spatial territories of ant species (Fig. 1). All six species were found foraging in pear trees and utilizing pear psylla honeydew as a food source and all, except *C. modoc*, also were predators of pear psylla.

However, ants differed in their reliance on pear psylla as a food source. *Formica neoclara* preyed almost exclusively on pear psylla (Paulson 1990) and collected large amounts of honeydew. Based on foraging intensity observed in the field, pear psylla honeydew was also an important food source for *L. pallitarsis*, but pear psylla (including honeydew) comprised only a small part of the diets of the other four species. Niches of each species within the orchard were further differentiated as the result of interspecific aggression and temporal mechanisms, especially ambient temperature and circadian cycles of behavior, which facilitated the coexistence of dominant and subdominant species (see below).

Nest sites of *F. neoclara*, *T. sessile*, *L. muscorum*, and *M. incompleta* also were spatially and temporally stable; nest locations (Fig. 2) of these species did not

In Washington, there are several key pests that affect orchard grown commodities, yet the beneficial role of ants in orchard systems has not been elucidated. One of the most damaging orchard pests is the pear psylla, *Cacopsylla pyricola* (Foerster). Heavy infestations can reduce yields by competing for available nutrients. Fruit production and value can be further reduced by the presence of honeydew, produced by the psyllids, which damages foliage and causes cosmetic russets on fruits, thereby decreasing their commercial value.

Presently, control of pear psylla is attained through the extensive use of pesticides. Chemical methods are not entirely successful, however. Spray programs fail when pesticide resistance develops in psylla populations. Damaging psylla population levels also may occur when pesticide use is discontinued prior to harvest. Ants can be valuable additions to a pear psylla management program. They remove substantial quantities of honeydew and are effective predators of pear psylla (Paulson 1990).

To effectively utilize ants in an integrated psylla control program, it is necessary to understand the structure of the ant community within a pear orchard. This study describes intra- and interspecific interactions within the ant community and the mediating effect of abiotic factors upon these interactions to form the ant mosaic.

MATERIALS AND METHODS

Field and laboratory studies elucidated the structure of the ant mosaic and the factors contributing to its formation and maintenance. Field studies were carried out from May–August during 1985–1989 in an organically managed orchard located near Peshastin, Washington. The study plot was initially 2 ha (approximately one-half of the orchard) of Bartlett pears (6 m × 6 m spacing), which was reduced to 1.5 ha in 1988 when most of the orchard was converted to pasture. Pear tree stumps, not removed from the pasture, sprouted. Therefore, after 1988, the study area was approximately 1.5 ha of mature pear trees and 0.5 ha of pasture/pear shrubs. Ground cover, predominantly grasses, was kept short by regular mowing. Irrigation was applied with undertree sprinkler heads rotated through the orchard on a weekly basis. The orchard had not been treated with pesticides for at least 10 years. Six species of ants inhabited the orchard: *Formica neoclara* Emery, *Camponotus modoc* Wheeler, *Leptothorax muscorum* (Nylander), *Lasius pallitarsis* (Provancher), *Myrmica incompleta* (Provancher), and *Tapinoma sessile* (Say).

The structure of the ant mosaic was studied by direct observation of spatial and temporal changes in foraging behavior of each ant species, and by placing pitfall traps throughout the orchard. From May to September each year, observations were made at least once each week during the following time periods: 2400–0800, 0800–1200, 1200–1600, 1600–2000, and 2000–2400 hours. During each observation period every tree in the study plot was carefully examined to determine: the presence or absence of ants, the species observed, the relative abundance, and the distribution of each species in the tree, and inter/intraspecific interactions such as aggression, recruitment, and trail following. Locations of ant nests in the orchard were recorded. Several nests of each species were examined to determine colony size and nest structure. Care was taken to avoid destroying the nests. Colony size was extrapolated from partial counts of individuals. Hourly

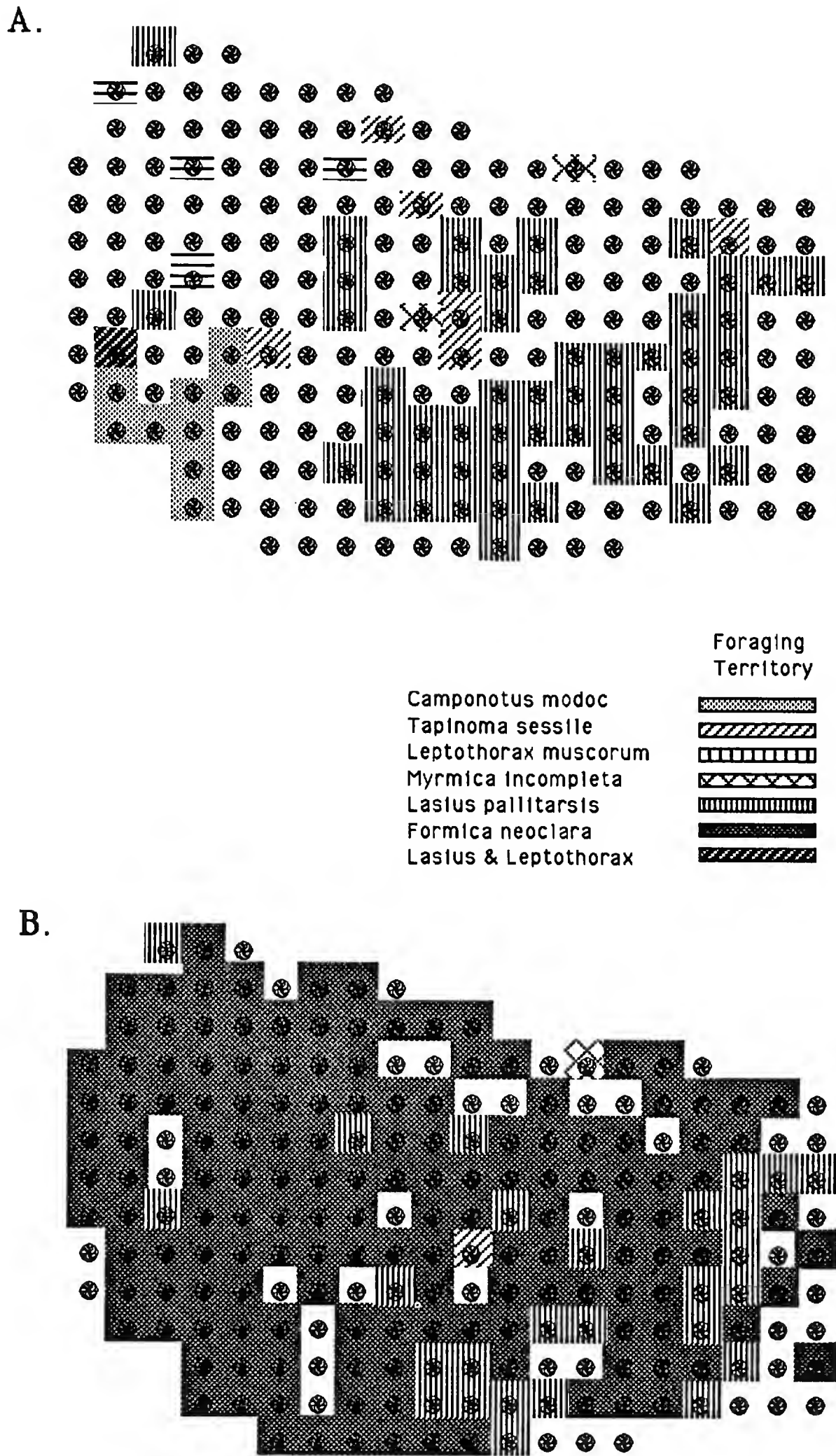
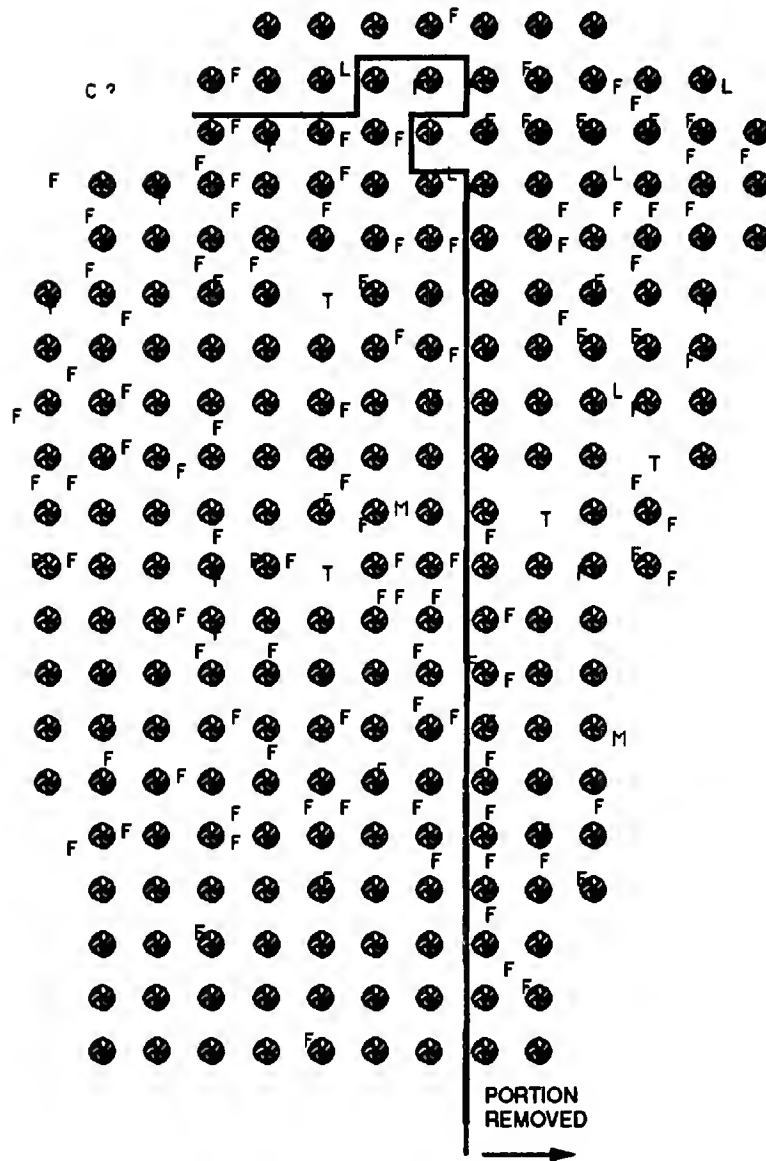


Figure 1. Foraging territories (A, B) in the ant mosaic of an organic pear orchard in Peshastin, Washington. Individual trees are represented by circular symbols.



Nest	
c	Camponotus modoc
T	Tapinoma sessile
L	Leptothorax muscorum
M	Myrmica incompleta
F	Formica neoclara

Figure 2. Nest sites in the ant mosaic of an organic pear orchard in Peshastin, Washington. Individual trees are represented by circular symbols.

change during this study. Of these species, *F. neoclara* had the greatest number of nests, 122, in the orchard. Only two nests of *M. incompleta*, four nests of *T. sessile*, and five nests of *L. muscorum* were found in the orchard. The nests of *Lasius pallitarsis*, a polygynous species, were difficult to locate and enumerate because the nests were cryptic and diffuse; the difficulty in discriminating nests may indicate the presence of a unicolonial nest assemblage. However, this possibility was not examined in this study. Due to the stability of the foraging areas of *L. pallitarsis*, it is reasonable to assume that its nest sites were also relatively stable. *Camponotus modoc* nests were never located.

Interspecific aggression was most responsible for the structure of the pear orchard ant mosaic. Vepsalainen & Pisarski (1982) divided the competitive hierarchy of ants into three levels. The bottom level, "submissives," defend only their nests. The intermediate level, "encounterers," also defend their food source. The

top level species, "territorials," additionally defend their foraging territories. Forager density (colony size) is positively correlated to competitive dominance (Savolainen & Vepsäläinen 1988). Based on their behavior and colony dispersion and size, the species inhabiting the pear orchard were categorized: *L. muscorum*, *T. sessile*, and *M. incompleta* were submissive species; *L. pallitarsis* were encounterers; and the territorial level of the competitive hierarchy in the orchard was occupied by *F. neoclara*, a polygynous species which had formed high density nests throughout the orchard. The role of *C. modoc* is discussed below.

Submissive Species.—Field surveys and pitfall traps indicated that *M. incompleta*, *T. sessile*, and *L. muscorum* all had stable nest sites and temporal stability in their foraging areas, but did not have long term stability in their foraging trails. Foraging trails of *L. muscorum* and *M. incompleta* were regularly encountered, but rarely persisted for more than 2 days (respectively, means \pm SD: 1.81 ± 0.08 d, $n = 26$; 1.58 ± 0.76 d, $n = 31$). *Tapinoma sessile* trails were slightly more persistent (2.12 ± 1.17 d, $n = 17$). Usually it was impossible to determine why a trail was terminated; however, on four occasions, *F. neoclara* was implicated as a probable cause for trail abandonment by *M. incompleta*. In these incidences *M. incompleta* were initially observed tending aphids. The following day both *F. neoclara* and *M. incompleta* were seen with the aphids. The ants did not appear antagonistic. During observation periods on subsequent days only *F. neoclara* were present and the aphid population declined until the aphids were gone. *Myrmica incompleta*, a submissive species, appeared to have been driven from the food resource.

In trail tests both *M. incompleta* and *T. sessile* responded most intensely to conspecific trails (Fig. 3). *M. incompleta* workers followed conspecific trails immediately (range <1 sec to 1 min), the number of ants responding to the trail was too intense to quantify. *Tapinoma sessile* workers responded to trails about as quickly as *M. incompleta* (range, 5 sec to 1 min), but less intensely. Maximum trail movement was about eight ants per minute moving toward the food source. The intensity and rapidity of recruitment to the food resource suggests that submissive ants exhibit a type of consumptive (exploitative) competition. When a food resource is located additional foragers are quickly recruited to maximize utilization of the resource before it is lost. The field observations described previously support this theory. Fellers (1987) reported that congeneric submissive (Fellers' "subordinate") species in a Maryland woodlot were also exploitative competitors.

In theory, exploitative ants should not recruit to food resources that are already being utilized by other ant species, especially those higher in the competition hierarchy, because there would be very little reward for the submissive ants. This was observed in the trail tests, further evidence that submissive ants are exploitative competitors. *Myrmica incompleta* workers appeared to sense the trails of other ant species. Workers would stop at the trails and have increased antennal movement, but did not follow those trails to the food. Similarly, *T. sessile* appeared to sense all the trails with which it was presented during this study, but it followed only conspecific trails and those of *M. incompleta* (response time, 2–3.5 min), another submissive ant.

Although reported (Smith 1928) to be polygynous, *T. sessile* colonies in this study were monogynous, as were all submissive species studied here. Nests of

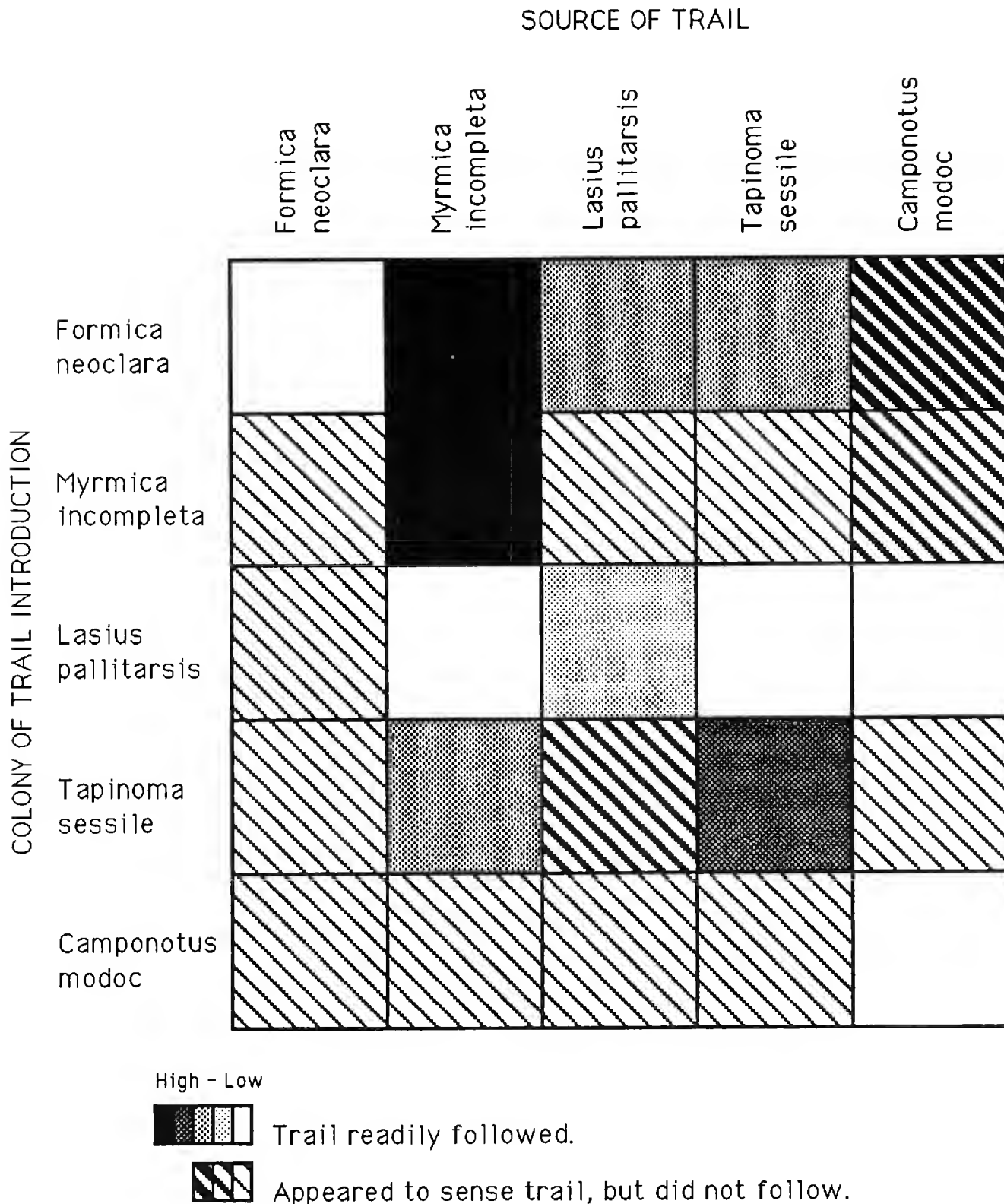


Figure 3. Matrix representing the relative intensity of ant worker response to foraging trails of five ant species.

submissive species were small. Average worker populations, based on estimates made during examinations of nests, were 1500 ($n = 2$, range, 500–2500) for *M. incompleta*, 5500 ($n = 3$, range, 2000–10,000) for *T. sessile*, and 2000 ($n = 3$, range, 1800–3000) for *L. muscorum*. Pitfall traps indicated that the submissive species had large foraging areas relative to colony size. All three species were generalist predators/scavengers. *Myrmica incompleta* was usually associated with aphids and was commonly found tending aphids infesting weeds in the orchard and the surrounding area.

Encounterer Species. — *Lasius pallitarsis* has many characteristics that indicate it is an encounter species. It is polygynous; nests were large and worker populations were estimated to be greater than 30,000. Nests and foraging territories had spatial

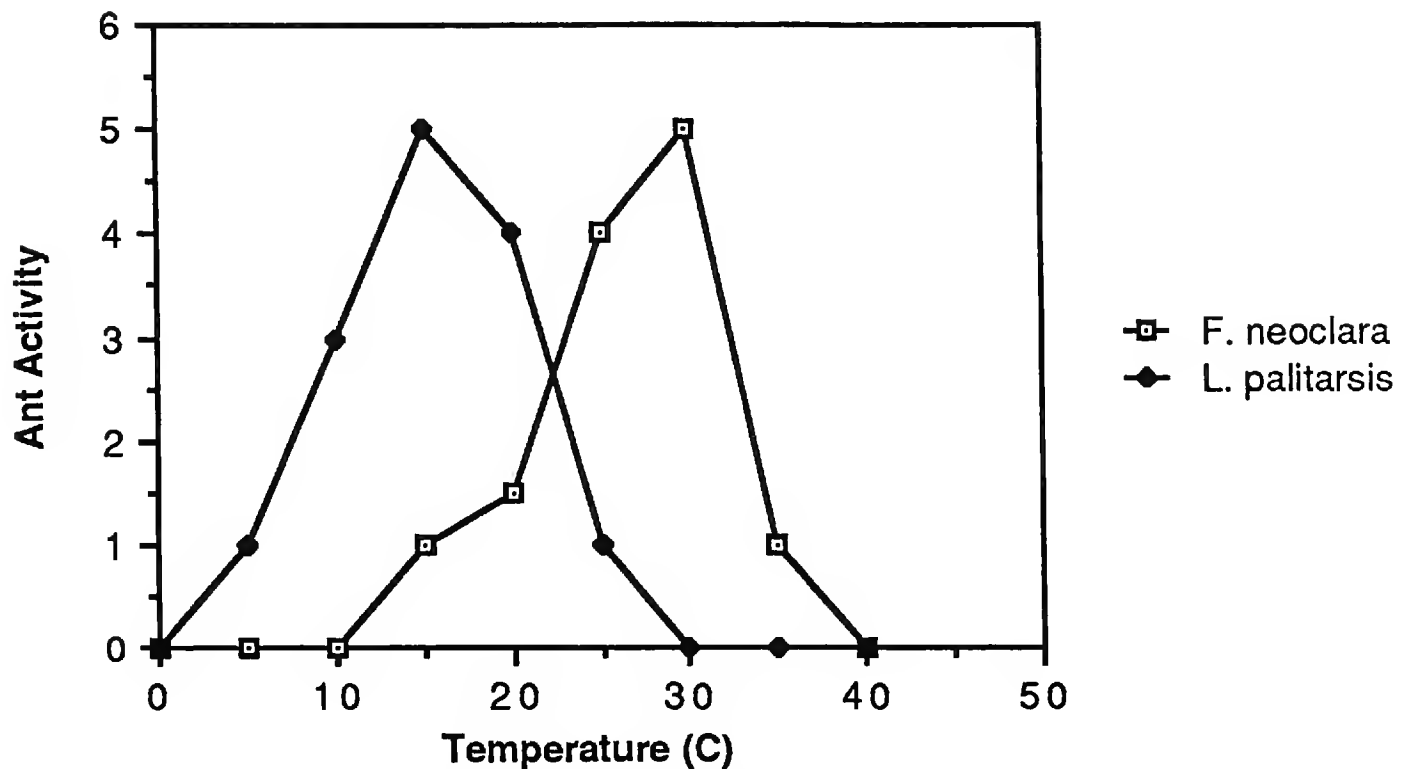


Figure 4. Relative foraging activity of *Formica neoclara* and *Lasius pallitarsis* in a pear tree at different tree canopy temperatures.

and long term temporal stability. Foraging trails were maintained for long periods which was taken as evidence that trails were defended and maintained as long as the resource offered sufficient rewards. In trail studies, *L. pallitarsis* responded most intensely to conspecific trails, forming new trails in 3.5–5 min. *Lasius pallitarsis* also readily followed trails established by submissive species (*M. incompleta* in 4–10 min, *T. sessile* in 4–7 min) and by *C. modoc* (6–10 min) but would not follow trails of *F. neoclara*. Apparently *L. pallitarsis* would challenge all but the dominant ant species for access to a resource.

Lasius pallitarsis foraged heavily in the litter and also collected extensive amounts of pear psylla honeydew. During good foraging conditions, it was common to find trail flow on pear tree trunks in excess of 75 ants, engorged with psylla honeydew leaving the tree each minute. Due to the cryptic nature of *L. pallitarsis* nests and the difficulty of observing foraging efforts in the leaf litter, the importance of pear psylla honeydew in the diet of *L. pallitarsis* was not determined. Although *L. pallitarsis* and *F. neoclara* both utilized pear psylla as a major food resource, competition was diminished by thermal and temporal niche differentiation. *Lasius pallitarsis* foraging activity was related to tree canopy temperature. Peak foraging occurred between 10–18° C, which occurred between 0400–0600 h. Above 25° C, *L. pallitarsis* activity is negligible. This pattern of activity is the inverse of that of *F. neoclara*, which is rarely active below 15° C and most active at temperatures above 23° C (Fig. 4). Talbot (1942) found similar patterns of above ground activity in congeneric species of ants in a Michigan forest.

Territorial overlap of *L. pallitarsis* and *C. modoc* was slight (Fig. 1). Probably there is little overlap in the resource niches of these species, due to the extreme difference in worker size. Although both species will collect pear psylla honeydew, the resource is not utilized at the same time of day. *Camponotus modoc* is a nocturnal forager and *L. pallitarsis* is diurnal.

Camponotus modoc does not fit into the ant hierarchy as readily as the other species. It may be a species that only occasionally forages in the pear orchard and,

thus, is not truly part of the pear orchard ant mosaic. Foraging areas of *C. modoc* were spatially and temporally stable but were located on the edge of the orchard. A *C. modoc* nest was never located in or near the orchard. In addition, *C. modoc* did not regularly forage in the orchard and was found only in low numbers. All of these factors seem to indicate that *C. modoc* has a transient role in the orchard ant mosaic. In trail studies, *C. modoc* only responded to conspecific trails. Only *L. pallitarsis* would follow trails established by *C. modoc*. Upon encountering *C. modoc* trails, *F. neoclara* became agitated and had increased ortho- and klinokinesis, which were interpreted as an alarm response. Other *F. neoclara* workers were quickly recruited to this response.

The role of *C. modoc* cannot be readily defined. Although most evidence indicates that *C. modoc* is only a transient part of the ant mosaic, the response of *F. neoclara* to *C. modoc* trails may indicate another possible role. *Camponotus modoc* may be a potential co-dominant that is severely limited by the availability of nesting sites in the orchard.

Territorial Species.—*Formica neoclara* foraged almost exclusively in pear tree canopies collecting psylla honeydew and preying heavily on immature pear psylla (Paulson 1990). Foraging *F. neoclara* were found in about 70% of the pear trees. Tree surveys and pitfall trap collections indicated that virtually the entire orchard was *F. neoclara* territory. Nests and foraging areas were spatially and temporally stable. Although *F. neoclara* is polygynous, it did not form a unicolonial nest assemblage in the pear orchard. Foraging and nearest-neighbor studies of *F. neoclara* showed that nests are discrete colonies with high tolerance for conspecific ants (Paulson 1990).

In the field, trails were maintained as long as the resource was available. Trail-following studies showed that *F. neoclara* had a more rapid and stronger response to trails produced by other ant species than to those produced by conspecifics. By responding to trails in this manner, *F. neoclara* may strengthen its dominance by reducing intraspecific aggression while excluding submissive and encounterer ant species from shared resources. In the laboratory, *F. neoclara* quickly followed trails produced by *L. pallitarsis* (2.5–5 min), *M. incompleta* (1 sec–1 min), and *T. sessile* (1–6 min), and established its own foraging trails (Fig. 3). *Formica neoclara* formed new trails in response to conspecific trails in about 5 min (range, 3–8.5 min). As mentioned previously, *C. modoc* trails were not followed by *F. neoclara* and elicited an alarm response from this ant.

In summary, the structure of the pear orchard ant mosaic was very stable. Niche differentiation of each species within the orchard appeared to be predominately the result of interspecific aggression and temporal mechanisms, especially ambient temperature and circadian cycles of behavior, which facilitated the coexistence of dominant and subdominant species.

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Pan-Pacific Entomologist Reviewers

Volume 67

Albu, R.	Griswold, C. E.	Peterson, R. V.
Andrews, F.	Hardy, A.	Pike, K. S.
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Gambino, P.	Nelson, C. R.	Warner, W. B.
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Gibson, G. A. P.	Opgenorth, D.	Wheeler, Q. D.
Gramaldi, D.	Parella, M. P.	Woolridge, D.
Granett, J.	Penrose, R.	

The Pan-Pacific Entomologist

Contents for Volume 67

- AKRE, R. D.—See PAULSON, G. S. 288
- ALLEN, R. K. & C. M. MURVOSH—A biogeographically based assessment of the potential mayfly fauna of Nevada 206
- ASOOUTH, A. & J. D. LATTIN—*Omanonabis*: a new genus of Nabidae (Heteroptera) from western North America, with a review of *Nabis edax* Blatchley 7
- ASQUITH, A. & J. D. LATTIN—A review of the introduced Lygaeidae of the Pacific Northwest, including the newly discovered *Plinththisus brevipennis* (Latreille) (Heteroptera: Lygaeidae) 258
- AYALA, R.—See BULLOCK, S. H. 171
- BALLING, S. S. & V. H. RESH—Seasonal patterns in a San Francisco bay, California, salt marsh arthropod community 138
- BARR, C. B.—See SHEPARD, W. D. 195
- BARRENTINE, C. D.—Post-egestive survival of *Sphenophorus phoeniciensis* Chittenden (Coleoptera: Curculionidae) egested by western toads 135
- BARZMAN, M. S.—see DAANE, K. M. 99
- BROWN, R. L. & J. A. POWELL—Description of a new species of *Epiblema* (Lepidoptera: Tortricidae: Olethreutinae) from coastal redwood forests in California with an analysis of the forewing pattern 107
- BULLOCK, S. H., R. AYALA, G. RODRÍGUEZ-GONZALEZ, R. PALACIOS-CHÁVEZ, D. RAMOS-ZAMORA, D. L. QUIROZ-GARCÍA & M. DE LA LUIZ ARREGUÍN-SANCHEZ—Nest provision and pollen foraging in three Mexican species of solitary bees (Hymenoptera: Apoidea) 171
- CALTAGIRONE, L. E.—See DAANE, K. M. 99
- CHAPCO, W. & P. R. RIEGERT—Maternal effects and egg hatchability in *Melanophus* (Orthoptera: Acrididae) 81
- CLARK, W. H.—Location of holotype of *Araeoschizus antennatus blaisdelli* Papp (Coleoptera: Tenebrionidae) 73
- DAANE, K. M., M. S. BARZMAN, C. E. KENNETT & L. E. CALTAGIRONE—Parasitoids of black scale in California: establishment of *Prococophagus probus* Annecke & Mynhardt and *Coccophagus rusti* Compere (Hymenoptera: Aphelinidae) in olive orchards 99
- DAHLSTEN, D. L.—See SWEZEY, S. L. 243
- DE LA LUIZ ARREGUÍN-SANCHEZ, M.—See BULLOCK, S. H. 171
- DELFINO, M. A.—A new species of *Uroleucon* (*Uroleucon*) and comments on *Uroleucon* (*Uroleucon*) *tucumani* (Essig) (Homoptera: Aphididae) 216
- DELGADO-CASTILLO, L. & M. A. MORÓN—A new genus and species of Trichiini from Mexico (Coleoptera: Melolonthidae) 181
- DOYEN, J. T. & F. T. HOVORE—Notes on two Pacific coastal species of Tenebrionidae (Coleoptera) 226
- FALCON, L. A.—See PITCAIRIN, M. J. 189
- FENG, M. G., R. M. NOWIERSKI, A. L. SCHAREN & D. C. SANDS—Entomopathogenic fungi (Zygomycotina: Entomophthorales) infecting cereal aphids (Homoptera: Aphididae) in Montana 55
- GOEDEN, R. D. & D. H. HEADRICK—Life history and descriptions of immature stages of *Tephritis baccharis* (Coquillett) on *Baccharis salicifolia* (Ruis & Pavon) (Diptera: Tephritidae) 86
- GRISWOLD, T. E.—A review of the genus *Microthurge* (Hymenoptera: Megachilidae) 115
- GUERTIN, D. S.—Atypical sex role behavior in the ball-rolling dung beetle, *Canthon pilularius* L. (Coleoptera: Scarabaeidae) 145
- HALSTEAD, J. A.—New species of *Aspirhina* Kirby from the Neotropical region (Hymenoptera: Chalcididae) 65
- HALSTEAD, J. A.—New species of *Notaspidium* Dalla Torre from the Nearctic and Neotropical regions 229
- HEADRICK, D. H.—See GOEDEN, R. D. 86
- HODKINSON, I. D.—First record of the Australian psyllid *Blastopsylla occidentalis* Taylor (Homoptera: Psylloidea) on *Eucalyptus* (Myrtaceae) in Mexico 72
- HOVORE, F. T.—See DOYEN, J. T. 226
- HUMBLE, L. M.—Occurrence of *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae) in central British Columbia 224
- KAMM, J. A.—Larval development of *Dargida procincta* (Grote) (Lepidoptera: Noctuidae) in the Pacific Northwest 20
- KEMP, W. P.—See O'NEILL, K. M. 177
- KENNETT, C. E.—See DAANE, K. M. 99
- KONDRATIEFF, B. C.—See WELCH, J. L. 124
- LATTIN, J. D.—See ASQUITH, A. 7, 258
- LIN, F. J.—See TSAUR, S. H. 24
- MANLEY, D. G. & G. O. POINAR, JR.—A new species of fossil *Dasymutilla* (Hymenoptera: Mutillidae) from Dominican amber 200

- MORÓN, M. A.—See L. DELGADO-CASTILLO 181
- MURVOSH, C. M.—See ALLEN, R. K. 206
- NOWIERSKI, R. M.—See FENG, M. G. 55
- O'NEILL, K. M. & W. P. KEMP—Foraging of *Stenopogon inquinatus* (Loew) (Diptera: Asilidae) on Montana rangeland sites 177
- OWEN, W. R.—New host for *Acanthoscelides aureolus* Horn (Coleoptera: Bruchidae) . . 74
- PACIFIC COAST ENTOMOLOGICAL SOCIETY, articles of incorporation and bylaws 1
- PACIFIC COAST ENTOMOLOGICAL SOCIETY, financial statement for 1988, 1989 78
- PACIFIC COAST ENTOMOLOGICAL SOCIETY, proceedings for 1988 147
- PACIFIC COAST ENTOMOLOGICAL SOCIETY, publications 80, 158
- PACIFIC COAST ENTOMOLOGICAL SOCIETY, sponsoring members for 1989 77
- PALACIOS-CHÁVEZ, R.—See BULLOCK, S. H. 171
- PAN-PACIFIC ENTOMOLOGIST, reviewers for volume 67 298
- PAN-PACIFIC ENTOMOLOGIST, notification of subscription renewals 157
- PAULSON, G. S. & R. D. AKRE—Behavioral interactions among formicid species in the ant mosaic of an organic pear orchard . . . 288
- PICKEL, C.—See PITCAIRIN, M. J. 189
- PITCAIRIN, M. J., C. PICKEL, L. A. FALCON & F. G. ZALOM—Development and survivorship of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) at ten constant temperatures 189
- POINAR, G. O. JR.—see MANLEY, D. G. . . 200
- POLHEMUS, J. T.—A new and primitive genus of Cryphocricinae (Heteroptera: Naucaridae) 119
- POWELL, J. A.—See BROWN, R. L. 107
- PRENTICE, T. R. & G. P. WALKER—Nocturnal clustering of the solitary wasp, *Chalybion californicum* (Saussure) (Hymenoptera: Sphecidae) 222
- QUIROZ-GARCÍA D. L.—See BULLOCK, S. H. 171
- RAMOS-ZAMORA, D.—See BULLOCK, S. H. 171
- RESH, V. H.—See BALLING, S. S. 138
- RIEGERT, P. R.—See CHAPCO, W. 81
- RODRÍGUEZ-GONZALEZ, G.—See BULLOCK, S. H. 171
- RUST, R. W. & P. F. TORCHIO—Induction of *Ascospaera* (Ascomycetes: Ascosphaerales) infections in field populations of *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae) 251
- SANDS, D. C.—See FENG, M. G. 55
- SAVARY, W. E.—See WILLIAMS, S. C. 272
- SCHAREN, A. L.—See FENG, M. G. 55
- SCHLINGER, E. I.—See SWEZEY, S. L. 243
- SHEPARD, W. D. & C. B. BARR—Description of the larva of *Atractelmis* (Coleoptera: Elmidae) and new information on the morphology, distribution, and habitat of *Atractelmis wawona* Chandler 195
- SORENSEN, J. T.—Phylogenetic character responses for shape component variance during the multivariate evolution of eulachnine aphids: redescription of *Pseudessigella* Hille Ris Lambers (Homoptera: Aphididae: Lachninae) 28
- SORENSEN, J. T.—Book Review: Oman, P. W., W. J. Knight & M. W. Nielson. 1990. Leafhoppers (Cicadellidae): a bibliography, generic-check-list and index to the world literature 1956–1985. CAB International, Wallingford, Oxon, United Kingdom, 368 pp 75
- SWEZEY, S. L., D. L. DAHLSTEN, E. I. SCHLINGER & S. M. TAIT—Pedation on Douglas-fir tussock moth (Lepidoptera: Lymantriidae) and white fir sawfly (Hymenoptera: Diprionidae) larvae by captive spiders from white fir in California 243
- TAIT, S. M.—See SWEZEY, S. L. 243
- THOMAS, D. B.—The Acanthosomatidae (Heteroptera) of North America 159
- TORCHIO, P. F.—See RUST, R. W. 251
- TSAUR, S. H. & F. J. LIN—A new *Drosophila* species in the *montium* Meijere subgroup of the *melanogaster* Meigen species-group in the subgenus *Sophophora* Sturtevant from Taiwan (Diptera: Drosophilidae) 24
- WALKER, G. P.—See PRENTICE, T. R. 222
- WELCH, J. L. & B. C. KONDRATIEFF—The Mydidae (Diptera) of Costa Rica 124
- WILLIAMS, S. C. & W. E. SAVARY—*Uroctonites*, a new genus of scorpion from western North America (Scorpiones: Vaejovidae) . . . 272
- ZALOM, F. G.—See PITCAIRIN, M. J. 189

The Pan-Pacific Entomologist

Index to Volume 67

- Abies concolor*, 243
Acanthoscelides aureolus, 73
Acanthosomatidae, 159
Acrididae, 81
Akre, R. D., 288
Allen, R. K., 206
Ancyloscelis wheeleri, 171
ant interaction, 288
Anthophoridae, 171
Aphelinidae, 99
aphid-pathogenic fungi, 55
Aphididae, 28, 55, 216
aphids, 28
Apis mellifera, 177
Apoidea, 171
Arachnida, 272
Araeoschizus antennatus blaisdelli, 73
Araneae, 243
Argentina, 216
Arizona, 272
arthropods, 138
Ascomycetes, 251
Ascospaera, 251
Ascospaerales, 251
Asilidae, 177
Aspirhina, 67
 A. alvarengai, NEW SPECIES, 69
 A. bifurca, NEW SPECIES, 67
 A. deceptor, NEW SPECIES, 70
 A. dubitator, 65
 A. spinosa, NEW SPECIES, 70
Asquith, A., 7, 258
Asteraceae, 107
Atractelmis, 195
 A. wawona, 195
atypical sex role behavior, 145
Australian psyllid, 72
Ayala, R., 171

Baccharis, 86, 216
 B. coridifolia, 216
 B. salicifolia, 86
Balling, S. S., 138
Barr, C. B., 195
Barzman, M. S., 99
bees, 115, 251
behavior, 288
bill bugs, 135
biogeography, 206
biological control, 99
biological control agents, 55
 biology, 86
 bird predation, 86
 Blastopsylla occidentalis, 72
 Book review, 75
 British Columbia, 224
 Brown, R. L., 107
 Bruchidae, 73
 Bufo boreas, 135
 Bullock, S. H., 171

California, 99, 107, 243, 272
Caltagirone, L. E., 99
Canthon pilularius, 145
cereal aphids, 55
Chalcididae, 65, 229
Chalcidoidea, 65, 229
chalk brood, 251
Chalybion californicum, 222
Chapco, W., 81
chemosensilla, 86
Clark, W. H., 73
coastal redwoods, 107
Coccinella septempunctata, 224
Coccinellidae, 224
Coccophagus, 99
Coleoptera, 73, 135, 145, 181, 195, 224, 226
competition, 288
Comptonotus modoc, 288
Convolvulaceae, 171
Costa Rica, 124
Cryphocricinae, 119
Curculionidae, 135
cutworm, 20
Cydia pomonella, 189

Daane, K. M., 99
Dahlsten, D. L., 243
Dargida procincta, 20
Dasymutilla dominica, NEW SPECIES, 201
De la Luz Arreguín-Sánchez, M., 171
Delfino, M. A., 216
Delgado-Castillo, L., 181
descriptions, 195
developmental rates, 189
Diprionidae, 243
Diptera, 24, 86, 124, 177
discriminant (function) analysis, 28, 216
disease, 251
distribution, 195
Dominican amber, 200
Douglas-fir tussock moth, 243

- Doyen, J. T., 226
Drosophila (Sophophora) austroheptica, NEW SPECIES, 24
 Drosophilidae, 24
 dung beetle, 145
- Elasmostethus*, 159
E. atricornis, 159
E. cruciatus, 159
E. interstinctus, 159
Elasmucha, 159
E. cordillera, NEW SPECIES, 163
E. flammatum, 159
E. lateralis, 159
 Elmidae, 195
 entomopathogenic fungi, 55
 Entomophthorales, 55
 Ephemeroptera, 206
Epiblema, 107
E. deverrae, NEW SPECIES, 110
E. hirsutana, 107
E. radicana, 107
Eucalyptus, 72
 Eucosmini, 107
 Eulachnina, 28
 Eulophidae, 86
Eupatorium buniifolium, 216
- Falcon, L. A., 189
 fecal pellets, 135
 feeding specialization, 171
 Feng, M.-G., 55
 floral records, 115
 foraging, 177
 forewing pattern, 107
Formica, 177, 288
F. neoclara, 288
F. subpolita, 177
 Formicidae, 288
 fossil, 200
- gall, 86
 geographical distribution, 206
 Goeden, R. D., 86
 grass pest, 20
 Griswold, T. E., 115
 Guertin, D. S., 145
- Halstead, J. A., 65, 229
Halticoptera, 86
 hatchability, 81
 Headrick, D. H., 86
 Heteroptera, 7, 119, 159, 258
 Hodkinson, I. D., 72
 Homoptera, 28, 55, 72, 99, 216
 Hovore, F. T., 226
 Humble, L. M., 224
- Hymenoptera, 65, 86, 115, 171, 222, 229, 243, 251
 immature stages, 86
 insect fauna, 124
 insects, 138
 introduced species, 258
Iridisoma, NEW GENUS, 181
I. acahuizotlensis, NEW SPECIES, 183
- Kamm, J. A., 20
 Kemp, W. P., 177
 Kennett, C. E., 99
 Kondratieff, B. C., 124
- larval growth, 20
Lassius pallitarsis, 288
 Lattin, J. D., 7, 258
 Leguminosae, 171
 Lepidoptera, 20, 107, 189, 243
Leptothorax muscorum, 288
 life history, 86
 Lin, F.-J., 24
 Logan's model, 189
 Lygaeidae, 258
 Lymantriidae, 243
- Madia*, 107
 Manley, D. G., 200
 maternal effects, 81
 mating behavior, 86
 mayflies, 206
 Megachilidae, 115, 251
Megalonotus, 258
Melanoplus, 81
Melitoma marginella, 171
 Melolonthidae, 181
Messiasia, 124
M. decor, 124
M. perpolita, 124
 México, 72, 171, 181
 microhabitat, 195
Microthurge, 115
M. boharti, NEW SYNONYM, 115
M. corumbae, NEW SYNONYM, 116
M. furcatus, NEW SPECIES, 118
M. pharcidontus, 115
M. pygmaeus, 115
 Montana, 55, 177
montium subgroup of *melanogaster*, 24
 Morón, M. A., 181
 morphology, 195
 morphometrics, 216
 multivariate evolution, 28
 Murvosh, C. M., 206
 Mutillidae, 200
 mycosis, 251

- Mydas*, 124
M. rufiventris, NEW SYNONYM, 132
 Mydidae, 124
Myrmica incompleta, 288
 Myrtaceae, 72
- Nabidae, 7
Nabis, 7
N. edax, 7
N. lovetti, 7
 natural selection, 28
 Naucoridae, 119
 Nearctic, 195, 299
Nemomydas, 124
N. lamia, 124
N. loreni, NEW SPECIES, 130
N. sponsor, 124
Neodiprion abietis, 243
 Neotropical, 65, 229
 nest provision, 171
 Nevada, 206
 Noctuidae, 20
 nocturnal clustering, 222
 North America, 159, 258
Notaspidium, 229
N. actum, NEW SPECIES, 237
N. bakeri, 229
N. boharti, NEW SPECIES, 240
N. braziliense, NEW SPECIES, 238
N. burdicki, NEW SPECIES, 236
N. formiciforme, 229
N. giganteum, NEW SPECIES, 232
N. grisselli, 229
N. hansonii, NEW SPECIES, 239
N. lineatum, NEW SPECIES, 239
N. mexicanum, NEW SPECIES, 241
N. minutum NEW SPECIES, 241
N. papuanum, 229
N. truncatum, NEW SPECIES, 238
N. villegasi, NEW SPECIES, 235
 Nowierski, R. M., 55
- O'Neill, K. M., 177
 Olethreutinae, 107
 olive, 99
Omanonabis, NEW GENUS, 7
O. lovettii, NEW COMBINATION, 10
Orgyia pseudotsugata, 243
 Orthoptera, 81
Osmia lignaria propinqua, 251
 Owen, W. R., 73
- Pacific coast, 226
 Pacific Northwest, 20, 258
 Palacios-Chávez, R., 171
Pan-Pacific Entomologist:
 Reviewers for Volume 67, 298
 Table of Contents for Volume 67, 299
- parasitoids, 86
 parasitoids of black scale, 99
 Paulson, G. S., 288
 Pacific Coast Entomological Society:
 Articles of Incorporation, 1
 Bylaws, 2
 Financial statement for 1988–89, 78
 Proceedings, 147
 Publications list, 80, 158
 Sponsoring members for 1989, 77
 Subscription renewal notices, 157
Phaleromela globosa, 226
P. variegata, 226
 phylogenetic characters, 28
 Pickel, C., 189
 Pitcairn, M. J., 189
Plinthisus, 258
P. brevipennis, 258
Pnigalo, 86
 Poinar, Jr., G. O., 200
 Polhemus, J. T., 119
 pollen foraging, 171
 population structure, 288
 Powell, J. A., 107
 pedation, 243
 Prentice, T. R., 222
 prey, 177
 principal components analysis, 28
Prococophagus, 99
Procryphocricos, NEW GENUS, 120
P. perplexus, NEW SPECIES, 120
Protomydas, 124
P. rubidapex, 124
Pseudessigella, 28
P. brachychaeta, 28
 Psylloidea, 72
 Peteromalidae, 86
Pteromalus, 86
- Quiroz-García, D. L., 171
- Ramos-Zamora, D., 171
 rangeland, 177
 Resh, V. H., 138
 Riegert, P. W., 81
 riffle beetle, 195
 Rodríguez-González, 171
 Rust, R. W., 251
- Saissetia oleae*, 99
Salicornia, 138
 salt marsh, 138
 San Francisco bay, 138
 Sands, D. C., 55
 Savary, W. E., 272
Scaphidem pictum, 226
 Scarabaeidae, 145, 177
 Scharen, A. L., 55

- Schlinger, E. I., 243
Scorpiones, 272
seasonal patterns, 138
seasonality, 138
seed bug, 258
seven spotted lady beetle, 224
Shepard, W. D., 195
solitary bees, 171
solitary wasp, 222
Sophophora, 24
Sorensen, J. T., 28
South America, 115
southern California, 86
Sphecidae, 222
Sphenophorus phoeniciensis, 135
spiders, 243
Stenopogon inquinatus, 177
stinkbugs, 159
strigulae, 107
Stygnocoris, 258
survival, 135
Swezey, S. L., 243
systematics, 272
- Tait, S. M., 243
Taiwan, 24
Tapinoma sissile, 288
taxonomy, 115, 159
Tenebrionidae, 73, 226
Tephritidae, 86
Tephritis baccharis, 86
Thomas, D., 159
threshold temperatures, 189
Tiliaceae, 171
- Torchio, P. F., 251
Tortricidae, 107, 189
Trichiini, 181
trophic, 138
tropical deciduous forest, 171
Tsaui S.-C., 24
- Uroctonites*, NEW GENUS, 273
U. giulianii, NEW SPECIES, 278
U. huachuca, NEW COMBINATION, 282
U. montereus, NEW COMBINATION, 281
Uroleucon (Uroleucon), 217
U. (U.) garnicai, NEW SPECIES, 217
U. (U.) tucumani, 216
- Vaejovidae, 272
Vaejovis, 272
V. huachuca, 272
V. montereus, 272
V. sequoia, 272
- Walder, G. P., 222
weevils, 135
Welch, J. L., 124
western North America, 272
western toads, 135
wetlands, 138
white fir, 243
white fir sawfly, 243
Williams, S. C., 272
- Zalom, F. G., 189
Zygomycotina, 55

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THE PAN-PACIFIC ENTOMOLOGIST

Volume 67

October 1991

Number 4

Contents

HALSTEAD, J. A.—New species of <i>Notaspidium</i> Dalla Torre from the Nearctic and Neotropical regions (Hymenoptera: Chalcididae)	229
SWEZEY, S. L., D. L. DAHLSTEN, E. I. SCHLINGER & S. M. TAIT—Predation on Douglas-fir tussock moth (Lepidoptera: Lymantriidae) and white fir sawfly (Hymenoptera: Diprionidae) larvae by captive spiders from white fir in California	243
RUST, R. W. & P. F. TORCHIO—Induction of <i>Ascospaera</i> (Ascomycetes: Ascosphaerales) infections in field populations of <i>Osmia lignaria propinqua</i> Cresson (Hymenoptera: Megachilidae)	251
ASQUITH, A. & J. D. LATTIN—A review of the introduced Lygaeidae of the Pacific Northwest, including the newly discovered <i>Plinthisus brevipennis</i> (Latreille) (Heteroptera: Lygaeidae)	258
WILLIAMS, S. C. & W. E. SAVARY— <i>Uroctonites</i> , a new genus of scorpion from western North America (Scorpiones: Vaejovidae)	272
PAULSON, G. S. & R. D. AKRE—Behavioral interactions among formicid species in the ant mosaic of an organic pear orchard	288
PAN-PACIFIC ENTOMOLOGIST REVIEWERS, Volume 67	298
CONTENTS FOR VOLUME 67	299
INDEX FOR VOLUME 67	301