The Semiaquatic and Aquatic Hemiptera of California
(Heteroptera: Hemiptera)

Edited by ARNOLD S. MENKE

With contributions by Harold C. Chapman, David R. Lauck,
Arnold S. Menke, John T. Polhemus, and Fred S. Truxal.
THE SEMIAQUATIC AND AQUATIC
HEMIPTERA OF CALIFORNIA

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ROBERT L. USINGER initiated this project but did not live to see it finished. Bob was an inspirational teacher and a dear friend to all of us, and it is with great affection that we dedicate this bulletin to his memory.
Contents

Preface, ix
Acknowledgments, x
Abbreviations, xi

INTRODUCTION, A. S. Menke
California Fauna, 1
Habitat and Ecology, 2
  Key to California semiaquatic and aquatic Hemiptera based on
  habitats and habits, 3
Economic Importance, 3
Biology, 4
  Eggs, 4
  Key to eggs and egg-laying habits of California semiaquatic
  and aquatic Hemiptera, 4
Nymphs, 5
  Key to nymphs of California families of semiaquatic and
  aquatic Hemiptera, 6
Parasites and commensals, 6
  Alary polymorphism and migration, 6
  Swimming and surface locomotion, 8
  Respiration, 9
  Stridulation, 10
Collecting Methods and Rearing Techniques, 10
Procedure, 10
Literature, 11
Morphology, 11
  Metathoracic scent glands, 12
Systematics, 13
  Infraordinal names, 13
  Phylogeny and classification, 13
  Key to adults of Nearctic families, 14

FAMILY SALDIDAE, J. T. Polhemus and H. C. Chapman 16
FAMILY HEBRIDAE, J. T. Polhemus and H. C. Chapman 34
FAMILY MESOVELIIDAE, J. T. Polhemus and H. C. Chapman 39
FAMILY HYDROMETRIDAE, J. T. Polhemus and H. C. Chapman 43
FAMILY MACROVELIIDAE, J. T. Polhemus and H. C. Chapman 46
FAMILY VELIIDAE, J. T. Polhemus and H. C. Chapman 49
FAMILY GERRIDAE, J. T. Polhemus and H. C. Chapman 58
FAMILY NEPIDAE, A. S. Menke 70
FAMILY BELOSTOMATIDAE, A. S. Menke 76
FAMILY CORIXIDAE, D. R. Lauck 87
| FAMILY OCHTERIDAE, A. S. Menke       | 124 |
| FAMILY GELASTOCORIDAE, A. S. Menke  | 126 |
| FAMILY NAUCORIDAE, J. T. Polhemus   | 131 |
| FAMILY NOTONECTIDAE, F. S. Truxal   | 139 |

*Literature Cited, 149*
*Index, 163*
Water bugs play an important role in fresh water ecosystems, and knowledge of them is essential for the study of fish biology and for the proper management of hatcheries. Furthermore, there is increasing evidence that certain groups may be utilized in the biological control of mosquitoes. Robert L. Usinger's book, "Aquatic Insects of California," published in 1956, summarized knowledge of the California semiaquatic and aquatic Hemiptera, but within a few years it was obvious that the treatment of some of the families in the book needed improvement. The water bugs were one of Bob's "first loves," and he wanted to see an updated manual on them in print, so in 1962 he approached Harold Chapman and Arnold Menke about doing a California Insect Survey Bulletin. David Lauck and Fred Truxal accepted invitations to join in the endeavor, and work started in mid-1962. Bob was to do the introduction and the Naucoridae and take care of editing the work. As often happens in a multiauthor project, some individuals had more time than others, and by 1967, when the first symptoms of the illness that would cut short Usinger's brilliant career became obvious, much of the bulletin still remained incomplete. After his death, the responsibility for insuring completion of the bulletin fell to Menke. John Polhemus agreed to write up the Naucoridae and help Chapman with the large task of completing the semiaquatic families. The 16-year gestation of this bulletin has resulted in some inconsistencies, but we hope that Bob would have been proud of the result.

Harold C. Chapman is on the staff of the Gulf Coast Mosquito Research Laboratory of the USDA at Lake Charles, La.; David R. Lauck is on the faculty of Humboldt State University, Arcata, Calif.; Arnold S. Menke is with the Systematic Entomology Laboratory, USDA, Washington, D.C.; John T. Polhemus is with the University of Colorado Museum, Boulder, Colo.; Fred S. Truxal is with the Natural History Museum, Los Angeles County, Los Angeles, Calif.
Acknowledgments

We have had the help of many individuals. Jerry A. Powell, University of California, Berkeley, devoted considerable time to the project, especially after Usinger's death. He arranged for the typing of rough drafts and the execution of those illustrations rendered by Celeste Green, also of the University. In addition, Jerry acted as a trouble shooter in many of those areas that plague a work as involved as this has been, and we owe him a special debt of thanks.

The late Carl J. Drake freely gave constructive advice on problems connected with various families in the Gerromorpha. Per Lindskog, University of Stockholm, Stockholm, Sweden; R. H. Cobben, Wageningen, Netherlands; I.M. Kerzher, Zoological Institute, Leningrad, U.S.S.R.; and Randall T. Schuh, American Museum of Natural History, New York, gave advice on special problems in the Saldidae. Margaret Parsons, University of Toronto, Toronto, Canada, and Helen Vaitaitis, Arlington, Virginia, furnished a complete translation of Popov's 1971 book without which it would have been impossible to include much information here about this important new work. Carl Muesebeck, U.S. National Museum, Washington, D.C., also did some translating for us. John Polhemus supplied up-to-date tabulations of total numbers of genera and species for the Gerromorpha and other useful information relating to the introduction. W. Aubrey Crich, Grimby, Canada, furnished the excellent photo of a male Belostoma with eggs. All figures taken from previously published works are acknowledged in the legends. Celeste Green rendered figures 11-12, 67-68, 80, 240-241, and 245-248. Biruta Akerbergs, Smithsonian Institution, drew figures 51-62, and E. Templeton, Los Angeles County Museum, drew figure 267. Figures 17-18, 27-28, 39-41 and 252-265 were drawn by Arnold Menke. The remaining figures are the work of the authors of each chapter. Douglass Miller, Ronald Hodges, and Ted Spilman, Systematic Entomology Laboratory, USDA, Washington, D.C., Robert Denno, University of Maryland and Harold Chapman, Lake Charles, Louisiana reviewed various portions of the manuscript and offered many useful suggestions for improvement. John Lawrence, Museum of Comparative Zoology, Cambridge, Massachusetts, furnished us with a photocopy of a rare Say paper. Karen Menke and Mary Pat Grimmnnitz did all of the manuscript typing. To all of these people we extend our deep appreciation.

We would like to thank the following people who furnished information on types or other critical specimens: Paul H. Arnaud, Jr., Vincent Lee, and Hugh Leech, California Academy of Sciences, San Francisco; Peter Ashlock and George Byers, University of Kansas, Lawrence; Howard Evans, Colorado State University, Fort Collins (formerly at Harvard University, Cambridge, Massachusetts); Richard Froeschner, U.S. National Museum, Washington, D.C.; Wayne Gagné and Frank Howarth, Bishop Museum, Honolulu, Hawaii; Jon Herring, Systematic Entomology Laboratory, U.S.D.A., Washington, D.C.; Ira La Rivers, University of Nevada, Reno; Jack Lattin, Oregon State University, Corvallis; Thomas Moore, University of Michigan, Ann Arbor; Joe Schuh, Klamath Falls, Oregon; Roy Snelling, Los Angeles County Museum of Natural History, California; Roy Danielson, Lunds Universitets Zoologiska Institution, Lund, Sweden; Nils Andersen, Universitetets Zoologiske Museum, Copenhagen, Denmark; C. Lyal, British Museum (Natural History), London, England; A. Kaltenbach, Naturhistorisches Museum, Vienna, Austria; C. Schmitz, Musee Royal de l'Afrique Centrale, Tervuren, Belgium; Bert Gustafsson, Naturhistoriska Riksmuseet, Stockholm, Sweden; and D. Guiglia, Museo Civico di Storia Naturale, Genoa, Italy.
Abbreviations

We gratefully acknowledge the cooperation of the following institutions and owners of private collections for making specimens available for study. The appended abbreviations are used to indicate deposition of the material seen in this study.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Institution/Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>American Museum of Natural History, New York</td>
</tr>
<tr>
<td>PDA</td>
<td>Ashlock Collection, Lawrence, Kansas</td>
</tr>
<tr>
<td>CAS</td>
<td>California Academy of Sciences, San Francisco</td>
</tr>
<tr>
<td>CDFA</td>
<td>California Department of Food and Agriculture, Sacramento</td>
</tr>
<tr>
<td>CNC</td>
<td>Canadian National Collection, Ottawa, Canada</td>
</tr>
<tr>
<td>HCC</td>
<td>Chapman Collection, Lake Charles, Louisiana</td>
</tr>
<tr>
<td>CNHM</td>
<td>Chicago Natural History Museum, Chicago</td>
</tr>
<tr>
<td>CU</td>
<td>Cornell University, Ithaca, New York</td>
</tr>
<tr>
<td>CLH</td>
<td>Hogue Collection, Eagle Rock, California (now in LACM)</td>
</tr>
<tr>
<td>ISU</td>
<td>Iowa State University, Ames, Iowa</td>
</tr>
<tr>
<td>ILR</td>
<td>La Rivers Collection, Verdi, Nevada (now in CAS)</td>
</tr>
<tr>
<td>DRL</td>
<td>Lauck Collection, Arcata, California</td>
</tr>
<tr>
<td>LACM</td>
<td>Los Angeles County Museum of Natural History, Los Angeles</td>
</tr>
<tr>
<td>HLM</td>
<td>McKenzie Collection (now in UCD)</td>
</tr>
<tr>
<td>ASM</td>
<td>Menke Collection (now in LACM)</td>
</tr>
<tr>
<td>NC</td>
<td>Nieser Collection, Utrecht, the Netherlands</td>
</tr>
<tr>
<td>OSU</td>
<td>Oregon State University, Corvallis, Oregon</td>
</tr>
<tr>
<td>JTP</td>
<td>Polhemus Collection, Englewood, Colorado</td>
</tr>
<tr>
<td>SDNHM</td>
<td>San Diego Natural History Museum, San Diego</td>
</tr>
<tr>
<td>JS</td>
<td>Schuh Collection, Klamath Falls, Oregon</td>
</tr>
<tr>
<td>SU</td>
<td>Stanford University, Palo Alto (now in LACM)</td>
</tr>
<tr>
<td>PHT</td>
<td>Timberlake Collection, Riverside, California</td>
</tr>
<tr>
<td>USNM</td>
<td>United States National Museum, Washington, D.C.</td>
</tr>
<tr>
<td>BC</td>
<td>University of British Columbia, Vancouver, Canada</td>
</tr>
<tr>
<td>CIS</td>
<td>University of California, California Insect Survey, Berkeley</td>
</tr>
<tr>
<td>UCD</td>
<td>University of California, Davis</td>
</tr>
<tr>
<td>UCLA</td>
<td>University of California, Los Angeles (now in LACM)</td>
</tr>
<tr>
<td>UCR</td>
<td>University of California, Riverside</td>
</tr>
<tr>
<td>FU</td>
<td>University of Florida, Gainesville, Florida</td>
</tr>
<tr>
<td>KU</td>
<td>University of Kansas, Lawrence, Kansas</td>
</tr>
<tr>
<td>UMMZ</td>
<td>University of Michigan, Museum of Zoology, Ann Arbor, Michigan</td>
</tr>
<tr>
<td>RLU</td>
<td>Usinger Collection (now in CIS)</td>
</tr>
<tr>
<td>ANSP</td>
<td>Academy of Natural Sciences, Philadelphia, Pennsylvania</td>
</tr>
<tr>
<td>BMNH</td>
<td>British Museum (Natural History), London, England</td>
</tr>
<tr>
<td>CSU</td>
<td>Colorado State University, Fort Collins, Colorado</td>
</tr>
<tr>
<td>CJD</td>
<td>Drake Collection (now in USNM)</td>
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<tr>
<td>Mus. Helsinki</td>
<td>Helsingin Yliopiston Eläintarhu, Helsinki, Finland</td>
</tr>
<tr>
<td>Mus. Eberswalde</td>
<td>Institut für Pflanzenschutzforschung Kleinmachnow, Eberswalde, German Democratic Republic</td>
</tr>
<tr>
<td>Mus. Brussels</td>
<td>Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium</td>
</tr>
<tr>
<td>LSL</td>
<td>Linnean Society of London, London, England</td>
</tr>
<tr>
<td>Mus. Turin</td>
<td>Museo ed Istituto di Zoologia Sistematica Turin, Italy</td>
</tr>
<tr>
<td>Mus. Genoa</td>
<td>Museo Civico de Storia Naturale, Genoa, Italy</td>
</tr>
<tr>
<td>MCZ</td>
<td>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts</td>
</tr>
<tr>
<td>Mus. Paris</td>
<td>Muséum National d'Histoire Naturelle, Paris, France</td>
</tr>
<tr>
<td>Mus. Vienna</td>
<td>Naturhistorisches Museum, Vienna, Austria</td>
</tr>
<tr>
<td>Mus. Stockholm</td>
<td>Naturhistoriska Riksmuseet, Stockholm, Sweden</td>
</tr>
<tr>
<td>Mus. Bucharest</td>
<td>Musée d'Histoire Naturelle Grigore Antipa, Bucharest, Romania</td>
</tr>
<tr>
<td>Mus. Naples</td>
<td>Musée Zoologico della Universita di Napoli, Naples, Italy</td>
</tr>
<tr>
<td>Mus. Tartu</td>
<td>Tartu State University, Tartu, Estonian S.S.R.</td>
</tr>
<tr>
<td>Mus. Copenhagen</td>
<td>Universitetets Zoologiske Museum, Copenhagen, Denmark</td>
</tr>
<tr>
<td>Mus. Oxford</td>
<td>University Museum, Oxford, England</td>
</tr>
<tr>
<td>Mus. Halle</td>
<td>Zoologische Institute, Martin Luther Universität, Halle, German Democratic Republic</td>
</tr>
<tr>
<td>Mus. Berlin</td>
<td>Zoologisches Museum der Humboldt Universität, Berlin, German Democratic Republic</td>
</tr>
<tr>
<td>Mus. Hamburg</td>
<td>Zoologisches Museum, Hamburg, Germany</td>
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</tbody>
</table>
INTRODUCTION

A. S. Menke

The California insect fauna is represented by 14 of the 16 major families of Hemiptera that are associated with aquatic environments. The missing elements are the Pleidae and Helotrephidae whose tiny members swim upside down. Pleids may eventually be found in the state because *Neopiea striola* (Fieber) is known in Utah (Drake and Chapman, 1953a), and the genus also occurs in northwestern Washington (Gagné, 1967). Because of their small size they may have escaped notice by collectors. The Helotrephidae are pantropical. Five of our families are totally aquatic leaving the water only during migratory dispersal flights: Nepidae, Belostomatidae, Corixidae, Naucoridae, and Notonectidae. Three families live on the surface film of water and are collectively called “water striders”: Hydrometridae, Veliidae, and Gerridae. The remaining six groups, the Saldidae, Ochteridae, Gelastocoridae, Hebridae, Mesoveliidae, and Macroveliidae, are littoral, dwelling on the damp shores of streams and ponds; however, some members of the last three families venture onto the water surface at times.

Two other families occur in California whose members are essentially terrestrial, but which have species that are sometimes found near water: the Leptopodidae (a saldid relative) and the Dipsocoridae. We do not treat these two groups in this bulletin. *Patatus spinosus* (Rossi), an adventive leptopodid from the Old World (Usinger, 1941a), is found in the Central Valley, and San Francisco Bay area. It occurs under rocks and debris remote from water, and sometimes on logs near streams. The body of this bug is covered with prominent spines which make recognition easy. *Cryptostemma usingeri* Wygodzinsky is a very tiny (1.5 mm long) dipsocorid found under stones along the shores of Hot Creek in Inyo County (Usinger, 1956). According to Usinger, a larger, undescribed species occurs at a hot spring in Death Valley.

1. In writing this section I have used some material from the introductory part of Usinger’s chapter on the semiaquatic and aquatic Hemiptera in his book “Aquatic Insects of California” but most of the information included here is new or extensively rewritten.

CALIFORNIA FAUNA

California has a diverse hemipterous fauna. Boreal elements common to the northern United States and Canada are found on the north coast and in the mountains (Transition Zone and above). Great Basin species are found on the east slope of the Sierra Nevada, including parts of Lassen County and in the Owens Valley. Species typical of the Sonoran Region occur along the Colorado River bordering Arizona. Of particular interest are the relict forms found in isolated springs in the southern deserts. These springs are mere vestiges of more extensive lakes and streams of former times. That the aquatic Hemiptera were not very different during the recent past, however, is indicated by species in the La Brea and McKittrick tar pits (Pierce, 1948) (Belostomatidae, Nepidae, and Notonectidae). These forms differ only slightly, if at all, from present-day species in the same area. The age of these fossils is presumably about 10,000 years.

Hungerford (1958) and Jaczewski and Kostrowicki (1969) mapped and discussed world patterns of distribution of the semiaquatic and aquatic Hemiptera. According to the latter authors, approximately 2,900 species are known, of which about 920 occur in the Holartic Region. Jaczewski and Kostrowicki did not include the approximately 230 species of Saldidae in their world survey; therefore, the total number of water bugs exceeds 3,100. The Nearctic fauna is richer than the Paleartic because of a larger infiltration of tropical elements. Jaczewski and Kostrowicki pointed out that the absence in North America of mountain ranges with an east-west orientation permits tropical forms to invade deeply into the Nearctic Region. As Table 1 shows, California has 113 species, or less than one-third of the 415 species known in America north of Mexico, although it has more than half of the genera. The disparity between the numbers of species in California and the ecologically less diverse eastern United States is probably due to the deserts which have presented a barrier to the tropical forms that have invaded the east.
TABLE 1: COMPARISON OF THE NUMBER OF SEMIAQUATIC AND AQUATIC HEMIPTERA IN AMERICA NORTH OF MEXICO AND IN CALIFORNIA

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of genera</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>North America</td>
<td>California</td>
</tr>
<tr>
<td>Saldidae</td>
<td>10</td>
<td>5(1)</td>
</tr>
<tr>
<td>Hebridae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Mesoveliidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Hydrometridae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Macroveliidae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Veilidae</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Gerridae</td>
<td>8</td>
<td>5(1)</td>
</tr>
<tr>
<td>Nepidae</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Belostomatidae</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Corixidae</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Ochteridae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Gelastocoridae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Naucoridae</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Notonectidae</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Pleidae</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>65</td>
<td>36(2)</td>
</tr>
</tbody>
</table>

Slater’s (1974) analysis of the water bug fauna of the northeastern United States allows comparison of the California fauna with an eastern area of comparable size. The number of genera is about the same in the two areas, but California only has two-thirds the number of species found in the northeast. The difference is found primarily in the Gerridae and Corixidae which are represented by twice as many species in the northeastern United States.

Holarctic species are known only in the Corixidae and Saldidae, and five in the latter family occur in California.

We have been unable to confirm the presence in California of 15 species recorded from the state by others (figures in parentheses on Table 1). Most of those in the Gerrormorpha are based on records published by the late Carl J. Drake. It is known that he occasionally mislabelled material, and this may explain our inability to confirm the presence in California of some of the species attributed to the state by Drake.

HABITAT AND ECOLOGY

The aquatic and semiaquatic Hemiptera occupy a wide variety of habitats from salt water pools to mountain lakes and from hot springs to large rivers. In general, they are intermediate stage predators in the food chains of their respective communities. Some, such as the surface striders, appear to be complete masters of their environment, whereas others, such as the relatively defenseless Corixidae, are generally preyed upon. Corixids are partly responsible for the primary conversion of plant material into animal food, but it is now clear that at least some of them cannot subsist on the “flocculent bottom ooze” alone but must take animal food, such as small mosquito larvae, as part of their diet.

The aquatic medium is a more restricted habitat than the terrestrial environment. Certainly the lives of aquatic organisms are more vulnerable to the activities of man and other agents than terrestrial life. This is particularly true of desert spring dwellers, and the continued existence of a few California species is rather fragile because they are confined to certain Death Valley hot springs. In fact, the following bugs could be classed as endangered species: the naucorid, *Ambrysus funebris* La Rivers (Travertine Spring and Cow Creek); and the belostomatids, *Belostoma saratogae* Menke and *Lethocerus angustipes* (Mayr) (Saratoga Spring). The *Ambrysus* is found in several small adjacent hot springs, but the species is flightless. Saratoga Spring is the only known habitat for the *Belostoma*, and, with the possible exception of hot springs in nearby Ash Meadows, Nevada, it contains the only North American population of *Lethocerus angustipes*, a Mexican species separated by a thousand air miles from the Death Valley colony. In the last few years Saratoga Spring has become a popular tourist spot, and swimmers have removed much of the aquatic vegetation from the main pool, thus considerably reducing the available habitat for the two belostomatids and other endemic life. Few *Lethocerus*
have been sighted in recent years, and the other inhabitants of the pool are much less abundant now than in the early 1950's when the hot spring was generally unknown to the public.

Although each genus of water bugs occupies a characteristic habitat and exhibits distinctive behavior patterns, such information cannot be easily organized in a useful way. Hungerford (1920) gave a "habitat key" which was updated by USinger (1956) for the California fauna. It is reproduced here with additional modifications, but, even so, it must be considered only a rough guide because several different groups inhabit similar situations or one group may be found in several different habitats. These problems occur primarily among littoral forms.

KEY TO CALIFORNIA SEMIAQUATIC AND AQUATIC HEMIPTERA
(Based on habitats and habits)

1. True aquatics, living beneath the surface film ....... 2
   Surface or shore bugs .................................. 11
2. Swimming venter up with long oarlike hindlegs ....... 3
   Notonectidae ........................................... 3
   Swimming dorsal up ................................... 4
3. Resting on submerged objects or at surface film, not in equilibrium with water, rising toward surface film when not swimming or holding onto substrate. Notonecta
   Resting poised in midwater, in equilibrium with water, not floating upward when resting. Buenoa ......... 5
4. Airstore replenished by breaking surface film with pronotum; usually feeding on bottom ooze ......... 6
   Corixidae ........................................... 5
   Airstore replenished by breaking surface film with tip of abdomen or by apical abdominal appendages; predatory forms ....................................... 6
5. In saline or brackish waters. Trichocorixa and some Corixella
   In fresh waters ..................................... other Corixidae ......... 5
6. Airstore replenished by breaking surface film with tip of unspecialized last visible abdominal segment. Nauocorididae ......... 7
   Airstore replenished by long, slender siphon or short, retractile straps at end of abdomen. ......... 8
7. Living among rocks in streams and lake margins. ....... Ambrusus
   Living amidst aquatic vegetation in ponds and springsoste .. Pelocoris ......... 7
8. Awkward slow swimmers; airstore replenished by long, slender, siphon tube ......... 9
   Nepidae ........................................... 9
   Strong swimmers; airstore replenished by retractile airstrips Belostomatidae ....................................... 9
9. Living in streams, clinging to rocks or hiding in watercress and other aquatic plants. Abedus
   Living in ponds and lakes ................................ 10
10. Eggs laid on backs of males. Belostoma
    Eggs laid on stems of rushes and other emergent vegetation. Lethocerus ......... 10
11. Surface bugs, walking or skating on surface film. ....... 12
    Shore bugs or on floating mats of vegetation (may run or walk on water when disturbed). ......... 17
12. Living on marginal waters of ponds and streams ....... 13
    Living on open water surface ................................ 14
13. Slow moving forms on long, stilllike legs in protected places
    Hydrometridae ................................ Hydrometra
    Rapid moving forms on short legs in open places; gregarious. resting on surface film near shore. Velidae ........ Micravelia
14. Living on ocean. Halobates
    Living on fresh waters ................................ Gerridae ................... Gellastocoridae
15. Living on ponds, lakes, and quiet waters of streams
    Gerridae .................................... Gerris, Trepobates
    Living on swiftly flowing streams, gregarious. ......... 16
16. Living on riffles of streams and small rivers. ......... Velidae
    Rhyzogelidae ........................................... 17
    Living on open water, usually of large rivers. ......... 18
    Gerridae .................................... Micravelia
17. Flying littoral forms. Saldidae ................................ Saldula, Pentacora, Micravelia
    Living in the open .................................. 19
    Hidden in cryptic, littoral situations. .................... 22
18. Found on mosses and other shore plants or on floating mats of vegetation. ......... 20
    Littoral forms living on sand or mud. .......... 21
19. Walking on water when disturbed. ......... 20
    Notonectid bugs seem to offer promise in the biological control of mosquitoes, for when given a choice, they apparently prefer mosquito larvae over other prey (Ellis and Bordon, 1970; Toth and Chew, 1972; Gittelman, 1974a). Bay (1974) experimented with Notonecta unifasciata Guérin-Ménéville and found that 10 to 12 adults in a 100-gallon tub that contained mosquito immatures gave nearly 100% control over mosquito emergence.

ECONOMIC IMPORTANCE

Water bugs of both the Nepomorpha and Gerrormorpha feed on mosquito larvae and adults. Jenkins (1964) gave an annotated list of over 80 references representing nine families of bugs that are mosquito predators. Notonectid bugs seem to offer promise in the biological control of mosquitoes, for when given a choice, they apparently prefer mosquito larvae over other prey (Ellis and Bordon, 1970; Toth and Chew, 1972; Gittelman, 1974a). Bay (1974) experimented with Notonecta unifasciata Guérin-Ménéville and found that 10 to 12 adults in a 100-gallon tub that contained mosquito immatures gave nearly 100% control over mosquito emergence.
Unfortunately, in the field, notonectids prefer fairly permanent waters while mosquito larvae are found often in temporary situations. The Old World nepid genus *Cercotmetus* Amyot & Serville was cited by Laird (1956) as a potentially valuable natural mosquito control agent. Members of this genus feed almost exclusively on wrigglers, and one adult can keep an area of five to six yards radius around itself almost clear of mosquito larvae. Some *Cercotmetus* are flightless and cannot easily escape from a pond and this enhances their usefulness.

The Old World belostomatid genus *Limnogeton* Mayr is important as an obligate feeder on freshwater snails that serve as intermediate hosts of human and veterinary schistosomiasis (Voelker, 1966). Some members of the New World genus *Belostoma* also feed on snails (Cullen, 1969) but the importance of this genus in biological control has not been investigated except in mosquito control (see Bay, 1974).

Many water bugs have little importance to man other than as natural food for fish. Aquatic families can be a nuisance in swimming pools, especially biting forms such as *Notonecta*, *Belostoma*, and *Lethocerus*, which may be attracted to lights around pools, and subsequently find refuge in their waters. Bugs of the families Corixidae and Belostomatidae are eaten by people of certain cultures, and corixids are extensively used in commercial pet foods for turtles and tropical fish. The fisheries industry sometimes must contend with large predatory bugs like *Lethocerus* (Wilson, 1958).

Jansson (1977) demonstrated that corixids can be used as indicators of water quality.

### BIOLOGY

In general, water bugs overwinter as adults, lay eggs in the spring and develop during the summer. Only a few exceptions are noted in the following chapters. Most bugs have five nymphal instars, but some species have only four, especially in *Microvelia*. Eggs are laid in a wide variety of places, each usually characteristic for a particular species or genus. Unlike many aquatic insects, water bugs do not deposit their eggs freely either on the water surface or beneath it. Instead the eggs are glued to various objects, including the backs of males, as in *Belostoma* and *Abedus*. Bug eggs can usually be recognized by the relatively tough, hexagonally reticulate chorion and by buttonlike or peglike micropylar processes. They are usually oval, occasionally spindle-shaped, and sometimes stalked.

**Eggs.** Usinger (1956) gave an incomplete, preliminary key to the eggs and egg-laying habits of California forms. Since then Cobben (1968) has described and figured eggs belonging to all of the families found in our state, allowing Usinger’s key to be updated.

### KEY TO EGGS AND EGG-LAYING HABITS OF CALIFORNIA SEMIAQUATIC AND AQUATIC HEMIPTERA

1. Eggs attached to substrate by a stalk ........................................ 2
   Eggs not stalked, inserted in plant tissues or glued to substrate .......... 3

2. Oviposition terrestrial; egg length about six times as long as greatest diameter, brown, with longitudinal fluting at middle, the tapered end reticulate (fig. 4) ........................................... *Hydrometra* 
   Oviposition aquatic; egg shorter, suboval, white, with the micropylar end briefly produced as a small nipple (fig. 3) ............................................................................. *Corixidae*

3. Two threadlike filaments at micropylar end, longer than the egg itself (fig. 2); egg inserted in submerged plant tissue with only the filaments projecting .................................................. *Nepidae* 
   Without threadlike filaments .......................................................... 4

4. Micropylar end of egg with a small cylindrical, bent, process (figs. 6.7); laid under water .......... *Notonectidae* 
   Micropylar end without a bent projection ........................................ 6

5. One end of egg with smooth, flattened, caplike, oval area; eggs inserted in plant tissue, the flat cap exposed (fig. 6) ............................................................................. *Buenoa* 
   Egg rounded at both ends, without smooth, flat area; eggs inserted in or glued to substrate (fig. 7) .................. *Notonecta*

6. Egg elongate, micropylar end curving up to a flat, exposed operculum, remainder of egg inserted in emergent stems (fig. 5) ................................................................. *Mesoveliidae* 
   Egg shape variable but without broad, flat micropylar operculum; usually not inserted in plant tissue .......... 7

7. Egg inserted in plant tissue .......................................................... some *Saldidae* 
   Egg not inserted in plant tissue .......................................................... 8

8. Egg attached at one end, perpendicular to substrate; laid in clusters, the eggs contiguous . *Belostomatidae* .......... 9

### FIGS. 1–7

Egg glued lengthwise to leaves of aquatic or shore plants, floating or submerged objects, or laid free on shore

9. Eggs laid on the folded hemelytra of male (fig. 8) .......................... *Belostoma*

Belostoma

Eggs laid in a mass above water on stems and other objects (fig. 9) .......................... *Lethocerus*

10. Egg oval, length about twice width or shorter .......................... 11

Egg elongate-oval or spindleshaped, length at least two and a half times width .......................... 14

11. Egg length twice width; glued to objects under water .......................... *Nausorinae*

Egg length less than twice width; laid out of water in sand or mud, or at bases of grass clumps .......................... 12

12. Egg laid in clumps of grass and roots .......................... *Ochteridae*

Egg laid in sand or mud .......................... *Gelastocoridae*

13. Egg laid among sand grains .......................... *Gelastocoris*

Egg laid in small holes in mud several feet from shore, beneath stones, the female “guarding” the eggs .......................... *Nerthra*

14. Egg laid just beneath the surface film on floating or emergent objects .......................... 15

Egg laid out of water at the bases of clumps of grass and other vegetation, or glued to moss .......................... 16

15. Egg length usually about one mm; often laid in rows. the individual eggs not contiguous .......................... *Gerridae*

Egg length less than one mm; laid individually or in irregular clusters .......................... *Veliidae*

16. Micropylar end of egg nipplelike .......................... 17

17. Egg spindle-shaped .......................... *Macroveliidae*

Orovelia

Egg elongate oval .......................... *Hebridae*

18. Egg length usually less than three times width, somewhat tapering or bent towards micropylar end which usually has a striate or reticulate “respiratory area,” one micropyle .......................... *Saldidae*

Egg length slightly more than three times width, spindle-shaped, narrowed towards both ends (fig. 1), reticulate zone absent, about 7 micropyles arranged in a circle .......................... *Macroveliidae*

**Nymphs.** Most nymphs of semiaquatic and aquatic bugs have one-segmented tarsi. This distinguishes them from apterous adults found in some families of the Gerrormorpha which have two or three segments, at least on the mid and hindlegs. The exceptions are nymphs of Ochteridae and Leptopodomorpha which have two. The tarsi of the latter appear one-segmented because the first segment is very small (Cobben, 1978). Herring and Ashlock (1971) and De Coursey (1971) provided keys to the nymphs of the North American families and subfamilies of Hemiptera. The following key to the nymphs of California semiaquatic and aquatic Hemiptera is based partly on these works. The nymphal keys to genera...
and species in Usinger (1956) have been incorporated in the appropriate family sections that follow. In most cases, the family key below should work for any instar, but fifth instars are easiest to key because some structures are difficult to see in the smaller, earlier nymphs. Trichobothria are rather prominent, individual sensory setae which occur in regular patterns on the heads of all Leptopodomorpha and Gerromorpha (fig. 11). They are absent in the Nepomorpha. In some groups these setae may be difficult to distinguish if the head is generally hairy. The location, number and pattern of the dorsal abdominal scent gland openings are easily seen and often are diagnostic.

**KEY TO NYMPHS OF CALIFORNIA FAMILIES OF SEMIAQUATIC AND aquatic hemiptera**

1. Antennae short, usually concealed beneath head where they often lie within pockets, but visible from above in Ochteridae; head without trichobothria; true aquatic and some shore bugs... (Nepomorpha) ........................................ 2

2. Antennae long, conspicuously exposed; face with three pairs of trichobothria (fig. 11); surface film or shore dwellers... 9

3. Labium triangular, unsegmented, but transversely sulcate (fig. 110); foretarsus one-segmented, scooplike (fig. 113); three pairs of abdominal scent gland openings present, located between terga III-IV, IV-V, and V-VI... Corixidae

4. Labium beaklike, three- or four-segmented; foretarsus not scooplike; scent gland openings absent, or present only between terga III-IV. ........................................ 3

5. Scent gland openings present (may be inconspicuous). .... 4

6. Scent gland openings absent. .................................. 5

7. Scent gland opening double; body flattened. ............. 6

8. Scent gland opening single; body strongly arched dorsally; tiny forms two mm or less; not known from California... Pleidae

9. Metapleura prolonged posteriorly around hindcoxae as flat plates, margins arcuate, ciliate (fig. 80)... Belostomatidae

10. Metapleura not prolonged. ........................................ 6

11. Apex of abdomen with a pair of long respiratory filaments that form a siphon channel; body long, slender.... Nepidae

12. Abdomen without filaments; body elongate oval or oval and flattened. ........................................ 7

13. Body strongly arched dorsally, elongate oval; hindlegs long, tibiae flattened, oarlike, tarsus apparently without claws; aquatic, swimming upside down... Notonectidae

14. Body oval, flattened; hindlegs not unusually long or oarlike, tarsus with two large claws; liturral. ................... 8

15. Forefemora enlarged, raptorial; head without spines; beak short, stout, reaching only to forecoxae... Gelastocoridae

16. Forefemora not enlarged; front of head with a crown of stout, upright spines; beak long, reaching hindcoxae... Ochteridae

17. A pair of abdominal scent gland openings located on suture between terga III and IV.. (Leptopodomorpha) .................. 9

18. Abdominal terga without scent glands, or with a single, median opening on tergum IV or on suture between terga IV-V.. (Gerromorpha) ........................................ 10

19. Tergum IV without scent gland opening... 11

20. Tergum IV with scent gland opening... 13

21. Head longer than thorax, very slender; claws apical... 12

22. Head not longer than thorax; claws subapical... (Terebrantia) Hydrometridae

23. Face with a median longitudinal line or groove... Velidiidae

24. Face without a line or groove... (Terebrantia) Gerridae

25. Antennal segment 1 length equal to or shorter than least interocular distance; venter of head with a groove for reception of beak... Hebridiidae

26. Antennal segment 1 length longer than least interocular distance; venter of head without a groove... (Nepomorpha). 14

27. Inner eye margins convergent anterad; legs spiny... (Mesoveliidae)

28. Inner eye margins parallel; legs without spines... (Macroveliidae)

**Parasites and commensals.** Aquatic and semiaquatic bugs are parasitized by immature stages of water mites belonging to several families. The saclike juvenile mites are attached to the exoskeleton of the host, and they can be very numerous; Riley, et al. (1957) counted over 500 *Hydrachna belostomae* Riley on a specimen of *Belostoma flumineum* Say. Jones (1967) and Smith and Oliver (1977) listed the known bug-mite associations, and the general life cycle of these mites was described by Harris and Harrison (1974) and Smith and Oliver (1977). Harris and Harrison (1974) found that of two mite species studied, one preferred attachment to the dorsum of its corixid host, while the other was most common on the legs of the host. Ectoparasitic fungi of the order Laboulbeniales occur on corixids, veliids, and mesoveliids (Poison, 1957) and macroveliids (Benjamin, 1967). Colonial ectocommensal Protozoa of the order Peritrichida (Lust. 1950) are common on many Nepomorpha, and leeches have been found on the belostomatid genus *Abedus* (Menke, 1960). Presumably the last are also commensals. Stewart, et al. (1970) have shown that water bugs play an important role in the dispersal to new habitats of small aquatic organisms such as algae and fungi.

A variety of endoparasites attack water bugs. Larsen (1938) and Southwood and Leston (1959) recorded nematode worms from corixids and notonectids, respectively, and Poison (1957) listed several species that infest gerrids, veliids, and nepids. Hymenopterous parasites of the families Sceionidae, Mymaridae, and Trichogrammatidae attack the eggs of aquatic and semiaquatic Hemiptera. These have been tabulated by Hoffmann (1932b) and Poison (1957), Cobben (1965a) described an unknown microorganism found in *Mesovelia* eggs and nymphs that he believed to be a symbiont. Poison (1957) has listed a variety of Protozoa that have been found in water bugs.

**Alary polymorphism and migration.** Alary polymorphism is expressed two ways in bugs: the degree of wing development (macroptery, brachyptery, and aptery) and flight muscle polymorphism. Wing polymorphism
is common in the water strider families. It occurs to some extent in most of the true water bugs (Nepomorpha) also, and although some naucorids are nearly apterous (micropterous), completely wingless forms are unknown. In the Gerromorpha apterous forms are often much more common than winged individuals, and consequently adults are sometimes mistaken for immatures. Among California semiaquatic Hemiptera, only the marine gerrid genus Halobates and the macroveliid Oravelia are always wingless in the adult, although winged forms of the latter may yet be discovered. The thoracic morphology of wingless forms usually differs considerably from that of winged individuals, and since the latter are sometimes less commonly collected, some genera are largely defined on the characteristics of the apterous forms.

The evolutionary significance of flightless forms is complex, but the essential consequence of brachyptery is that it insures continued usage of the immediate resource. Generally, flightless morphs are found in permanent habitats such as rivers, lakes, and large ponds. Reduced flight capability in dwellers of such habitats is favored by natural selection. Brachyptery insures that at least a part of the population will survive, and it may also allow more energy to be allocated to the process of reproduction instead of having to share it with flight muscle and wing developmental processes. In his studies of flight muscle polymorphism in corixids, Young (1965b, 1969) found that flightless morphs had definite advantages over macropters. They could swim faster and they lived longer when starved. These and other aspects of flightlessness have been discussed in detail by Guthrie (1959), Brinkhurst (1959, 1963), Larsén (1970), Vepsäläinen (1971b), Scudder and Meredith (1972) and Andersen (1973).

In temporary habitats the ability of at least a part of the population to migrate is favored by selection. True migration usually occurs at the start of adult life according to Southwood (1962), who defines it as movement away from the home territory at which time the individual does not respond normally to stimuli such as food, a mate, or shelter. Southwood feels that the prime evolutionary advantage of migration lies in enabling a species to keep pace with habitat changes; flight is often obviously necessary to reach hibernation sites, for dispersal to new habitats, and for gene exchange. In the last analysis the production of macropters should be proportional to the instability of the habitat.

During the summer months in the Sacramento and San Joaquin Valleys, corixids (Corisella) and to a lesser extent, belostomatids (Lethocerus), are frequently attracted to lights, sometimes in large numbers. Presumably these bugs are drawn to lights during migratory movements. The generally held belief that bugs fly only on moonlit nights is not always true. Callahan (1974) found gerrids flying at night in the San Francisco Bay area when there was no moon.

Considerable work has been done on wing polymorphism in Gerris, especially in Europe. Generally univoltine Gerris species are monomorphic. Those inhabiting continuous waters (rivers) are nearly always apterous, while univoltine species living on isolated habitats (ponds, lakes) are usually macropterous (Brinkhurst, 1959; Vepsäläinen, 1973). Obviously river dwellers can reach new habitats simply by skating and wings are unnecessary for dispersal. Vepsäläinen indicated that the only univoltine Gerris that exhibit wing polymorphism are those species that inhabit semipermanent situations, while this phenomenon is characteristic of bivoltine Gerris that inhabit unstable habitats. In these, dimorphic forms occur mainly in the first generation (spring-summer) which lives under unstable conditions. Usually the second generation (overwintering) is macropterous because wings are needed for migration to hibernation sites in the fall and to new habitats in the spring. For further discussion of the adaptive significance of wing polymorphism in Gerris, and especially the various hypotheses that have been proposed to explain it, see Järvinen and Vepsäläinen (1976).

A full understanding of the factors that produce wing or muscle polymorphism has not been achieved. The studies and experiments of contemporary workers, most of whom have confined their researches to Gerris, have produced conflicting theories of the causes of these phenomena. It seems probable that a variety of environmental cues act separately or in concert to control a "genetic switch" mechanism which in turn leads to alternative developmental pathways for the wings. The best developed hypothesis is that of Vepsäläinen (1974, a,b). According to him, wing length in Gerris is controlled by photoperiod acting on the genetic switch, which may be influenced also by temperature under certain conditions. Vepsäläinen (1974a) indicated that the genetic switch is formed by two alleles at one locus, or by a pair of super genes, the dominant allele being the gene for shortwing. Basically then, two factors can control polymorphism in Gerris: (1) a genetic switch mechanism, and (2) various environmental cues (day-length, temperature, etc.) which affect the switch through hormonal agents. Galbreath's (1975) studies of wing polymorphism in Mesovelia (Mesoveliidae) reveal that temperature, not photoperiod, is the prime environmental influence in this bug, and her statement that the "causation of morphs in gerroids is not likely to be explicable on the basis of any one environmental variable" is undoubtedly true.
Some authors (e.g., Southwood, 1961) have theorized that short-winged forms are "juvenile" adults (neoteny) that fail to develop fully because of an imbalance between juvenile and other hormones, but this is discounted by Brinkhurst (1963) at least in Gerris, because of the absence of juvenile characters in apterous and brachypterous morphs. Most Hemiptera have five nymphal instars, but some Microvelia species may have four or five. The adults resulting from four instars are always apterous and Southwood feels that these forms are really juveniles with "adult" characters. i.e., paedomorphic.

Flight muscle polymorphism in aquatic and semiaquatic bugs is common but less well known than wing polymorphism. Although reduced indirect flight muscles are often associated with brachyptery or aptery, reduction also occurs in macropterous individuals. Until recently most authors have explained the situation in terms of muscle degeneration, but according to Young (1965b) and Scudder (1971a) nonflying macropterous corixids are produced simply because normal muscle development is arrested in the teneral and post-teneral adult; low temperature triggers arrested flight muscle development, at least in corixids. In subsequent field studies, Scudder and Meredith (1972) found that adults of Cenocorixa with juvenile flight muscles occurred only in the fall. Experimentally they demonstrated that indirect flight muscles remained undeveloped if the bugs were kept in water maintained at 5°C. Arrested muscle development is not a one-way process. Scudder and Meredith found that muscle development was initiated if they subjected cold water bugs to water temperatures of 15°C continuously for more than 24 hours.

An interesting behavior involving the wings occurs in some macropterous rhagadotarsine and trepobatine Gerridae and some Mesoveliidae which break off the membranous portion of the forewings (Torre-Bueno, 1908; Jordan, 1951). The break occurs along a transverse cleavage line in gerrids. Two theories were proposed by Torre-Bueno to explain this autotomy. One is that after bugs have migrated to a new habitat they no longer need their wings. It is well documented that macropters in Gerris resorb their flight muscle after spring populations are established (Brinkhurst, 1959; Andersen, 1973) and this fact adds credence to this theory. Torre-Bueno's second hypothesis is that wings hinder copulation, and a mechanism has developed enabling them to be broken off.

Swimming and surface locomotion. True water bugs propel themselves through the water with synchronous, oarlike movements of the hindlegs as in the Corixidae, Notonectidae, Pleidae, and Naucoridae, or by synchronous stroking of the middle and hind pair of legs, each pair working alternately, as in the Nepidae and Belostomatidae. During periods of vigorous swimming, belostomatids stroke with both pairs of legs in unison. The Nepidae are the weakest swimmers. Their slender middle and hindlegs are not designed for efficient underwater propulsion; thus, nepids swim with slow, awkward movements. The legs of naucorids are also not very well adapted for swimming; consequently these bugs must move them rapidly to swim. The corixids, notonectids, and belostomatids are excellent swimmers. The hind tibiae and tarsi are broad, flattened, and fringed with long swimming hairs. The hairs collapse on the return stroke, minimizing drag, but spread as a result of pressure on the propulsive stroke. The belostomatids, especially members of the genus Lethocerus which have the broadest swimming legs of all the bugs, are the strongest swimmers. The corixids are probably the most agile, being able to svwee abruptly. The notonectids, which swim upside down, move with graceful sweeps of their oarlike hindlegs.

Residence on the surface film by members of the Gerromorpha is made possible by water repellent hydrofuge hair piles on the tarsi and sometimes also the tibiae. By laying the tarsi flat on the film, the insect maximizes weight distribution. The claws are wettable (Baudoin, 1955) and in the most specialized families, the Velidae and Gerridae, they are subapical and can be folded against the tarsal surface. In Gerris the claws lie at the base of a notch into which they can be withdrawn when on the water surface (Brinkhurst, 1960).

The water surface offers the advantage of very weak resistance to movement. This is accentuated by its horizontal plane which reduces the energy required to overcome the force of gravity. However, a completely nonwettable leg would make it difficult for a surface dweller to gain "traction." According to Baudoin (1955), Darnhofer-Demar (1969), and Andersen (1976), semiaquatic bugs overcome this problem by using their wettable claws to penetrate the surface film, thus gaining resistance for movement. Part of the tarsal hair also penetrates the film (Andersen, 1976).

Most of the surface bug families walk slowly on the surface film, each leg moving alternately with its mate in a normal "tripod" walk. However, gerrids "skate" or row on the surface film by synchronous, oarlike movements of the middle legs (Caponigro and Eriksen, 1976). During this time the hind tarsi contribute little to the forward motion. Their purpose is mainly to provide support and directional stability. There are two kinds of movement in Gerris: gliding and leaping; steering is accomplished by unequal strokes of the midlegs while the hindleg on the inside of the turn acts as a pivotal point (Caponigro and Eriksen. 1976). Veliids of the
subfamilies Rhagoveliinae (Bacon, 1956), Veliinae (Andersen, 1976), and Haloveliinae (Kellen, 1959) also propel themselves with synchronous rowing movements of the middle pair of legs. Occasionally some Microvelia row also, but their gait is normally tripodal.

The physical means by which skating surface forms produce forward thrust has only recently been explained. Brinkhurst (1960) suggested that in Gerris “the surface film becomes ‘packed up’ behind each tarsus during the rowing stroke and the resulting build-up of surface pressure imparts a forward thrust.” This mechanism was clarified by Darnhofer-Demar (1969) and Andersen (1976). To initiate the acceleration phase, the middle tarsi are abruptly pressed down on the water surface which results in a circular surface wave. The middle tarsi then push backward against the wave at a speed greater than that of the wave. This heightens the wave crest giving the legs a better abutment for imparting forward thrust.

Genera in the veliid subfamily Rhagoveliinae have special tarsal modifications that aid in propulsion. The apical tarsal segment of the midleg is deeply cleft (fig. 10B). In Rhagovelia and Trochopus Carpenter this cleft contains a pair of plumes, each composed of numerous featherlike branches, and a pair of modified bladelike claws (fig. 10A, C). According to Cobben (1968) the plumes are highly modified parempodia, but Andersen (1976) disagrees. In repose the plumes are folded within the tarsal cleft, but when rowing the plumes unfold, fanlike, and project through the surface film, thus serving as paddles or “swimming fans” (Torre-Bueno, 1907; Andersen and Polhemus, 1976; Andersen, 1976). A few other veliid genera possess modified tarsal structures which probably aid in their progression over the water surface.

Brinkhurst (1960) described an intriguing phenomenon in Velia Latreille: after struggling to make headway against a strong current without progress, bugs would stop all movement, but instead of being swept downstream, they suddenly shot forward. Linsenmair and Jander (1963) found that in Velia the saliva discharged from the beak acts as a detergent, lowering the surface tension. The insect is thus carried forward (or sideways or in an arc) by the contracting surface film. Direction of movement apparently is controlled by the highly mobile beak (Andersen, 1976). He said that “expansion skating” is found in adults and nymphs and that it is also known in Microvelia and Rhagovelia.

Respiration. Each of the truly aquatic families has a distinctive type of respiration which will be discussed in detail in their respective chapters. Most water bugs are dependent on atmospheric oxygen obtained at the water surface through tubes (Nepidae), air straps (Belostomatidae), the tip of the abdomen (Notonectidae, most Naucoridae), or the pronotum (Corixidae). Air layers, whose size and distribution may vary from one species to another, adhere to the bodies of these insects when they are submerged. A large part of the stored air is usually concealed dorsally between the wings and the abdominal dorsum, and another part is exposed on the ventral surface of the body where it is held in place by hydrophuge hairs. Bugs with these exposed ventral airstores can extract dissolved oxygen from the water because the airstore acts as a physical gill. In most Nepomorpha the airstores gradually diminish in volume and must be periodically renewed at the water surface. This type of respiration has been reviewed in detail by Thorpe (1950) and Popham (1960). Parsons (1974) terms the nepids and belostomatids “siphon” bugs and the others “air-bubble” bugs in reference to their mode of obtaining air. Nymphs generally have modes of respiration different from adults (Parsons, 1971).
A few naucorid bugs derive their oxygen from the water and are thus independent of atmospheric oxygen and can remain submerged indefinitely. The Old World naucorid \textit{Aphelocheirus} Westwood is the classic example, but there is good evidence that the New World naucorid \textit{Cryptocricos} also uses this mode of respiration (Parsons and Hewson, 1975). These bugs respire exclusively with dissolved oxygen obtained through a very thin, submicroscopic, permanent, exposed air layer or "plastron." The plastron is retained by short, densely packed hairs, which do not allow it to diminish in volume; under optimal conditions (well-aerated water) the bug does not have to renew its stored air at the surface because enough dissolved oxygen is obtained by means of the gill effect of its plastron. A few intertidal saldids also respire through a plastron (Polhemus, 1976c).

Some surface bugs such as \textit{Rhaboevelia} (Veliidae) and members of the Gerridae occasionally enter the water to escape predators or to lay eggs. These bugs are covered with a fine hair pile that traps a layer of air when they dive under water. Presumably when submerged they respire by means of this air layer which appears as a silvery sheen over the body.

\textit{Stridulation}. Sound production in the Gerromorpha is known only in the Veliidae, but a number of authors have mentioned hearing songs in most of the aquatic families of the Nepomorpha (Leston and Pringle, 1964). Stridulatory structures have been described in the Corixidae, Notonectidae, and Nepidae, and the corixids have received considerable study.

\textbf{COLLECTING METHODS AND REARING TECHNIQUES}

True aquatic bugs should be collected with a net that has a straight outer margin (hoop D-shaped). This maximizes the surface area of the bottom that can be effectively covered while dragging the net over it. If the net is to be dragged through tangled roots, coarse debris, or other objects that would rip the net material, the bag should be shrouded with an outer shield of canvas open at the end to permit the flow of water. In some situations a metal screen may be more suitable. A subaquatic light trap such as the one designed by Hungerford, Spangler, and Walker (1955) can be an effective collecting device. A fine mesh fishnet held between two people and pulled through a pond will capture belostomatids and other large bugs. Stream dwellers that hide under stones, such as \textit{Abedus} and \textit{Ambrusus}, can be collected by holding the net on the bottom downstream and dislodging the bugs above the net by turning over rocks. Water striders and open water aquatic forms, such as backswimmers, that do not live on the bottom can be caught with a simple round hoop net equipped with a nylon bag. For shore bugs and species that live at the water's edge, painstaking search must be made beneath rocks, and in moss and other marginal plants. Small bugs that hide in mosses and floating vegetation can be exposed by pressing the plants underwater. This forces the bugs to the surface. Cryptic forms such as ochterids, hebroids, and certain saldids are often most easily collected by splashing water on the bank to flush them out of crevices. Some kind of suction tube may be an effective collecting aid for these small littoral forms. A simple white dipper can be used to capture small bugs such as hebroids and veliids that hide on the underside of overhangs along stream and pond margins, or for reaching into tree holes and similar crevices. By depressing the dipper slowly beneath the water, bugs will be carried into it by the water flow. An atomizer loaded with ethyl acetate or 70% ethanol is an effective device for "shooting" fast running saldids. Berlese funnels can also be used for plant and debris inhabitants.

Any water bug may be preserved in alcohol, but most study collections consist of pinned or pointed specimens. In most cases it is useful to have some specimens dried and others in alcohol. The latter are ideal for dissection and for careful study under the higher powers of the dissecting microscope. When pinning long-legged forms like gerrids and nepids, the legs should be held close to the body with paper retainers or bracing pins until dry.

Water bugs, like other aquatic insects, should be transported alive in containers with moist water plants rather than in jars of sloshing water. They do well in home aquaria if cared for daily. However, the mortality is usually quite high during successive molts, and very few species have been reared through many generations. For the true aquatics a constant supply of fresh air is desirable and can be maintained by bubbling air through a line from an aquarium aerator. Shore bugs do well in small jars containing a substrate of plaster of Paris darkened with lampblack. Excess moisture must be avoided, lest the small nymphs become entangled in the surface film. Most bugs must be kept in individual containers to avoid cannibalism and to keep track of cast skins.

\textbf{PROCEDURE}

In a group that has attracted as much taxonomic attention as the water bugs, it is surprising to learn that certain aspects of good taxonomic procedure have often
been ignored. We found that the deposition of type material and the sex of the holotype were frequently not given in the original description. In some cases lectotypes have never been selected and designated, even for well-known forms, leading one to question the accuracy of some North American species interpretations. Because of this, we have had several goals beyond the minimum requisites of the CIS Bulletin series. One was to provide complete data on holotypes and lectotypes, including sex and deposition, so far as possible. In spite of our efforts, this information is incomplete for a few California species. Second, we wanted to indicate the type-species for each genus, and in the case of subsequent type-species designation, the authority and date. Third, we have endeavored to give complete lists of all generic and specific synonyms for our taxa; however, we have not provided the type data mentioned above for these names.

In general we give complete distribution records, i.e. place, date, number of specimens, collector, depository, only for species with few California records. There is some inconsistency from family to family in the completeness of such data. Our arrangement of families and subfamilies conforms roughly to current ideas of phylogeny. Species are alphabetical.

Our keys to genera and species include all United States forms wherever practical. We have also included Usinger’s (1956) nymphal generic keys which have been modified in some cases. Many of the illustrations used here are original, but we have borrowed some of the fine figures found in Usinger’s “Aquatic Insects of California,” following his original suggestion that we do so.

Initially, Usinger encouraged us to make the introductory sections for each family as broad in scope as possible, and we have thus included a broad array of information that should have wide appeal. Special attention has been given to problems of family definition in the Gerromorpha, an area of water bug systematics that needs much more study.

LITERATURE

Important literature pertaining to each family is cited within each chapter. However, there are a number of general works that cover a broad spectrum of biology, ecology, morphology, and taxonomy that may be of interest to students of the California fauna. These are Hungerford (1920), Blatchley (1926), Poisson (1924, 1951, 1957), Southwood and Leston (1959), and Miller (1971). These papers plus those of Macan (1965) and Nieser (1968, 1975), which include keys to the species of Britain, the Netherlands, and the Guyana region, respectively, contain useful bibliographies. Keys to the aquatic and semiaquatic Hemiptera of other parts of the United States and adjacent areas are: Alayo (1967, 1971), Cuba; Brooks and Kelton (1967), central Canada; Bobb (1974), Virginia; Chapman (1958) and Herring (1950-51), Florida; Ellis (1952) and Gonsoulin (1973-75), Louisiana; Froeschner (1949, 1962), Missouri; Hilsenhoff (1975), Wisconsin; and Wilson (1958), Mississippi. Most of these also contain biological data.

Popov’s (1971) book on the Nepomorpha is a milestone in aquatic hemipterology, but it is entirely in Russian.2 The book contains six chapters which cover the taxonomic history of each family, geology and geography of fossil forms, comparative external and internal morphology, history of higher classification of the suborder Hemiptera in general and of the semiaquatic and aquatic bugs in particular, classification of the Nepomorpha families including fossil forms, and finally, the phylogeny of the Nepomorpha. The extensive bibliography contains many references of east European workers that are little known to westerners. His history of classification and treatment of extinct forms is comprehensive and current (many previously unknown fossil forms are described, representing families, genera, and species), and these sections along with the chapter on phylogeny are particularly valuable. In his view the Nepomorpha, Gerromorpha, and Leptopodomorpha arose in the Triassic, and he feels that the ancestral stocks of the modern superfamilies all had diverged by the end of the Jurassic.

MORPHOLOGY

Figures 11-12 show the external structures of a saldid. Other bugs vary in details, but these drawings will suffice for a general understanding of water bug morphology. The beak, which is labial in origin, consists of four segments; however, the first is often quite short and usually concealed so that the beak appears to be three-segmented in many groups. The area of the face between the eyes is often called the interoculus or interocular space. The anteculus is the facial area projecting in front of the eyes that bears the beak. Some authors use the term metaxyphus for the metasternum, but we prefer the latter term. The first visible abdominal sternum is part of the true second segment, thus some authors refer to it as sternum I and so on. The last sternum, true VII, is often called the subgenital plate. The lateral plates of the abdomen which are often reflexed upward are usually referred to by hemipterists by the collective term “connexiva.” We have used the more descriptive terms paratergite and parasternite for these plates.

2. An English translation can be obtained from Margaret Parsons, University of Toronto, Toronto, Canada.
The genital capsule is usually concealed and is in the ninth segment. Male genitalia are used for the separation of species in most groups of aquatic Hemiptera. The genital segment can be removed in dried specimens by softening the tip of the abdomen in a solution of phenol (1/3), water (1/3), and alcohol (1/3). A dissecting needle with its tip bent should be inserted at the side of the eighth segment and then twisted and drawn out, pulling the genital segment. For specimens preserved in alcohol the operation is simpler. Genitalia, including the claspers and aedeagus, are best studied in fluid, but in a few cases the structures are hard enough for study in a dried condition. The genitalia can be glued to a card beneath the specimen, but those of some water bugs should be mounted in balsam on microscope slides or between cover slips on small cards or points beneath the specimen. Perhaps the best method of preserving genitalia is in polyethylene microvials containing glycerine. These are stoppered with long, cylindrical silicone rubber stoppers, and they are held on the pin below the insect.

Measurements of body length and width can be made with a metric rule, but comparative measurements of various structures should be made with an ocular micrometer. Total length is the over-all length of the insect in one plane, excluding appendages. Measurements of antennal segments do not include the small, intercalary, ringlike segments seen in some forms.

**Metathoracic scent glands.** A short review of these glands, which are often referred to in family character discussions in the Gerromorpha, is appropriate because they are sometimes difficult to locate. According to Brindley (1930) most Hemiptera have two glands in the metathorax that empty into a single reservoir. The reservoir empties via two ducts, each of which opens beside one metathoracic coxa. Each opening, or ostiole, is sometimes surrounded by tufts of setae which presumably help to disseminate secretions. In some water bugs the two ostioles have migrated from their primitive lateral position to a more median location on the metasternum. As such they are often referred to as metasternal scent glands. China (1955) discussed their evolution in water bugs in some detail. In the Veliidae the two ostioles are close to one another, and they are difficult to see except under very high magnification or dissection, but their median location on the sternum is pinpointed by a pair of channels (appearing suturelike or groovelike) that extend laterad to a point on the pleuron in front of the metacoxa (fig. 13). Presumably the function of these channels is dissemination and...
evaporation of secretions. These evaporative channels may terminate laterally with prominent, raised lips that are tufted with setae. In the Gerridae the pair of osti-oles are united in a common opening usually termed the "omphalium." The omphalium is often elevated or tuberclelike (see cross-section in Brinkhurst, 1960 and photos in Andersen, 1975). Most gerrids have lost the lateral evaporative channels and possess only the omphalium (fig. 14). However, even the omphalium is absent in two subfamilies of the Gerridae (Matsuda, 1960 and Andersen, 1975). Cobben (1968, 1978), Carayon (1971), and Andersen (1975) offer considerable evidence that the evolutionary progression just outlined is incorrect. They feel that the median scent gland opening without lateral channels is the primitive condition. Thus, lateral channels develop and eventually the osti-oles move apart laterally in more advanced bugs. The function of the scent glands is not known. Most authors imply a defense action by calling them "stink glands," but they may also be involved in the production of pher-omones. Brinkhurst (1960) suggests that in Gerris they may produce the oil film that helps waterproof the body. Staddon and Thorne (1973) suggested that the glands of the naucorid Ilyocoris cimicoides (Linnaeus) as well as those of some other water bugs, may produce a chemical that disinfects the outer body surface. See Cobben (1978) for a current review of possible gland functions.

SYSTEMATICS

Infraordinal names. Since Dufour (1833), hemipterists have traditionally split the suborder Hemiptera into three divisions: the Geocorises or land bugs, the Amphibricorises or semiaquatic bugs, and the Hydrocorises or true water bugs. The names Gymnocerata and Cryptocerata of Fieber (1851) are sometimes used for the latter two groups. It has become increasingly clear that these divisions do not reflect the relationships of the major phyletic lines. Furthermore, these names are not formed from generic names. Leston, Pendergrast, and Southwood (1954) made the first modern attempt to rectify both situations when they proposed dividing the Geocorises into two groups, the Cimicorpha and Pentatomomorpha. These infraordinal "morpha" names have gained acceptance by most hemipterists and Stys and Kerzhner (1975) in their excellent review of the higher taxa of the Heteroptera, recognize seven such groups. Three of these are of concern here: the Leptopodomorpha, the Gerromorpha (=Amphibricor-ises, Gymnocerata), and the Nepomorpha (=Hydrocor-ises, Cryptocerata). Only the Leptopodomorpha, which contains the Saldidae and a few closely related families, needs some discussion here. Traditionally the saldids and their allies have been associated with the Gerromorpha, but contemporary workers have disassociated the Saldidae from the water striders and their relatives in varying degrees. Cobben (1968) implied infraordinal status for the Saldidae and its close relatives, and Stys and Kerzhner (1975) used the infraordinal name Lep-topodomorpha (first proposed by Popov, 1971) for these bugs. This rank was accepted by Cobben (1978).

The Leptopodomorpha and Gerromorpha have long conspicuous antennae which are inserted in front of the eyes. The Nepomorpha have short antennae that are inserted beneath the eyes and usually concealed from view. All truly aquatic bugs belong in the Nepomorpha, and two families of littoral bugs, the Ochteridae and Gelastocoridae, are also included. The antennae of the Ochteridae and the exotic naucorid genus Apheloch-eirus, though short, are partially exposed to view.

Phylogeny and classification. Hemipterists disagree as to the phylogenetic relationships of the three infra- orders and their component families. Until recently, the work of China (1955) was the basic contemporary discussion of this subject. He regarded the Gerromorpha and Nepomorpha as having evolved from separate, littoral ancestral stocks. According to his view a saldidlike ancestor gave rise to the Gerromorpha and an ochterid-like group led to the Nepomorpha. Parsons (1962), after a study of the head capsule, cast doubt on the correctness of placing the saldids at the base of the Gerromorpha. Cobben (1968, 1978) put forth the novel idea that the ancestral stock of the Gerromorpha gave rise to all other Hemiptera, a theory that is contrary to previous ones. Popov (1971) feels that the Gerromorpha and Nepomorpha arose from a common, saldidlike ances- tor, and he regards the Saldidae as the most primitive living family of Hemiptera.

Clearly, the higher classification of the water-loving families of Hemiptera is not yet completed. Cobben
(1968) indicated his belief that the Leptopodoidea, the leptopodomorph superfamily in which the Saldidae is placed, is a “natural group sharply defined from others” and that it is equivalent to other major divisions such as the Gerromorpha and Nepomorpha. Stys and Kerzhner (1975) excluded the Saldidae from the Gerromorpha and placed the family in the Leptopodomorpha, an action that seems warranted based on the studies of Cobben, Popov, Parsons, Carayon, and others.

Exclusion of the Saldidae makes the Gerromorpha a more homogeneous group. However, Cobben (1968) suggested that the single superfamily Gerroidea may have to be divided into two or more superfamilies. Most of the gerroid families contain a few genera whose characters transcend accepted family boundaries, and it is apparent that more investigation of family limits is necessary. On a world basis, separation of the Velidae and Gerridae is particularly difficult (China, 1957).

The phylogeny and classification of the Nepomorpha has received more attention than that of the Gerromorpha and Leptopodomorpha, but the relationships and origins of the various families are by no means settled. Popov (1971), like China, derived the Nepomorpha from ochteridlike ancestors, but he feels that the latter arose from a saldidlke stock. Both authors regard the ochterids and gelastocorids as the most primitive families of the Nepomorpha. However, Parsons (1966a, b, c), who has been making detailed studies of the comparative morphology of the families of the Nepomorpha, suggested that the Ochteridae and Gelastocoridae are more specialized than admitted by Popov and China, and that they may even have become littoral secondarily. The close relationship between the Nepidae and Belostomatidae is well documented, and they are placed in the superfamily Nepoidea. Parsons regarded the siphon respiration, the rather simple food pump and epiphiaryngeal filter, the unmodified antennae, and the narrow labium to be generalized characters of the Nepoidea; she suggested that the superfamily was the first offshoot of the littoral ancestor of the Nepomorpha. Rieger (1976) and Popov concur.

The phylogeny of the Corixidae has puzzled phylogeneticists. Börner (1904) proposed a separate division for the family, the Sandaliorrhyncha. However, it is now well established that the Corixidae belongs in the Nepomorpha. Both Parsons (1966a) and Popov (1971) indicated divergence of the Corixidae after the Nepoidea on their phylogenetic dendrograms.

Cobben tentatively divided the Nepomorpha into five superfamilies, the Nepoidea for the Nepidae and Belostomatidae, the Corixoidea for the Corixidae, the Notonectoidea for the Notonectidae, Pleidae and Helotrephidae, the Naucoroidea for the Naucoridae, and the Ochteroidea for the Ochteridae (and presumably the Gelastocoridae). Parsons (1966a) placed the ochterids and gelastocorids on the same evolutionary branch in her phylogenetic dendrogram. Popov (1971) recognized the same superfamilies as Cobben except that the name Gelastocoroidea is used in place of Ochteroidea. On the basis of the gross structure of the food pump, Parsons (1972a) recognized three main assemblages within the Nepomorpha: the Nepoidea, the Corixoidea, and a group consisting of the Notonectidae, Naucoridae, Gelastocoridae, and Ochteridae. She further subdivided the last assemblage into two groups, one of which consists of the Ochteridae and Gelastocoridae. Thus there is close agreement between Cobben, Popov, and Parsons as far as major groupings are concerned, and in this bulletin we have adopted the five superfamilies recognized by Cobben and Popov: Nepoidea, Corixoidea, Notonectoidea, Naucoroidea, and Ochteroidea.

Rieger (1976) in his intensive study of the Ochteridae and the cladistic relationships of the Nepomorpha superfamilies, has arrived at a classification that differs little from the schemes of Cobben, Parsons, and Popov. He used the name Telmatobia for the Gelastocoridae, and recognized an additional superfamily, the Aphelocheiroidea, for the naucorine genus Aphelocheirus.

### KEY TO ADULTS OF NEARCTIC FAMILIES OF SEMIAQUATIC AND AQUATIC HEMIPTERA

| Antennae shorter than head, inserted beneath eyes, not visible from above (figs. 79, 84, 240-241, 251, 272) except in Ochteridae (fig. 239): head without trichobothria: true aquatics and a few shore bugs ... (Nepomorpha) | 2 |
| Antenna longer than head, inserted in front of eyes and plainly visible from above (fig. 11); head with 3 pairs of trichobothria (fig. 11); shore bugs and surface bugs | 9 |
| Beak short, triangular, unsegmented, scarcely differentiated from rest of head (fig. 110); front tarsus one-segmented, scoolike, fringed with rake setae (fig. 113) | 3 |
| Beak cylindrical, with at least three visible segments; front tarsus neither scoolike nor fringed | 4 |
| Apex of abdomen with a pair of flat, retractile, respiratory appendages, or with a slender, cylindrical respiratory siphon composed of two filaments ... (Nepoidea) | 5 |

**1. Antennae shorter than head, inserted beneath eyes, not visible from above (figs. 79, 84, 240-241, 251, 272) except in Ochteridae (fig. 239): head without trichobothria: true aquatics and a few shore bugs ... (Nepomorpha).**

**2. Antenna longer than head, inserted in front of eyes and plainly visible from above (fig. 11); head with 3 pairs of trichobothria (fig. 11); shore bugs and surface bugs.**

**3. Beak short, triangular, unsegmented, scarcely differentiated from rest of head (fig. 110); front tarsus one-segmented, scoolike, fringed with rake setae (fig. 113).**

**4. Beak cylindrical, with at least three visible segments; front tarsus neither scoolike nor fringed.**

**5. Apex of abdomen with a pair of flat, retractile, respiratory appendages, or with a slender, cylindrical respiratory siphon composed of two filaments.**

**6. (Nepomorpha)**
4. Apex of abdomen with a nonretractile, cylindrical siphon (fig. 79); tarsi one-segmented .............. Nepidae
   Apex of abdomen with a pair of flat, retractile airstrips (fig. 109); tarsi two or three segmented .......... Belostomatidae
5. Ocelli present; middle and hind legs without fringes of swimming hairs; shore bugs (Ochteroidea) .............. 6
   Ocelli absent; hind legs and usually the middle legs fringed with long swimming hairs; water bugs ................... 7
6. Front legs slender, similar to middle legs, not raptorial; beak reaching to or beyond hind coxae; antennae exposed ......... Ochteridae
   Front legs raptorial, femora broadened; beak short, not reaching hind coxae; antennae concealed from above .... Gelastocoridae
7. Front legs raptorial, femora broadened (fig. 266); body dorsoventrally flattened . (Naucoroidea) .......... 8
   Front legs slender, femora not broadened (fig. 272); dorsum of body strongly convex . (Notonectoidea) ........... 14
8. Elongate forms with long, oarlike hind legs; claws of hind tarsus greatly reduced, inconspicuous; body 5 mm or longer .......... Notonectidae
   Oval forms with all legs similar; hind legs with two well-developed claws; body less than 3 mm long ........ Pleidae
9. Hind coxae large, transverse, broadly joined to thoracic pleura (fig. 12); wing membrane with four to five similar cells (fig. 21) (Leptopodomorpha; Leptopodoidea) .......... 10
   Hind coxae small, conical or cylindrical, freely rotatory in sockets; wing membrane usually without veins, or if cells present, not similar . . . (Gerromorpha, Gerroidea) .......... 11
10. Claws of at least front tarsus inserted before apex .......... 12
11. Hind femur short, distal end scarcely, if at all, surpassing end of abdomen; midlegs inserted about midway between front and hind pair; metasternum with a pair of closely spaced scent gland openings from which a pair of groove-like or suturelike channels extend laterad, ending on pleura in front of hind coxa (fig. 13); face usually with a median, longitudinal sulcus or shiny glabrous line ....... Veliidae
   Hind femur long, distal end greatly exceeding end of abdomen; midlegs inserted closer to hind legs than to forelegs; metasternum or metasternal area with single median, scent gland opening, lateral channels absent (fig. 14); face usually without median groove or line ........... Gerridae
12. Head as long or longer than thorax along middorsal line; body long, slender, cylindrical ........... Hydrometridae
   Head not exceeding combined lengths (along middorsal line) of pronotum and scutellum (or pronotum alone in wingless forms); body short, stout .......... 13
13. Tarsi two-segmented; venter of head with longitudinal groove for reception of beak .......... Hebridae
   Tarsi three-segmented; venter of head without groove .......... Hebridae
14. Inner margins of eyes converging anteriorly; femora with at least 1 or 2 stiff, erect, black bristles; winged forms with an exposed, bipartite scutellum .......... Mesoveliidae
   Inner margins of eyes arcuate, diverging anteriorly and posteriorly; femora without erect bristles; winged forms with scutellum concealed by pronotum .......... Macroveliidae

5. Except in Rhagovelia and Trochopus which have the last tarsal segment of the mid leg deeply cleft, the cleft containing featherlike structures (fig. 10); and in Husseyella Herring which has four blade-like appendages in place of claws on the last tarsal segment of the mid leg.
Saldids are oval or elongate-oval bugs with moderately long legs fitted for running and jumping. The head is short, declivant and the beak is apparently three-segmented, the tip reaching back to the hindcoxae or beyond. Ocelli are present except in the Old World genus *Aepophilus* Signoret, and the compound eyes are large and notched at the inner posterior angle. The long antennae are four-segmented. The hemelytra are divided into a clavus and corium, and the membrane has veins which delimit 4 or 5 cells, at least in macropterous forms. A single scent gland ostiole is located on the sternum of the metathorax except in the genus *Aepophilus*. The hindcoxae are large and transverse, and all tibiae are generally spinose. The tarsi are three-segmented, and the claws are apical. The abdominal spiracles are located ventrally, and a pair of eversible glands are found at the posterolateral corners of the seventh sternum (absent in *Aepophilus*) (Cobben, 1957; Drake, 1962). Nymphs of many saldids have a pair of “larval organs” on abdominal sternum III which open mesad of the spiracle (Cobben, 1957). These glands persist as rudimentary form in some adults. Male saldids have paratergites II and III modified into a clasping organ which is used to hold the female during copulation (see Cobben, 1957; Leston, 1957). Most shore bugs are dull black or brown, but some species have conspicuous white, yellow, or even reddish markings.

The family Saldidae contains 19 genera and about 230 species. The present classification of the family is based on the work of Cobben (1959, 1961) who recognizes three subfamilies: Aepophilinae, Chiloxanthinae, and Saldinae. The first of these is a monotypic Old World group, but the other two are widespread. Cobben (1971) established a fourth subfamily for the fossil genus *Leptosalda* Cobben, and Popov (1973) proposed the Saldoniinae for a new fossil genus, *Saldonia* Popov. The intertidal dwarfbugs of the genera *Onania* Horvath and *Corallocoris* Cobben, although related to the Saldidae, have been placed in a separate family, the Omaniidae, by Cobben (1970). Polhemus (1976c) gave an excellent review of the biology and systematics of the Saldidae and related forms.

The Saldidae is now generally regarded as one of the most primitive families of living Hemiptera (Mivamoto, 1961; Parsons, 1962, 1963; Popov, 1971). Although the saldids have been associated with the water strider families in past classifications, most evidence indicates that Cobben’s (1965b, 1966, 1970) placement of the family in the Leptopoidea is correct. Seudder’s (1959) suggestion of a relationship between the saldids and mesoveliids has been discounted by Gupta (1963a), Cobben (1968), and others. The Saldidae have structures that are found nowhere else in the Hemiptera: the eversible glands of the seventh sternum, the peculiar male coupling device of the second and third paratergites (present in Omaniidae also), and the presence of both an r-m and an m-cu crossvein in the hindwing, for example.

The Saldidae is a very difficult group taxonomically. The generic division of the family has changed little since the work of Reuter (1912), although several additional genera have been described. Generic limits are not settled and several species complexes, especially in *Salidula*, continue to be problems for specialists in the family. No comprehensive revision of the North American species has been published since Uhler’s (1877) work, but Hodgden’s (1949a) unpublished thesis is a comprehensive survey of the Nearctic forms. Regional treatments of the Saldidae containing keys are Chapman (1962) for Nevada, Schuh (1967) for the Great Lakes Region, and Brooks and Kelton (1967) for the Prairie Provinces of Canada. Drake and Hoberlandt (1951) published a family checklist but it contains serious nomenclatorial errors. The family is a nomenclatorial morass because of the many varietal and color form names that have been proposed, and because some of the older names have been ignored. This is especially a problem in the Old World, but because some European species are Holarctic and occur in California, we have attempted to present correct synonymies for these forms. Particularly useful in checking old saldid names are the works of Reuter (1888, 1896) and Stichel (1960).

As their common name implies, most saldids are
littoral, inhabiting lake shores, beaches, and stream banks. However, the variety of habitats utilized by the Saldidae is much wider, ranging from the intertidal zone to dry land far from water and even to the moss on the trunks of rain forest trees. A few ocean shore dwellers may be submersed by the tide for several hours and these saldids can almost be considered as aquatics. In fact, the Marine Bug, *Aeophillus*, lives most of its life under water (Brown, 1960). Cobb (1968) and Lindskog (1975) hypothesized that ecological radiation in the Saldidae has been from semiaquatic to terrestrial environments. Terrestrial species are predominantly in the Saldinae which contains the most advanced forms morphologically. Because the littoral species are in general very quick, running or flying at the slightest disturbance, and the secretive forms are very difficult to detect, these bugs are rarely taken by the general collector and are poorly represented in most collections.

Habitat preference varies markedly with season. Observable population densities are highest during the reproductive period, which for many Nearctic species is confined to spring or early summer. These populations are usually restricted to firm, moist substrates having stable moisture conditions. Later in the season, during the migratory phase, the same species range onto much drier ground, sometimes far from water. Lindskog (1968) showed that the ability of *Saldula saltatoria* (Linnaeus) to keep its water content above a critical value varied by a factor of 5 to 6 over the imaginal life period. and is reflected in an ability to invade a greater variety of habitats. This behavior pattern with respect to moisture content of the habitat substrate is strongly developed in a number of North American species including most Salda species, *Saldula saltatoria*, and especially *S. bouchevillii* (Provancher) which is found on dry ground late in the summer, paralleling the habitat sequence often noted for the Old World species *S. orthochila* (Fieber).

California species of *Pentacora* prefer saltwater habitats. The genus *Saldula* is the largest in the family and most of the California saldids belong in it. Our 21 species collectively inhabit most fresh water and some salt or brackish water littoral habitats. Only some brine and alkaline situations lack *Saldula* species. The Holarctic *S. pallipes* (Fabricius) is eurytropic, inhabiting a great variety of habitats and life zones. Members of one primarily tropical species group in *Saldula* are largely saxicolous, living on large stones or rock walls rising from the water.

*Saldula villosa* (Hodgden), *luctuosa* (Stål) and *fernaldi* Drake are exclusively salt marsh species and are regularly washed by high tides. Presumably all undergo submersion for many hours without ill effects, but this has been confirmed only for the last species which was studied in Oregon by Stock and Lattin (1976) (as *S. palustris*). Brown (1948) observed tidal submergence in the Old World species, *Saldula palustris* (Douglas). In California Lane and Gustafson (1969) found that *Saldula fernaldi* was driven to the tops of *Spartina* stems by the rising tide, but Polhemus (unpublished notes) confirmed tidal submergence in this species at Tomales Bay, Marin Co. Brown's studies and those of Stock and Lattin indicate that these bugs can tolerate submergence for up to 14 hours in the case of *S. palustris* and up to 9 hours in the case of *S. fernaldi*.

Species of the genus *Salda* are mostly slow to fly, and are often brachypterous. They live in damp meadows among sparse grasses. While they are usually found at low to moderate elevation, some species are found at timberline.

The saldid species that have colonized the intertidal zone span all three subfamilies and range from primitive to specialized, hence it is apparent that they have independently invaded this habitat, and that most or all intertidal saldids are derived from littoral ancestors (Polhemus and Evans, 1969).

Saldids are probably best described as predators or scavengers. Most feed on organisms found in the damp surface layers of the substrate. There are few published notes on feeding behavior. Ekblom (1926) saw *Saldula saltatoria* feed on fly larvae both above ground and in the soil. Lindskog's (1968) observations on the same species agreed with those of Ekblom and he added enchytraeid worms as a food source and noted that chironomid midges resting or stuck on the ground were an important food source for this and other saldids. Polhemus has reared fourth and fifth instar nymphs of several saldid species to adult on a damp soil substrate augmented with a variety of soft-bodied insects which were readily accepted. Hungerford (1920) kept saldids on a diet of dead flies, and Wiley (1922) reared two species on dead flies, mirids, and cicadellids. Ussinger (1956) reared saldids on katydids, and Rimes (1951) found that they will feed on their own eggs.

The ability of saldids to leap many times their body length is attributable to the large, transverse posterior coxae. All saldids are morphologically similar with respect to leg structures, including tarsi and claws. Saldids that inhabit open areas such as sandy or muddy shores, stones, or tide flats usually run rapidly over the surface, then leap when disturbed and simultaneously take to wing, flying some distance before landing. Bugs that hide in cryptic habitats tend to exhibit reduction of flight wings and a lessened propensity to jump. *Micrantha utahensis* Drake & Hottes, which inhabits mouse tunnels in dense grass, scarcely moves when disturbed. The final step in this reduction progression is exhibited by some intertidal saldid species: *Enalosalda*
mexicana (Van Duzee) has the flight wings reduced to small membranous strips, and the hemelytra are coriaceous; Aepophillus has the elytra reduced to short triangles and the flight wings are absent.

Wing polymorphism is a common phenomenon in saldids with several forms often occurring together in the same population. The degree of wing development is so variable that such terms as submacropterous and semibrachypterous are often used. The reduction in flight wings is accompanied by a reduction in thoracic musculature, resulting in a narrowed pronotum, and a greater body width with respect to length. Wing polymorphism has not been seen in the truly intertidal saldids.

Macropterous saldids are strong fliers. Many records of Saldula opiparia Drake & Hottes in California are from light traps, and Micracanthia humilis (Say) has been taken in Kansas in both black light and white light traps. Saldula species have been taken on ships lying offshore (Drake and Viado, 1952; Polhemus, 1968). There is considerable evidence that a substantial exchange of species took place across the Bering Strait area (Oman and Krombein, 1968).

The life histories of Saldula pallipes and Salda lugubris (Say) (as Saldula major) were studied by Wiley (1922). The eggs were laid at the base of the grass blades or inserted through them. The egg of Saldula pallipes was 0.6 mm by 0.15 mm, elongate cylindrical, one end broadly rounded, the other end much smaller, tapered and dorsally arched. The eggs hatched in 7 to 9 days and required 16 days to pass through the 5 instars, each instar being of about equal duration. The egg of Salda lugubris was about twice as large, 1.2 mm x 0.3 mm, of the same shape, and required about 12 days to hatch. About 17 days was required to reach the imago stage, and the duration of each nymphal instar was about equal.

The most extensive studies of saldid eggs and oviposition have been made by Cobben (1968). He found that most eggs are of the shape described by Wiley (1922), but Calacanthia Reuter and some species of Saldula have cylindrical eggs with the cephalic pole as blunt as the basal pole. Most saldids insert their eggs into plant tissue when available, but will glue them superficially to other surfaces, and species with cylindrical eggs ordinarily lay them in the latter way.

Studies on nymphal morphology have been largely neglected but can be valuable taxonomically as well as biologically. For example, Salda coloradensis Polhemus and Salda littoralis (L.) are virtually inseparable on the basis of external imaginal morphology, but S. coloradensis nymphs have many long dorsal setae, which are absent in S. littoralis nymphs. Similarly, in sympatric populations of Salda buenoí (McDunnough) some adults are very similar to S. coloradensis, but nymphs of the two species can easily be separated in the same way (Polhemus, 1967).

Copulation in saldids is side-by-side rather than with the male on top as in the Gerronornpha (see photograph in Jordan and Wendt, 1938). In most saldids, the female has an embolar notch or a patch of short coarse pubescence at about the middle of the hemelytral border that couples with the male grasping organ. This male structure consists of a granular plate on the posterior margin of paratergite II and a row or patch of pegs or spines on the anterior margin of paratergite III. These were first described by Drake and Hottes (1951b) as a stridulatory apparatus, but were later correctly diagnosed by Cobben (1957) and Leston (1957) as a male-female coupling device. Attachment is also made at the genitalia, where the male parameres (copulation hooks of Ekblom, 1926) grasp the female ovipositor (fig. 15). When attached in this manner, the male can be transported by the female, and they can leap a short distance without disengaging (Hungerford, 1920).

Nearctic saldids overwinter in several ways. The genera Teloleuca, Lampracanthia Reuter, and Salda overwinter in the egg stage, with the first adults being seen at the end of May. Certain species, such as Lampracanthia crassicornis (Uhler) and Salda obscura Provancher, appear as adults only briefly in early summer and are rare or absent later. The same life cycle was noted for Salda littoralis (Jordan and Wendt, 1938) but Southwood and Leston (1959) noted that this species also overwinters as an adult; perhaps due to a different climate and geographical location. Many species of Ioscytus, Micracanthia, and Saldula overwinter as adults, but others almost certainly overwinter as eggs (Wroblewski, 1966). Some species such as Saldula pallipes and S. comatula Parsley are active during warm periods throughout the winter, becoming quiescent in cold periods. Three salt marsh species of Saldula have been collected in the San Francisco region in February, so it is likely that they remain active all year.

Most saldids are positively phototropic. Saldula retreat into the gravel or vegetation during cloudy weather and at night. We have collected them at night by shining a light on the loose, dry sand along a river. Saldids sometimes carry mites. A population of Pentacora saratoga Cobben studied in Death Valley was heavily infested with red mites, and many specimens were unable to fly because the mites interfered with the wings. Saldids carry other organisms also; they have been identified as a dispersal agent for both blue green and green algae (Stewart et al., 1970).
Our treatment of genera is more liberal than the schemes of Cobben (1959, 1960) and Lindskog (1975) both of whom treat Teloleuca and Lampracanthia as no more than subgenera of Salda. Lindskog suggests that species groups are sufficient in Salda and Saldula for infrageneric groupings. We have retained Teloleuca and Lampracanthia as genera. Cobben’s (1959) preliminary generic revision separates the tribes of the subfamily Saldinae on the basis of structures of the aedeagus and the structure of the “larval organ,” an organ on the dorsum of the nymph which is visible externally as an oval swelling mesad of the spiracle on tergum III (Cobben, 1957). This scheme is not completely utilitarian because males must be used and the nymphal character is not always diagnostic. In the following key, California genera can be identified without dissecting males, provided females are available, but the eastern Saldula lugubris (Say) will key to Saldula on the basis of external characters. Females are identified by their narrow ovipositor which protrudes behind sternum VII (fig. 12).

KEY TO NEARCTIC GENERA OF SALDIDAE

1. Membrane with five closed cells in macropters; hindmargin of last female sternum essentially straight for most of its breadth, sometimes with mesal notch (fig. 18); base of filum-gonopori of male curved up in a bow or at most forming one closed ring (fig. 20) ... (Chiloxanthinae) ... Membrane with four cells in macropters; hindmargin of last female sternum triangular (fig. 17); base of filum-gonopori of male coiled like a watch spring (fig. 19) ... (Saldinae) ... 
2. Brachypterous, hemelytron thickened, corium and membrane not clearly differentiated, the latter reduced and not or scarcely overlapping when wings folded, cells indistinct; intertidal forms. Gulf of California
   Enoladesa Polhemus
   Macropterus, hemelytron normal, corium and membrane clearly delimited, the latter broadly overlapping when wings folded, cells distinct (fig. 21) ... 3
3. Sublateral cell of membrane short, petiolate posteriorly, not reaching apices of adjoining cells; Arctic Region
   Chiloxanthus Reuter
   Sublateral cell of membrane not petiolate (fig. 21) ... Pentacora Reuter, p. 20

4. Pronotum with two prominent, conical tubercles on front lobe; southeastern U.S. ... Saldina Osborn
   Pronotum without conical tubercles on front lobe ... 5
5. Lateral margin of pronotum concave, humeral angle produced; body shiny black; eastern North America to British Columbia ... Lampracanthia Reuter
   Lateral margin of pronotum convex, humeral angle rounded ... 6
6. Innermost cell of membrane produced cephalad one-half its length beyond base of second cell; dorsum more or less extensively pale; lateral pronotal margins pale; first and second antennal segments of male flattened, oval in cross section, the flattened sides glabrous; Alaska, Canada ... Calacanthus Reuter
   Innermost cell of membrane produced cephalad only slightly, not more than one-third of its length beyond base of second cell or if produced more than one-third cephalad, then dorsum without extensive pale markings and pronotum unicolorous; first and second antennal segments of male not flattened, round in cross section, evenly pubescent or setose over entire surface ... 7
7. Second segment of tarsi usually nearly half again as long as third; innermost cell of membrane short, usually reaching only four-fifths of the distance to apex of adjacent cell; outer corium with large pale spots; clavus with yellow spot on each side in velvety black area ... Teloleuca Reuter, p. 32
   Second segment of tarsi subequal or slightly longer than third segment; innermost cell of membrane long, usually reaching almost to apex of adjacent cell; outer corium with or without pale spots; clavus with or without yellow spot on each side in velvety black area ... 8
8. Males longer than 5.5 mm, females (fig. 12) longer than 6 mm, if shorter, then innermost cell of membrane produced two-fifths to one-half its length cephalad beyond base of second, and dorsal surface unicolorous or with a few small pale spots on corium and membrane ... Salda Fabricius, p. 31
   Males shorter than 5.5 mm, females shorter than 6 mm; innermost cell of membrane produced cephalad only slightly beyond base of second or if inner cell is produced more strongly cephalad, then dorsum has more or less extensive pale markings ... 9
9. Antennae relatively thick, the third and fourth segments thicker than the distal end of the second segment ... Isocyamus Reuter, p. 22

FIG. 15. male genital capsule of Saldula pallipes; 16, 3/4 view of head of Saldula pallipes.
Antennae relatively slender, the third and fourth segments not thicker than the distal end of the second segment. 10
Veins of corium more or less distinct; body more than 3 mm long. .............................. Saluda Van Duzee, p. 23
Veins of corium obsolete; body usually less than 3 mm long ................................. Micracanthia Reuter, p. 22

Subfamily Chiloxanthinae

The subfamily Chiloxanthinae was founded by Cobben (1959) who included two genera, Chiloxanthus Reuter and Pentacora Reuter. Three more genera belonging to this subfamily have been described subsequently: Pelachoris Drake (1962), Enalosalta Polhemus (in Polhemus and Evans, 1969) and Paralosalda Polhemus and Evans (1969). The first of these is a fairly typical member of the subfamily as defined by Cobben, but the other two, while clearly belonging in the Chiloxanthinae, require a redefinition of the subfamily. Cobben's characterization included a membrane with five cells and a truncate female subgenital plate (fig. 18) with a shallow median notch. In Enalosalta the membrane is reduced, coriaceous, and it has a variable number of cells (usually three). Paralosalda has four cells. All three of these newly described genera have a deep median notch on the female subgenital plate, and the notch is well formed in some Pentacora (fig. 18).

The following combination of characters is diagnostic for the Chiloxanthinae: Larval organ usually present mesally; embolar fracture long; sixth female sternum indented posteriorly; no small crescent-shaped sclerite adjacent to eversible gland; apicolateral endosomal sclerites absent; filum gonopori coiled one turn at most (fig. 20); female subgenital plate truncate, base of ovipositor exposed; dilation of ductus ejaculatorius with accessory glands; spermatheca pump flange absent; transverse swelling of head weak or absent. See Polhemus and Evans (1969) and Polhemus (1972) for additional discussion.

Genus Pentacora Reuter

Type-species: Salda signoretii Guérin-Méneville, 1857, original designation.

The genus Pentacora is distinguished from the other Nearctic saldids by the five elongate cells of the membrane. Its closest relative is the curious intertidal genus Enalosalta known only from the Gulf of Lower California.

In California, members of the genus Pentacora are almost always found in saline or alkaline habitats, hence they are found mostly along the coast, around the Salton Sea, and in Death Valley. These saldids are usually agile and quick to fly. Five species occur in the Nearctic, and three of these are known from California.

KEY TO CALIFORNIA SPECIES OF PENTACORA

1. Side margins of thorax and embolium with black setae (fig. 21) ........................... signoretii (Guérin-Méneville)
   Side margins of thorax and embolium without black setae .............................. 2

2. Length more than 5.2 mm; pronotum and scutellum not shining; second antennal segment usually subequal to segments three and four together .......................... saratogae Cobben
   Length less than 5.2 mm; pronotum and scutellum shining; second antennal segment about three-fourths the length of three and four together .......................... sphacelata (Uhler)

Pentacora saratogae Cobben


The larger size and longer second antennal segment separate P. saratogae from P. sphacelata. In addition, the base of the first antennal segment is usually dark in P. saratogae.

Geographic range. California.


Searches were made at Bad Water in February, 1964, and October, 1964, but no specimens were found; however, in April, 1961, the species occurred in swarms at the same locality, indicating that it is very seasonal or remains dormant until the proper moisture conditions prevail. The Davis specimens were most likely collected in a salt marsh north of that city that has now been cultivated.

Pentacora signoretii signoretii (Guérin-Méneville) (Figs. 18, 20, 21)


This is the largest saldid occurring in California and it is easily separated from other species by the black setae that occur along the margins of the embolium. Our form is the typical subspecies. The subspecies P. yucatana Hodgden occurs on the Yucatan Peninsula of Mexico.

Geographic range. Southern California to Florida, north to Canada in eastern North America; Mexico; Greater Antilles.

California records. IMPERIAL CO.: Salton Sea Beach, IX-24-60


This small pale species is separated from P. saratogae by its smaller size and shorter second antennal segment.

Geographic range. California, Connecticut, Maryland, Massachusetts, Mississippi, Missouri, New Jersey, New York, Texas, Utah, Mexico, West Indies, Trinidad, Galapagos Islands, and Mediterranean region of Europe.


This species is usually halophilous but Polhemus collected specimens around fresh water near Cleveland, Texas, about 50 miles from the nearest brackish water bay, and it tolerates wide changes in salinity in the coastal marsh near Galveston, Texas.

Subfamily Saldinae

Cobben (1959) redefined the Saldinae on the basis of larval organ characteristics, aedeagal features, a produced female subgenital plate (fig. 17), presence of a postclypeus (fig. 16), and a hemelytral membrane with four cells. The aedeagal structures used by Cobben are shown in figure 19. The distinction in hemelytral cells between the Saldinae and Chiloxanthinae is not constant (see Chiloxanthinae). Additionally, the Old World genus Salduncula Brown, included in the Saldinae, seems to lack a postclypeus (Polhemus and Evans, 1969). This is a second discrepancy in Cobben’s subfamily characterization.

The following combination of characters is diagnostic for the Saldinae: Larval organ usually present laterally, adjacent to spiracle; embolar fracture short; sclerite adjacent to eversible gland present, small, crescent shaped; apicolateral endosomal sclerites present; filum gonopori coiled one to four times (fig. 19); female subgenital plate lengthened caudad, base of ovipositor concealed; dilation of ductus ejaculatorius without accessory glands; spermatheca pump flange usually present.

The Saldinae contains the majority of saltid genera and it is divided into two tribes. The tribe Saldoidini (= Chartoscirtini of Cobben) includes among its many genera the following from North America: Calacanthia, Ioscytus, Micracanthia, Saldoida, and Saldula. The tribe Saldini includes only Salda, Lampracanthia, and Teloleuca.

Tribe Saldoidini

We have used Saldoidini because it is an older name than Chartoscirtini.
Genus *Zoscytus* Reuter


Type species: *Salda polita* Uhler, 1877, original designation.

Species of the genus *Zoscytus* have the third and fourth antennal segments swollen. They are generally shiny, and have long dorsal hairs. These saldids inhabit a variety of habitats, but each species seemingly prefers a restricted ecological niche. *Zoscytus politus* prefers an alkaline habitat, while *Z. franciscanus* prefers coastal bogs. *Z. nasti* occurs around streams and ponds, usually at high elevations.

Five of the six known species occur in the United States. Three of these species occur in California. *Zoscytus cobbeni* is included in the key as it is widely distributed through the high desert regions of the southwest.

**KEY TO *ZOSCYTUS* OF CALIFORNIA AND ADJACENT STATES**

1. Clavus of hemelytron without golden pubescence ............
   *cobbeni* Polhemus

   Clavus of hemelytron with golden pubescence ............ 2

2. Third antennal segment more slender, about 1/6 as thick as long. .................. *franciscanus* (Drake)

   Third antennal segment very stout, about 1/4 as thick as long 3

3. Clavus and thorax with dense golden pubescence; thorax not shiny. .................. *nasti* Drake & Hottes

   Clavus and thorax usually with sparse golden pubescence; thorax normally shiny (fig. 22) .................. *politus* (Uhler)

**Zoscytus franciscanus** (Drake)


The third and fourth antennal segments are much more slender than in the other species of *Zoscytus*.

**Geographic range.** California and Oregon.


*Z. nasti* occurs along the damp margins of streams and ponds in the Sierra Nevada.

**Zoscytus politus politus** (Uhler)

(Fig. 22)


Typical *I. politus* possesses a red coriun with a black embolium which easily separates it from related species.

**Geographic range.** Arizona, California, Oregon, and Nevada.


Several of our collections (Coachella and South Dos Palos) contained numerous specimens that were very dark and some individuals were completely black. Some specimens from Mono and Inyo counties have a completely pale embolium and a reddish coriun. Reuter (1912) gave Utah specimens with this color pattern the name *I. flavicosta*. However, specimens from the type locality (Salt Lake, Utah) and Colorado are consistently smaller and more rotund than California and Nevada specimens as well as paler.

**Genus Micracanthia** Reuter


*Micracanthia* is characterized by the corium having no apparent forked vein, or the median vein not forked apically. Otherwise the genus is very similar to *Salda*. *Micracanthia* has about 13 species, several of them Holarctic. Eleven species occur in the Nearctic, two of these are reported from California, one of which, *M. humilis*, we have been unable to confirm. A third, *M. utahensis*, probably will be found in the state.

**KEY TO *MICRACANTHIA* OF CALIFORNIA AND ADJACENT STATES**

1. Base of femur dark; outer embolium of hemelytra mostly dark, except where interrupted by two plate spots. .................. *quadrinodulata* (Champion)
   Base of femur pale; entire length of outer embolium of hemelytra pale; western Nevada or southeast Oregon ........... 2

**Genus Micracanthia** Reuter


*Micracanthia* is characterized by the corium having no apparent forked vein, or the median vein not forked apically. Otherwise the genus is very similar to *Salda*. *Micracanthia* has about 13 species, several of them Holarctic. Eleven species occur in the Nearctic, two of these are reported from California, one of which, *M. humilis*, we have been unable to confirm. A third, *M. utahensis*, probably will be found in the state.

**KEY TO *MICRACANTHIA* OF CALIFORNIA AND ADJACENT STATES**

1. Base of femur dark; outer embolium of hemelytra mostly dark, except where interrupted by two plate spots. .................. *quadrinodulata* (Champion)
   Base of femur pale; entire length of outer embolium of hemelytra pale; western Nevada or southeast Oregon ........... 2
2. Inner corium usually concolorous, or with at most one apical pale spot; southeast Oregon, or with at most one apical pale spot: southeast Oregon ............... 1
   Inner corium with three or four pale or pruinose spots; clavus with pale or pruinose apical spot. ..................... 3
3. Pronotum rugulose; ocelli large, separated by no more than an ocellus diameter; width of interocular space distinctly less than eye width: hemelytra never with bluish pruinose areas ........................................... 3
   Pronotum almost smooth, shining; ocelli small, usually separated by more than an ocellus diameter; interocular space usually subequal to eye width; hemelytra often with bluish pruinose areas ........................................... utahensis Drake & Hottes

Micracanthia humilis (Say)


Micracanthia humilis resembles most closely M. quadrimaculata (Champion), but may be separated from it by the key characters.

M. humilis inhabits many types of habitats, but usually prefers sparsely vegetated sandy soil near water. It apparently overwinters as an adult, as specimens have been collected in the winter months in the southern U. S. and in October and May in more northern latitudes.

Micracanthia quadrimaculata (Champion) (Fig. 23)


The silver pubescence and four-spotted hemelytra are distinctive in M. quadrimaculata (fig. 23).

Geographic range. Western U. S. and Canada, Mexico and Central America.

California records (map 1). Specimens have been examined from 20 counties (Trinity to Los Angeles). Damp margins of streams, ponds, and lakes are common habitats of this species: it occurs up to 6,000 feet.

Micracanthia utahensis Drake & Hottes


The pruinose spots on the hemelytra, pale embolar area, and very large eyes characterize this species.

Geographic range. Nevada, New Mexico, Utah, and Durango, Mexico.

California records. Not known from California but included here because it occurs only a few miles from the California border near Reno, Nevada.

This species has been found only around springs and seeps in heavy vegetation, sometimes in dark mouse tunnels in matted grass. The species is slow moving but not easily seen.

Genus Saldula Van Duzee

Saldula Van Duzee, 1914, Can. Entomol. 46:386. Type-species: Cicimex saltatorius Linnaeus, 1758, original designation.


Macroscalcula Southwood & Leston, 1959, Land and water bugs of...
KEY TO CALIFORNIA SPECIES OF SADULATA


Species for some of our species have been illustrated by...

MAP 1. California distribution of Microceratha quadrinota.
MENKE: THE SEMIAQUATIC AND AQUATIC HEMIPTERA OF CALIFORNIA

Thorax and hemelytra smooth or with only short pubescence, sometimes appressed ........................................ 9

2. Eye with a few short, erect hairs ........................................ 3

Eye bare ........................................ 5

3. Length 4.5 mm; base of clavus with pale spot; large pruinose blue spot on corium adjacent to apex of clavus

villosa (Hodgden)

Length 3.5 mm; base of clavus without pale spot; corium adjacent to apex of clavus without large pruinose blue spot ........................................ 4

4. Lateral pronotal margins almost straight; hairs on hindtibia subequal to tibial width .................. severissi Harris

Lateral pronotal margins curved; hairs on hindtibia at least twice tibial width .................. orbiculata (Uhler)

5. Hemelytra often pale except for dark transverse band at middle; dorsal surface very shiny; narrowest portion of vertex and one eye shorter than second antennal segment length .................. andreii Drake

Hemelytra pale or dark but without dark transverse bands at middle; dorsal surface not especially shiny; narrowest portion of vertex and one eye equal to or greater than second antennal segment length .................. 6

6. Dorsum appearing shaggy, pubescence long, coarse, abundant, especially evident towards side margins of pronotum; length 4.5-5 mm; pubescence on hindtibia longer than tibial width .................. comatula Parshley

Dorsum appearing less shaggy, pubescence shorter, finer, and much less abundant; length about 4 mm; pubescence on hindtibia not very noticeable, much shorter than tibial width .................. 7

7. Embolium and all of corium shining; pronotum more than 1.5 times head width, including eyes ........... lucidus (Stål)

Only embolium shining, corium dull like clavus; pronotum width less than half head width, including eyes ........... 8

8. Clavus with well-defined apical spot (fig. 25) ............. pecs Drake

Clavus without well-defined apical spot; eyes small, interocular space wide .................. usingeri Polhemus

9. Lateral margins of pronotum pale .................. 10

Lateral margins of pronotum concolorous with rest of pronotum, without pale areas .................. 12

10. Pronotum pale except for median portion; body length less than 3.5 mm .................. bulli Drake

Pronotum normally pale only along lateral margins; body length more than 3.5 mm .................. 11

11. Clavus dark, interrupted with pale at middle and at apex .................. varicos Drake & Hottes

Clavus dark, interrupted with pale only at apex .................. optiparia Drake & Hottes

12. Foretibia with frontal, fuscous stripe which is interrupted near middle, or with fuscous marking only at base ........................ 13

Foretibia with uninterrupted frontal, fuscous stripe which extends to near apex ........................ 16

13. Foretibia with fuscous stripe interrupted near middle .................. 14

Foretibia with fuscous marking only at base .................. 15

14. Pale marginal mark before middle of hemelytra forming a distinct "C" .................. "c-album (Fieber)

Pale marginal mark before middle of hemelytra not forming a distinct "C" .................. saltatoria (Linnaeus)

15. Length usually more than 4.4 mm; dorsal pubescence more or less shaggy, coarse, golden; inner part of hypocostal area (ventral surface of embolium at hemelytra base) pruinose basally .................. fernandi Drake

Length usually less than 4.2 mm; dorsal pubescence of uniform length, fine; inner part of hypocostal area not

FIG. 24. Clinal variation in hemelytral markings in Saldula, middle figure represents common pattern: A-E, arenicola; F-J, pallipes (redrawn from Wagner, 1950).

pruinose, entire hypostomal area at least faintly shining ........................................ opacula (Zetterstedt)

16. Narrower portion of vertex and one eye shorter than second antennal segment length .................. nigrita Parshley

Narrower portion of vertex and one eye longer than second antennal segment length .................. 17

17. Length usually less than 3.5 mm .................. 18

Length more than 3.5 mm .................. 19

18. Labrum all or mostly black; membrane dark, smoky, and opaque with no pale spots .................. ourayi Drake & Hottes

Labrum usually mostly pale; membrane usually pale with dark spots .................. basingeri Drake

19. Side margins of pronotum with broadly explanate; lateral margin of embolium usually entirely dark .................. explanata (Uhler)

Side margins of pronotum narrowly explanate; extreme lateral margin of embolium usually with pale area .................. 20

20. Corium dull with gray pubescence; pale areas of hemelytra when present, tending to form a transverse band, not especially interrupted with fuscous (fig. 24A-E) .................. arenicola (Scholz)

Corium glabrous with gold to black pubescence; pale areas of hemelytra, when present, not forming a marked transverse band but interspaced with fuscous (fig. 24 F-J) .................. pallipes (Fabricius)

Saldula andreii Drake


The shining dorsum is distinctive in S. andreii.

Geographic range. Western U. S. and Canada, Mexico.

California records. No California specimens have been seen, but
Drake & Hottes (1950) reported this species from the state. Chapman collected it along the Colorado River in southern Nevada. *Saldula andrei* is primarily saxicolous, however we have also collected it on sandy stream beds and along damp margins of rivers and a lake.

*Saldula arenicola arenicola* (Scholz)  
(Fig. 24 A-E)


The variation in the hemelytral pattern is shown in figure 24 A-E. Figure 24 C shows the commonest California pattern. Several subspecies of *arenicola* are recognized in the Old World, but the names listed in the above synonymy are regarded as *arenicola s. s.*

*Geographic range.* In the U. S. this Holarctic species is known from California, Colorado, Nevada, Oregon, and Utah.

*California records.* MONO CO.: Mono Lake, VII-2 (Wickham, CJD); VI-8 (Wickham, JTP).

*S. arenicola* occurs in saline situations.

*Saldula balli* Drake


Long series of *S. balli* and *S. varionis* Drake & Hottes appear to intergrade and it is possible that these species are not distinct. The almost completely pale thorax of *S. balli* separates this small species from other *Saldula*.

*Geographic range.* Arizona, California, Colorado, Kansas, Nebraska, Nevada, New Mexico, and Utah.

*California records.* RIVERSIDE CO.: Needles, VI-21-64 (H. C. Chapman, HCC); Palm Springs, VII-10-63 (E. I. Schlinger, UC). SAN DIEGO CO.: Borrego, III-30-57 (J. T. Polhemus, JTP).

These are the first California records for *balli*.

*Saldula basingeri* Drake

*Saldula basingeri* Drake, 1949, Psyche 56:190. Holotype♂: Riverside, California (CJD), original spelling. We have emended Drake’s name to *basingeri* because it is clear in the original description that the species was named in honor of A. J. Basinger.

The pale hemelytra and small size are peculiar to this species. It is possible that *S. basingeri* is merely a small, light color phase of *S. pallipes*.

*Geographic range.* California and Colorado.

*California records* (map 2). Specimens were examined from 19 counties. All localities are at low elevations.

*Saldula c-album* (Fieber)


*Salda gamma* Fieber, 1864, Wiener Entomol. Monat. 8:212.

*Saldula c-album reuteri* Stichel, 1934, Illustrierte Bestimmungstabellen der Deutschen Wanzen Lief 10, p. 300, not Jakowleff, 1889.  

The prominent “C” mark of the outer corium of the hemelytra is distinctive. According to Lindskog (in litt.) true *S. c-album* is strictly an Old World bug. Thus the New World species masquerading under this name is undescribed.


Saldula comatula Parshley


The shaggy appearance and hairy legs and antenna separate this large species from its congeners.

Geographic range. Most states west of the Rocky Mountains including California, also western Canada.

California records (map 3). Specimens have been taken widely through the state except in the deserts. Some records were from localities exceeding 10,000 feet.

*Saldula explanata* (Uhler)


Syntypes (sex unknown): City Cañon [= American Fork Canyon], Ogden and Alta, Utah (USNM, types lost).

The explanate margins of the pronotum and very dark dorsum are diagnostic for this species, but some specimens approach and are extremely difficult to separate from *S. pallipes*.


California records (map 4). *S. explanata* has been taken in 20 counties. It occurs primarily in the Sierra Nevada but it is known from the White Mountains (10,500 feet), and the San Jacinto Mountains of southern California.

*Saldula fernaldi* Drake


*Saldula palustris* of authors, not Douglas, 1874.

The pruinosity of the inner part of the hypocostal area (= venter of embolium) and the tibial markings will usually separate *S. fernaldi* from related species. The dorsal pubescence varies, specimens from the central coastal area of the state being the shaggiest.

The salt marsh populations of *S. fernaldi* have been long misidentified as the Old World species *S. palustris* Douglas. Both species are quite variable and similar in overall appearance, but their sclerotized aedeagal structures differ. *S. fernaldi* differs from *S. palustris* in having a large pruinose area on the underside of the forewing.

The biology of *S. fernaldi* was treated by Stock & Lattin (1976) who used the name *S. palustris*.

MAP 3. California distribution of *Saldula comatula* Parshley.

MAP 4. California distribution of *Saldula explanata* (Uhler).
**Geographic range.** Primarily coastal from Alaska to Baja California, and from eastern Canada to New England.


Drake & Hottes (1950) reported this species from Marin and Santa Cruz counties. S. fernaldii is primarily a halophilous species occurring in coastal marshes, tidal flats, and sloughs. It is most abundant in the mid-tidal zone where it regularly undergoes submersion. Populations also occur inland, some at high elevations, but these specimens may represent another species.

**Saldula luctuosa** (Stål)


The shining embolium and corium, along with the erect pubescence will separate *S. luctuosa* from related species.

**Geographic range.** California.


*Saldula luctuosa* is restricted to coastal areas. Chapman collected many specimens at the edge of a salt water slough, and this series of specimens contained both light and dark, shining, bluish black forms.

**Saldula nigrita** Parshley


The long second antennal segment and dark color are distinctive features of this large species.

**Geographic range.** Most states west of the Rocky Mountains, Canada, east to New Hampshire and Newfoundland.


All examples of this saxicolous species were from the central and northern part of the state.

**Saldula opaculata** (Zetterstedt)

*Saldula opaculata* Zetterstedt, 1838, Insecta Lapponica, column 268. Holotype $\sigma$: Dovre, Lappland (Norway) (Mus. Lund).

*Saldula costalis* P. Dahlberg, 1848, Monographia Geocorisarum Fenniae, Helsinki p. 152.

*Saldula opaculata marginata* Puton, 1880, Synopsis Hémiptères Hétéroptères France 1(3):197, not Herrich-Schaeffer, 1853.


The pale outer embolium, short golden pubescence of the hemelytra, and tibial markings separate *S. opaculata* from related species.

*Saldula opaculata* exhibits a remarkable degree of habitat induced polymorphism. The species commonly inhabits bogs, and in most populations the exocorium and other markings are light yellow brown against a soft brown ground color, but those inhabiting peat bogs exhibit reduction in body size and a high degree of melanism.

**Geographic range.** This Holarctic species is widely distributed in Canada, the northern United States, northern Europe, and Siberia. In the west it is known from Alaska, California, Colorado, Nevada, Oregon, and Utah.

**California records.** SISKIYOU CO.: Mt. Shasta, VI-30-47 (R. L. Usinger, CIS). Only one California specimen of this bog-inhabiting species is known.

**Saldula opiparia** Drake & Hottes


*Saldula coxalis* of authors, in part, not Stål, 1873.

The pale, broad, lateral stripe that extends to the base and apex of the pronotum will distinguish *S. opiparia* from its congeners.

**Geographic range.** Rocky Mountains westward, sw. Canada, and Baja California.

**California records** (map 5). *Saldula opiparia* occurs from the 39th parallel south to Imperial County over a broad range of altitudes reaching high elevations east of the Sierra Nevada (12,500 in the White Mts.) (Lower Sonoran to Alpine). The species is commonly
taken in light traps. Drake (1950) recorded this species from California under the name Saldula xanthochila limboza Horvath.

**Saldula orbiculata** (Uhler)


The hairy eyes, rounded thoracic sides, and long hair on the hindtibia separate *S. orbiculata* from related species.

**Geographic range.** California, Nevada, Texas, and much of the eastern U.S.; also Mexico.

**California records.** FRESCO CO.: Coalinga, XI-30-63 (H. B. Leech, CAS). Drake & Hottes (1954) recorded specimens from Calaveras and San Diego Counties.

**Saldula ourayi** Drake & Hottes


The small size, dark labrum and smoky membrane without fuscous spots will identify *S. ourayi*.

**Geographic range.** California, Colorado, Idaho, Oregon, Nevada, Utah, Washington, and Canada.


The preferred habitat for this species is the margins of highly alkaline areas.

**Saldula pallipes** (Fabricius)

(Figs. 15, 16, 17, 19, 24 F-J)


*Acanthia pallipes* Fabricius, 1794, Entomol. Syst. 4:71. Holotype †: Denmark (Mus. Copenhagen).


*Saldula tropicalis* Champion, 1900, Biologia Centrali-Americana. Rhyndota 2:341.


*Saldula pallipes* varies greatly in size and color and tends to grade into many allied species (fig. 24 F-J). While it is difficult to fix limits of variation for this species, the dark spot on the embolium is fairly constant (arrow on fig. 24 H), and will separate *S. pallipes* from *S. fernaldia*, a closely related species. Figure 24 H represents the predominant color form in California. Very dark specimens are extremely difficult to separate from *S. explanata*.

It has been overlooked by saldid workers that the name *S. pallipes* is unavailable under the provisions of Art. 59(b)(i). Apparently the species should be called *S. marginalis* Turton although Geoffroy's *S. pellucidus* may qualify as an earlier name. We anticipate that some action will be taken to conserve *S. pallipes*. Therefore, we have not used the name *S. marginalis*.

**Geographic range.** Europe, Asia, Africa; North, Central, and South America and West Indies. The most widely distributed saldid in the U.S.

**California records** (map 6). This is the most common and widespread saldid in California. Habitats range from salt marshes to elevations of 10,200 feet. It is marginal in desert areas.
MAP 6. California distribution of *Saldula pallipes* (Fabricius).

*Saldula pexa* Drake

(Fig. 25)


The small size, the long, erect hairs on dorsal surface, and dull corium separate *S. pexa* from related species. *Saldula pexa* is the species referred to by Usinger (1956) as *Saldula hirsuta* (Reuter) and *S. hirsuta pexa* Drake. Usinger's figure 7:40a was erroneously labelled *S. comatula* Parshley.

**Geographic range.** Arizona, California, Oregon, Nevada, and Mexico.

**California records** (map 7). Specimens have been seen from 22 counties. These records range from Lake County in the north to Inyo and San Diego counties in the south. This species is very common in the foothills.

*Saldula saltatoria* (Linnaeus)

*Cimex alpinus* Scopoli, 1763, Entomologia Carniolica p. 129.

The body shape, tibial markings, large callosities of the pronotal lobe, and corial markings identify this species.

**Geographic range.** This Holarctic species is widespread in North America and extends south to Colombia. In the west it is known from California, Colorado, Nevada, and Oregon.

**California records.** SAN MATEO CO.: La Honda, V-16-22 (E. O. Essig, CIS). Half Moon Bay, V-16-22 (S. E. Flanders, CIS). SISKIYOU CO.: No date or collector (CAS). We have seen only eight California specimens. Often found in shady places, this saldid overwinters as an adult.

*Saldula severini* Harris


The straight sides of the prothorax and short hair on the hind tibia separate *severini* from *S. orbiculata*. 
This species was listed as a synonym of *orbiculata* by Usinger (1956).

**Geographic range.** California, Colorado, Iowa, Nevada, New Mexico, South Dakota, Tennessee, and Wyoming.

**California records.** CALAVERAS CO.: Calaveras, no date (Osten Sacken, MCZ). LOS ANGELES CO.: no date (Coquillett, USNM).

This species was recently restored to specific status (Polhemus, 1976); heretofore it had been synonymized with *Saldula orbiculata*. *S. severini* has not been reported previously from California.

*Saldula usingeri* Polhemus


*Saldula usingeri* may be recognized by the small eyes and wide interocular space. The clavus lacks the well-defined apical spot found in *S. pexa*.

**Geographic range.** California.

*Saldula pexa*, female, dorsal view (from Usinger, 1956).

*Saldula pexa* is known only from one hot spring area. It is a sluggish species. In February, Polhemus found many specimens in the debris at the foot of a concrete wall and in the crevices above where sulphur laden water seeped on the face of the wall.

*Saldula varionis* Drake & Hottes


The pale lateral pronotal markings, visible at least beneath, and the larger size will usually distinguish *S. varionis* from *S. balli* Drake, with which it is sometimes found. *S. varionis* is very similar to *S. balli* and may prove eventually to be a synonym.

**Geographic range.** California, Colorado, Kansas, and Utah.

**California records.** SAN DIEGO CO.: Borrego, III-30-57 (J. T. Polhemus, JTP). This is a new saldid record for California. *Saldula varionis* and its close relative *S. balli* are normally found on light-colored sandy shores in desert areas.

*Saldula villosa* (Hodgden)


*Saldula villosa*: Usinger, 1956, Aquatic Insects Calif.:226.

The long erect hair of the dorsal surface, the hairy eyes, and the presence of extensive pruinose areas on the hemelytra will separate *S. villosa* from its congeners.

**Geographic range.** California and Oregon.


Hodgden (1949b) reported *S. villosa* from San Francisco and Sonoma Counties. All specimens of this rarely collected species were from the San Francisco Bay area and salt marshes seem to be the preferred habitat.

**Tribe Saldini**

**Genus Salda Fabricius**


*Sciodoptera* Amyot and Serville, 1843, Histoire Naturelle des Insectes, Hémîptères p. 404.

Cobben (1959) defined *Salda* on the basis of new characters: filum-gonopori coiled 2½ to 4 times, the median sclerotized structure of the aedeagus complex,
and the larval organ always absent. Reuter's (1912) concept of the genus was based on the anteriorly elongated inner cell of the hemelytral membrane, a characterization still valid for the western U.S. *Salda* species (fig. 26), but not for some European species, or the Nearctic *Salda lugubris* Say which does not occur in California.

These are medium to large sized black saldids that inhabit seeps, springs, and meadows with sparse to dense vegetation. While no detailed biological field studies have been made of *Salda* species, all available evidence indicates that our species overwinter in the egg stage.

KEY TO CALIFORNIA SPECIES OF SALDA

Entire dorsal surface excepting membrane, shining, clothed with thinly scattered minute pubescence. **provancheri** Kelton & Lattin

Entire dorsal surface, excepting membrane, dull, clothed with very abundant, very short, reclining brownish pubescence. **buenoi** (McDunnough)

Salda buenoi (McDunnough)

(Fig. 26)


Geographic range. Transcontinental in the northern United States and southern Canada.


All specimens seen were from moderate to high elevations in the eastern portion of the state. Brachypterous forms are common.

Salda provancheri Kelton & Lattin


_Salda provancheri_ Kelton & Lattin, 1968, Nat. Can. 95:664. New name for _coriacea_ Uhler, not _Salda coriacea_ (Fabricius), 1776. _Salda bouchervillei_ of authors, not Provancher, 1872.

This large saldid is characterized by its shining dorsal surface and robust shape. A related species, _Salda obscura_ Provancher, has been found in Nevada and Oregon; while it is similarly shining, it differs in being smaller and having the upper surface of the second antennal segment pale instead of concolorous as in _S. provancheri._
UISTICA COLLECTIONS AND ITS PRESENCE IN THE STATE: NEEDS VESTIGEATION.

WESTERN U.S., WHERE THEY ARE FOUND IN MOUNTAINOUS PINE
AND HEMLOCK (1961). BOTH ARE KNOWN FROM THE NORTH.

THE FORMER SPECIES WAS REPORTED FROM THE SHOLE BY DR. BAJER.
SHEEP RANCH AND WE HAVE BEEN TOLLED FROM CALIFORNIA.

 crist a occurs in the Northern region, both are con-

UIU SPECIES: J. PHYSICUS AND J. PROFUSION (FABR).

Two species: J. Physicus and J. Profusion (Fabr).

Characters as noted in the generic key.

The proclivity of slender leaflets and other
characteristics are noted in the generic key.

The inclusion of Tofolana as a separate genus is characterized by

the broad ranges of the genus. Some members of the
genus exhibit close resemblance of their forms and

except for the distinct yellow and black appearance.

Hebrids are small (2.5 mm or less), inconspicuous, stout-bodied bugs that are densely covered with a velvety hydrofuge pile. The short legs are equally spaced and the tarsal claws are apical. The antennae are four or five segmented. The beak rests in a groove on the underside of the head and prothoracic sternum. The ocelli and scutellum are well developed in winged forms, but bugs with reduced wings have the ocelli reduced or absent and the scutellum reduced. The clavus and membrane of the forewing are devoid of veins or cells, but the corium has a single cell. There is a single median metathoracic scent gland opening on the sternum. Many species have prominent white markings on the hemelytra, but the general ground color of hebrids varies from dull grey, brown, reddish brown, greenish to violet.

This family is closely related to the Mesoveliidae, but the groove on the venter of the head for the reception of the beak is diagnostic. Apterous hebrids have a scutellum, unlike wingless mesoveliids.

The Hebridae contains about 125 species divided among five genera, three of which are found only in the Old World. Two genera, Hebrus and Merragata, are widespread and are represented in the New World by 34 species and nine species, respectively. Both genera occur in California. The last revisionary work on the New World hebrids was by Drake and Harris (1943), but it contains no keys. An unpublished thesis by Porter (1950) contains much useful information. Several regional treatments key species of the eastern and southern United States (Blatchley, 1926; Chapman, 1958; Froeschner, 1949; and Wilson, 1958). Various authors have contributed to the taxonomy of North American hebrids (Porter, 1952a and b, 1954; Polhemus and Chapman, 1966, 1970; and Drake and Chapman, 1953b, 1954, 1958). The last paper includes a catalog of American species.

Hebrids occupy two types of habitats: Moist places at shorelines, and floating plants. The commoner North American Merragata and the only California species, M. hebroides White, typically are found in the latter situation, and Drake (1917) stated that they are found walking on the surface, on the undersides of floating leaves, and even in the submerged roots of floating plants. An air film surrounding submerged bugs allows them to remain underwater for some time. Hebrus and some Merragata species inhabit detritus or sparsely vegetated moist earth along shorelines, where they are secretive and seldom seen. Vigorously splashing water on their habitat will dislodge them, carrying them onto the surface where they may be seen.

While hebrids ordinarily are associated with fresh water habitats, some species of Hebrus and Merragata have a tolerance or preference for brackish or saline situations (Chapman, 1958; Polhemus and Chapman, 1970). Wilson (1958) collected Merragata hebroides in a saline tidal pool (salinity 6.6%), and in the Nether-lands Antilles this species inhabits both fresh and brackish waters (Drake and Cobben, 1960).

Hebrids are carnivorous, feeding on Collembola, other small insects, and perhaps other arthropods (Brooks and Kelton, 1967; Southwood and Leston, 1959). Hungerford (1920) fed them plant lice, midges, and mosquitoes in the laboratory. Hebrids are attacked by predaceous bugs and beetles (Porter, 1950), Mesovelia species, and even by each other (Williams, 1944).

The life histories of Hebrus buenoi Drake & Harris, H. burmeisteri Lethierry & Severin, H. sobrinus Uhler, Merragata brunnea Drake, and M. hebroides have been studied by Porter (1950), and Hungerford (1918, 1920) recorded the egg laying of H. concinnus Uhler. Hebrus species lay their eggs on moss, usually secreting them in leaf axils or between closely spaced leaves; they are attached with a gelatinous glue. Eggs are elongate oval and about twice as long as wide with rounded ends. They are pearly white when laid, but change to yellowish white as the embryo develops. Hebrus eggs are laid on moss, usually secreting them in leaf axils or between closely spaced leaves; they are attached with a gelatinous glue. Eggs are elongate oval and about twice as long as wide with rounded ends. They are pearly white when laid, but change to yellowish white as the embryo develops. Hungerford (1918) noted the large size of hebrid eggs (0.625 mm by 0.25 mm) compared to the size of the female (0.925 mm across the prothorax). One female carried only four eggs. Eggs are laid over a two-month span. Incubation takes from 8 to 12 days, but may be less at higher
temperatures. Cobben (1968) gave the incubation time for *Hebrus ruficeps* Thomson, an Old World species, as 12 days at 22° C. and six and a half days at 30° C. He also stated that incubation and successful hatching can occur when the egg is continuously under water or in moist air. In the laboratory, *Merragata* species lay their eggs on moss leaves or under algae. In nature Porter (1950) found eggs under filaments of algae on stones, and in surface holes of the stones. Incubation time in *Merragata* also lasts about 8 to 12 days.

Hebrids have five nymphal instars. Each *Hebrus* instar typically lasts about one week. Development time from egg to adult requires 34 to 62 days for *Hebrus buenoi* and *H. sobrinus*. *Merragata hebroides* develops faster, each instar averaging 2 to 7 days, with adults appearing after 20 to 36 days (Porter, 1950).

*Hebrus buenoi* and *sobrinus* overwinter as adults at Denver, Colorado, appearing in numbers in late March or early April. In the southern United States, both *Hebrus* and *Merragata* are active during the winter months (Chapman, 1958). According to Hungerford (1918), mating occurs in late June at Ithaca, New York, but undoubtedly this varies with locality and climate. Egg laying is spread over several months and adults are present throughout the summer.

No one appears to have recorded flight in hebrids, but since winged forms are common and they are often found in isolated habitats, flight undoubtedly plays a part in their dispersal. The dispersal of small insects by wind as aerial plankton has been discussed by numerous authors (see Fernando, 1964a), and is a possible dispersal mechanism for hebrids. Dispersal by man is possible. For example, *Merragata hebroides* is thought to have been introduced to Hawaii in plants.

Wing polymorphism is a common phenomenon in hebrids. In *Hebrus* macropterous individuals ordinarily are more prevalent than brachypterous or apterous forms. A few *Hebrus* species are known only from brachypterous (*H. amnicus* Drake & Chapman, *H. obscurus* Polhemus & Chapman) or apterous forms (*H. tuckahoonus* Drake & Chapman). Individuals of *Merragata hebroides* are usually macropterous.

The only hebrid parasite known is *Rhizopodomyces merragatae* Thaxter, a fungus of the family Laboulbeniaceae. It has been found on *Merragata hebroides* collected at Victorville, California, and also on a *Hebrus* species from Palm Springs, California (Benjamin, 1967).

**KEY TO NEARCTIC GENERA OF HEBRIDAE**

- Antenna five-segmented (fig. 27) .................................. *Hebrus* Curtis, p. 35
- Antenna four-segmented (fig. 28) ............................... *Merragata* White, p. 37
- Key to California species of *Hebrus*

| Length of 3rd and 4th antennal segments combined usually clearly shorter than width of head through eyes; male genital capsule with long hairs projecting posterolaterally | *sobrinus* Uhler |
| Length of 3rd and 4th antennal segments combined subequal to width of head through eyes; male genital capsule without long hairs projecting posterolaterally (presence in California not confirmed) | *concinnus* Uhler |
| Median pit of second transverse pronotal pit row prolonged posterad nearly to hindmargin of notum; body large, usually more than 2.2 mm long (presence in California not confirmed) | *major* Champion |
| Median pit of second transverse pronatal pit row at most weakly prolonged posterad; body usually less than 2.2 mm long | *hubardi* Porter |
| Head without median, longitudinal sulcus, frons smoothly arcuate in front view | 3 |
| Head with median, longitudinal sulcus as seen in front view | 2 |
| Length more than 1.6 mm; only macropterous forms known | *buenoi* Drake & Harris |
| Length less than 1.6 mm; only brachypterous forms known | *obscurus* Polhemus & Chapman |
| Anterior margin of pronotum paralleled by a continuous transverse row of small pits | 4 |
| Anterior margin of pronotum without adjacent row of continuous pits | 5 |

**KEY TO CALIFORNIA SPECIES OF HEBRUS**

1. Head with median, longitudinal sulcus as seen in front view
2. Head without median, longitudinal sulcus, frons smoothly arcuate in front view
3. Length more than 1.6 mm; only macropterous forms known
4. Anterior margin of pronotum paralleled by a continuous transverse row of small pits
5. Median pit of second transverse pronatal pit row prolonged posterad nearly to hindmargin of notum; body large, usually more than 2.2 mm long (presence in California not confirmed)
6. Median pit of second transverse pronatal pit row at most weakly prolonged posterad; body usually less than 2.2 mm long
7. Length of 3rd and 4th antennal segments combined usually clearly shorter than width of head through eyes; male genital capsule with long hairs projecting posterolaterally
8. Length of 3rd and 4th antennal segments combined subequal to width of head through eyes; male genital capsule without long hairs projecting posterolaterally (presence in California not confirmed)

**Genus Hebrus Curtis**

*Naeogena* Laporte, 1833, Mag. Zool. (Guerin) 2(suppl.):34.
*Hebracella* Poisson, 1944, Rev. Fr. Entomol. 10:111 (= subgenus.)

*Hebrus* is identified by its five-segmented antenna. Short, intercalary rings are usually found between segments II-III, III-IV, and IV-V but these, except the one between segments II-III, are not likely to be noticed except under very high magnification (fig. 27).

The genus is cosmopolitan and contains over 100 species, of which 12 are Nearctic. Usinger (1956) recorded two species of *Hebrus* from California, and we have been able to add two more. Two other species, *H. major* and *concinnus*, have been reported from California, by early authors, but we have been unable to confirm their presence in the state.

A number of subgenera have been described from Africa, and the infragenic categories of *Hebrus* need review.
Hebrus buenoi buenoi Drake & Harris

Hebrus buenoi Drake & Harris, 1943, Notas Mus. La Plata, Zool. 8:52. Holotype ♂: White Plains, New York (CJD).

The long deep, median sulcus on the head separates H. buenoi from other California species.


This is the first record of H. buenoi from California. Long series of H. buenoi have been seen from several locations in Idaho and Oregon. These, and the California locality, are the only records for this species west of the Continental Divide. Records of H. buenoi from the southern United States and Mexico refer to the subspecies H. furvus Polhemus and Chapman (1970).

Hebrus hubbardi Porter

(Fig. 29)


Hebrus hubbardi typically occurs along the shaded banks of small, freshwater streams. The Banner locality is a wooded area.
Hebrus major Champion


With a length of 2.2 mm or more, H. major is larger than any other hebrid found in the United States.

Geographic range. Arizona, California, Texas, and Mexico.

California records. Drake and Chapman (1958) list major from California. According to Dr. Jon Herring, Systematic Entomology Laboratory, Washington, D.C., a female in the Drake Collection bears a label "Cal." The presence of major in California needs verification.

Hebrus obscurus Polhemus & Chapman
(Fig. 30)


This is a very small (1.6 mm or less), brachypterous species with distinctive male parameres (fig. 30).

Geographic range. Arizona and California.


In California both obscurus and hubbardi are known only from these sites.

Hebrus sobrinus Uhler
(Figs. 27, 31)


The large male genital capsule with long, erect, posterolateral hair is diagnostic in this species. Polhemus (1975a, 1977a) clarified the status of the above names.

Geographic range. Arizona, California, Colorado, Georgia, Missouri, Nevada, New Jersey, New Mexico, Texas, Vermont, and Virginia.


Judging by the scattered records, this species is widely distributed in California. Hebrus sobrinus is found rather commonly along the damp margins of freshwater springs, lakes, and streams in the western foothills of the Sierra Nevada.

Genus Merragata White


Merragata is separated from Hebrus by the antennal difference noted in the generic key. Usinger (1956) sug-
gested that this distinction may prove untenable. There are short intercalary rings between segments II and III. and III and IV. Merragata is a widespread genus containing 11 species of which two of the three Nearctic species have been reported from California, but the presence of one needs confirmation.

**KEY TO CALIFORNIA SPECIES OF MERRAGATA**

Last antennal segment clublike, broader than second segment (fig. 28) .................................................... hebroides White

Last antennal segment slender, not broader than second segment brevis Champion

**Merragata brevis** Champion

*Merragata brevis* Champion, 1898, Biologia Centrali-Americana. Rhynchota 2:122. Nine syntypes, sex unknown: Ventanas, Durango, Mexico; La Noria, Sinaloa, Mexico; San Gerónimo, Guatemala; Guatemala City, Guatemala; Rio Naranjo, Guatemala; Tola, Panama; Panama City, Panama (BMNH).

**Geographic range.** ? California, Florida, Mississippi, and Texas and south to Panama.

**California records.** Drake and Harris (1943) reported *M. brevis* from Los Angeles County. Their specimens cannot be located, and the occurrence of *M. brevis* in California needs verification. In Mississippi and Florida this species has been taken in the vicinity of brackish and saline areas.

**Merragata hebroides** White

(Figs. 28, 32)


Holotype: Oahu, Hawaii (BMNH).


**Geographic range.** Throughout the Americas from southern Canada to Argentina, but not Chile; also West Indies, Hawaiian Islands, and Canary Islands.

**California records (map 9).** This is the commonest hebrid in the state. We have seen it from 26 counties ranging from Shasta in the north to Imperial in the south. While more common at low elevations, *M. hebroides* is found in foothill springs and ponds up to 4,000 feet. Collection dates range from March to December.

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**FIG. 32.** *Merragata hebroides*, dorsal view (from Zimmerman, 1948).

**MAP 9.** California distribution of *Merragata hebroides* White.
All mesoveliids have apical tarsal claws except the extralimital genus *Mesoveloides* Hungerford. The saw-like female ovipositor which is about one-fourth the length of the body, and the three-segmented tarsi may be the only consistent family characters on a world basis. Macropterous mesoveliids usually have two or three closed cells in the forewing, usually have ocelli, and the scutellum is exposed. In apterous forms the ocelli are absent or greatly reduced, and the thorax is divided into three simple segments with no differentiation of a scutellum or wing pads. In America north of Mexico this family is represented only by *Mesovelia*. Members of this genus are elongate bugs with spiny legs, and the inner eye margins converge anterad. Winged forms of *Mesovelia* have ocelli, but they are not as common as apterous individuals.

The Mesoveliidae contains five genera. Since the works of Horvath (1915, 1929) no one has made a comprehensive study of the family, and the relationships of the three genera described since his last paper (*Mesoveloides*, *Speovelia* Esaki, and *Paraphrynovelia* Poisson) remain unclear. The exposed scutellum in winged forms and the two or three closed cells in the forewing distinguish the Mesoveliidae from the winged members of the Macraveliidae, but the separation of wingless forms of these two groups is not so easy on a world basis. China and Miller (1959) joined the two families, but we feel that further study of the component genera is needed before a final judgment can be made. The aberrant genus *Mesoveloides* which China and Miller placed in the monotypic subfamily Mesoveloiideinae, is known only from winged individuals. Ocelli are absent in this genus, a condition that normally occurs only in wingless forms in other genera. Furthermore, lateral metathoracic scent gland channels are present in *Mesoveloides*, a character which links the genus with the Veliidae. The slightly preapical tarsal claws of this genus differ from the apical claws found in other mesoveliids. The African genus *Madeovelia* Poisson which Poisson (1959) placed in the monotypic family Madeoveliidae, has both of these features also, and there may be a relationship between the two genera. Cobben (1968) shares this opinion. According to Poisson, *Madeovelia* links the Mesoveliidae and the Veliidae.

Mesoveliids occupy a variety of habitats. The widespread species, *Mesovelia mulsanti* White, lives on the surface of ponds, bog lakes, and other types of standing water in California. This species prefers waters that have floating or partially submerged vegetation. Bugs forage on the plants and run over open water with amazing agility. They walk by moving the opposite legs alternately. *Mesovelia mulsanti* is found on both fresh and brackish waters in the Netherlands Antilles (Cobben, 1960b) and Polhemus has collected it on saline waters around mangroves in Panama. The other California species, *M. amoena* Uhler, although occurring in the same general area as *M. mulsanti*, occupies a different habitat. It is secretive, often hiding in vegetation, crevices, and loose earth, and it is rarely found on open water. The other genera of the family range from cavernicoles to truly terrestrial.

*Mesovelia* are carnivorous and feed on a variety of dead or disabled insects found on the water surface or floating vegetation. They may also feed on weaker members of their own kind. Hungerford (1917a) and Ekblom (1928) found that ostracods are occasionally attacked. According to Hungerford, the crustaceans are speared through the surface film. Williams (1944) noted that *M. mulsanti* preyed on the hebrid *Merragata hebroides* White.

The life history of *Mesovelia mulsanti* was studied by Hungerford (1917) and Hoffmann (1932a). The latter also studied *M. amoena* (as *douglasensis*) and *M. cryptophila* Hungerford. Ekblom's (1928) paper contains much interesting data on the biology of Old World species. Eggs are inserted in plant tissue at the waters edge by means of the well-developed, sawlike ovipositor which pierces stems by means of rocking motion of the body. The egg is elongate oval and the micropylar end curves up to a flat operculum or lid which is exposed when the egg is deposited. When laid, the egg is white but it becomes transparent as the embryo develops.
Mesovelia mulsanti lays about 100 eggs, while M. amoena lays from 100 to 200 (Hoffmann, 1932a). Detailed figures of the eggs may be found in Cobben (1968).

Incubation of the egg takes 7 to 9 days in M. mulsanti and 12 days in M. amoena (Hoffmann, 1932a), but Mesovelia eggs laid late in the summer or early fall may overwinter and hatch in April or May (Southwood and Leston, 1958). According to Ekblom (1928) and Cobben (1968) complete incubation and successful hatching can occur underwater as well as in moist air. Unlike most Gerrimorpha which have a sharp egg burster, the mesoveliid embryo develops a bladderlike outgrowth in the frontal region which pushes off the egg cap. The nymph then struggles free and swims to the surface, breaking through the surface film easily (Ekblom, 1928).

Most Mesovelia have five nymphal instars, but Hoffmann found only four in M. cryptophila. The adult stage is reached in 18 to 25 days and there may be several generations per year.

Hungerford (1920) described copulation in Mesovelia mulsanti. "In mating, the male mounts the female, clasps his forelegs around her mesothorax in front of her middle legs, rests his middle legs upon the water film or other supporting surface, and holds the hindlegs poised in the air. The copulatory organ of the male is long and curves around the side of the tip of the female's body to come in contact with the genital opening." According to Hoffmann (1932a), the male of Mesovelia amoena makes a quick jump onto the back of the female, then slides back quickly to engage her. Hungerford (1924a) said that in amoena, the male, once connected is supported by the genitalia alone, with all of the legs poised in the air.

Mesovelia eggs are parasitized by the trichogrammatid wasp Hydrophilia aquilovolans (Matheson and Crosby) (Hoffmann, 1932b). Cobben (1965a) found what appeared to be some kind of symbiotic microorganism in mesoveliid eggs, a condition unknown in other Gerrimorpha. Benjamin (1970) recorded parasitic fungi (Laboulbeniales) in the abdomen and legs of Mesovelia mulsanti.

Hoffmann (1932a) found that eggs could withstand freezing, and Galbreath (1973) stated that nymphs and adults of M. mulsanti do not survive hard freezes. Thus in colder climates Mesovelia overwinters in the egg stage. Hungerford (1920), Hoffmann (1932a), and Neering (1954) could not find overwintering adults in Kansas, and Hoffmann only found first instar nymphs in May; however, Froeschner (1949) noted that adults of M. mulsanti are found all year in Missouri. In the southern United States, including the desert areas of California, adults of M. amoena and M. mulsanti are active all year. M. mulsanti has been taken in February as far north as Lake County, California.

Apterous individuals far outnumber winged forms in Mesovelia. The absence of wings is accompanied by reduction or loss of the ocelli, and simplification of the thoracic dorsum. Gupta (1963b) hypothesized that alate forms require the visual supplement provided by the ocelli; on the other hand, the absence of ocelli in apterous forms may be genetically linked with some other structure affected by wing degeneration. Macronpterous forms of Mesovelia have been taken at lights.

The forewing membrane of winged forms is often broken off in Mesovelia (fig. 36). According to Hungerford (1917a) this is accomplished by rubbing the hind tibiae against the wings. The spines of the leg are probably important in this task (Jordan, 1951). The forewing veins are strong and resist breakage and they form a natural cleavage line. The reason for this unusual form of autotomy is unknown. As Jordan points out, the wings of the female may hinder copulation and loss of the membrane might therefore be beneficial, but both sexes exhibit membrane loss and there is no apparent benefit to the male.

Genus Mesovelia Mulsant and Rey


The type-species of Mesovelia is incorrectly spelled furcata in most publications.

Mesovelia is distinguished from the other genera in the family by the following combination of characters: head elongate, blunt anteriorly; eyes many faceted and not touching the anterior pronotal margin; inner eye margins converging anterad; beak reaching midcoxae; hindmargin of pronotum straight, pronotum shorter than mesonotum; legs with scattered black spines. The morphology of Mesovelia has been described by Gupta (1963b).

The genus is cosmopolitan, and some species are broadly distributed: M. mulsanti ranges from Canada to Brazil and M. vittigera Horvath occurs throughout tropical Africa and Asia. Nine of the approximately 20 species occur in the New World; four of these are found in North America and two in California. Jaczewski (1930) keyed most of the New World species. Drake (1949) listed all of our forms with the exception of a species described subsequently by Hungerford (1951) and one described by Polhemus (1975b).

Species of Mesovelia are easily distinguished by char-
acters of the penultimate abdominal sternum (VIII) of the male (figs. 34-35). The presence or absence and number and arrangement of setal tufts on the surface are diagnostic for most species. The length of the beak and forewing venation are also useful.

KEY TO MEOVELIA OF AMERICA, NORTH OF MEXICO

1. Front and middle femora armed beneath with a row of black spines; male with two black tufts of minute setae on apparent sternum VII (true sternum VIII) (fig. 35) mulsanti White
   Front and middle femora without a row of black spines beneath; male without black setal tufts on apparent sternum VII (fig. 34).

2. First antennal segment length equal to nine-tenths width of head through eyes or more... cryptophila Hungerford

3. First antennal segment length equal to no more than three-fourths width of head through eyes... amoena Uhler

Mesovelia amoena Uhler
(Figs. 34, 36)

Syntypes. 99: Grenada, West Indies (BMNH, USNM).


This small species (1.8-2.1 mm long, 0.6-0.8 mm wide) is about half the size of M. mulsanti, but it is robust for the genus. The appendages are stouter than in the other North American species. In contrast to other Mesovelia, M. amoena is brown instead of green.

Jaczewski (1930) surmised that M. douglasensis was a synonym of M. amoena, but as Hungerford (1953) pointed out, West Indian males must be compared with M. douglasensis males before this synonymy can be confirmed.

Geographic range. Mesovelia amoena is known from the West Indies, Panama, and Brazil (Harris and Drise, 1941), and M. douglasensis occurs from Quebec, Canada, to Florida. Usinger (1956) recorded M. amoena from Mississippi, Louisiana, and Texas and several California localities. We have also seen material from Nevada and Hawaii.


Mesovelia amoena occurs on moss-covered rocks of hot spring caves in Death Valley, and in crevices along edges of ponds and oasis springs. This species is more secretive than M. mulsanti and is seldom collected on open water. These two occur together in some desert springs.

In the tropics and in Hawaii, M. amoena is apparently parthenogenetic; at least males are unknown. (Cobben, 1960b; Gagné and Howarth, 1975).

Mesovelia mulsanti White
(Figs. 33, 35, 37)

Mesovelia mulsanti is the largest North American species (more than 3 mm long). It is readily identified by the row of black spines on the ventral side of the front and middle femora, and the two black tufts of minute setae on the eighth abdominal sternum of the male (fig. 35). The male hair tufts and the prongs and lobes of the female abdomen are variable, and Jaczewski (1930) established four subspecies based on this variation. Herring (1950) found no justification for these forms, and Neering (1954) studied over 3,800 specimens in an effort to correlate the three characters subspecifically, but concluded that the morphological differences had no taxonomic significance.

Geographic range. Southern Canada to Argentina, the West Indies and Hawaii.

California records (map 11). The species has a scattered distribution throughout the state, and occurs in a variety of habitats. Mesovelia mulsanti is found up to 5,200 feet and is very abundant in foothill ponds, but it is not common in the Sierra Nevada, although Usinger (1942) first recorded the species in California from Swamp Lake in Yosemite Valley. Nymphs and adults are often found on open water, especially around mats of algae and duckweed.

MAP 11. California distribution of Mesovelia mulsanti White.
This family is represented in North America by the genus *Hydrometra*. These are fragile, sticklike bugs with threadlike legs and very elongated heads that are about as long as the thorax (fig. 38). *Hydrometra* means “water measurer” and refers to the slow measured gait of these bugs as they traverse the surface film. The lengthening and narrowing of the body and appendages in hydrometrids is evidently an adaptation to life on the surface film because weight is reduced and distributed over a large area of the water surface (China, 1955). The antennae are four-segmented in our forms but some extralimital genera have five segments. Ocelli are absent except in one exotic species. The tarsi are three segmented and the claws are apical except in one extralimital genus. Metasternal scent gland openings are absent in the Hydrometrinae, but are present in the other two subfamilies. Wing polymorphism is common and varies from apterous to macropterous; the hemelytra of winged morphs have two closed cells in our forms.

The Hydrometridae contains about 110 species and they are divided among three subfamilies and six genera (China and Usinger, 194%). The Hydrometrinae, which is worldwide, contains the majority of the species of the family, about 100, and most of these belong in the genus *Hydrometra*. The Limnobatinae contains the single monotypic Neotropical genus *Limnobatoides* Hussey which is of interest because it has dorsally located, preapical tarsal claws (Hussey, 1925). The Heterocleptinae contains a single, terrestrial, African genus, *Heterocleptes* Villiers, with three species (China, Usinger, and Villiers, 1950). China and Usinger (1949a) assigned it to the Hydrometridae but they, as well as China (1963), have indicated that *Heterocleptes* has affinities with the Macroveliidae. China (1955) considered this genus to be primitive because of certain features not found in other hydrometrids: vestigial ocelli, paired metathoracic scent gland openings, three hemelytral cells, and no arolia (instead, the parempodia have weak pads as in some terrestrial bugs—see Cobben, 1968, p. 366).

*Hydrometra* are most often found on quiet waters having abundant emergent vegetation which provide protection for them. Usually these bugs venture onto open water only when disturbed. In the Colorado River area *H. australis* Say is most common in small drainage pools choked with vegetation but lacking fish. The ab-
sence of a metathoracic scent gland may render them susceptible to fish predation, but this remains to be determined (Usinger, 1956). *Hydrometra* walk over the water and vegetation by moving the opposite legs alternately, primarily in a horizontal plane. Although these bugs are typically inhabitants of fresh water, *H. australis* has been found occasionally in saltwater tide pools in Florida (Herring, 1949), and in brackish water ponds in Texas (Polhemus, unpublished).

Hydrometrids are carnivorous, feeding upon dead or disabled insects and other invertebrates that they find on the water or floating vegetation. Victims are impaled on the beak and held by the retrorsely barbed mandibles while the juices are sucked up through the maxillary stylets. Saliva injected into the prey contains enzymes which liquefy the tissues; a victim which is attacked and almost immediately released soon dies. Smaller prey are speared with the bugs' rostrum and carried to shore for feeding. Larger prey are fed upon in situ. Southwood and Leston (1959) suggested that hydrometrids locate prey by sensing vibrations caused by the struggling animal. According to Hungerford (1920) and Sprague (1956) common prey of hydrometrids include emerging midges, mosquito wrigglers, blood worms, cladocerans, and collembolans. Their predation on *Anopheles* larvae led F. X. Williams to consider their introduction as biological control agents (Usinger, 1956).

While hydrometrid nymphs undoubtedly fall prey to other predators, and cannibalistic predation upon them has been noted, the adults have fused thoracic and abdominal segments which reduce their vulnerability to small predators (Sprague, 1956). However, *Mesovelia* is known to attack them (Butler, 1923).

A number of *Hydrometra* life histories have been published, but virtually all deal with two species, the Old World *H. stagnorum* (L.) or the North American species *H. martini* Kirkaldy, which may prove to be conspecific with *H. australis*. Sprague (1956) has summarized the earlier works and given much valuable new data along with a complete morphological study. Egg details are illustrated in Sprague (1956) and Cobben (1968), and good photographs are found in Hungerford (1920). The eggs of *H. martini* are about 2 mm long and 0.28 mm wide, spindle shaped, beautifully sculptured and borne on a stalk (fig. 4). Eggs are laid singly on almost any object, usually just above the surface of the water, although Takahashi (1921) often found *Hydrometra* eggs under water in Japan. The female exudes a glistening drop of a gummy substance from the genital opening, which she then presses against the oviposition site where it hardens rapidly. The base of the egg stalk follows this fluid, and as the egg emerges, the female lifts her body drawing the egg out perpendicular to the support. Eggs are pearly white, but turn brown upon exposure to moist air or wet surfaces. One female produced up to 11 per day, with a total of 173 over 37 days. Thus each ovariole may produce about one egg per day (Hungerford, 1920). The incubation time varies from about 7 to 23 days, depending on temperature, with the average being 11 to 13 days. Hydrometrid embryos split the shell with a sclerotized egg burster, then thrust the head through the slit. Successful hatching can take place either in the water or above it.

The five nymphal instars require about two weeks to reach adulthood. Hungerford (1920) gave the minimum life cycle as 15 days, but 21 to 35 days is typical. There are apparently three broods per summer in the northern United States, and perhaps five or more from Kansas south. Mating begins in the spring and continues throughout the warm season. Copulation takes place with the smaller male on top of the female, his genitalia bent down to engage her (see figure in Ekblom, 1926). While *in copulo*, the female walks about and feeds occasionally. The male may remain mounted for as long as 15 minutes, but six minutes is the norm.

Overwintering adults appear in the spring, often in mid-March. *Hydrometra martini* often live seven to nine months in the laboratory, and Torre-Bueno (1905) kept one individual alive for 15 months. The only known parasite of hydrometrids is the mymarid wasp *Litus cynipeus* Haliday which parasitizes the eggs of Old World species (Poisson, 1957).

Flight in Western Hemisphere hydrometrids is not a commonly recorded event, but it undoubtedly plays an important role in their dispersal. In North America winged forms make up perhaps only two or three percent of a given population (Torre-Bueno, 1926; Sprague, 1956); and there is no record of sudden increases in macropters due to external influences such as drying of ephemeral habitats, as has been noted in gerrids. Wing development varies greatly among hydrometrids. In *H. martini* both apterous and macropterous forms are rather rare, the predominant form being micropterous. The tiny wing pads are sometimes visible only under high magnification. In macropterous forms, the wings rarely reach the fifth abdominal segment. In the laboratory, Sprague (1956) found that winged females produced fewer eggs and were shorter lived than wingless individuals.

Subfamily Hydrometrinae

This subfamily contains four genera of which only one, *Hydrometra*, occurs in North America. The lack of
MENKE: THE SEMIAQUATIC AND AQUATIC HEMIPTERA OF CALIFORNIA

a scent gland opening on the metasternum and the four-segmented antennae are characteristic of this subfamily.

Genus Hydrometra Latreille

Hydrometra Latreille, 1796. Précis caractères génériques des insectes p. 86 (no species). Type-species: Cimex stagnorum Linnaeus, 1758, designated by Latreille, 1810 (one of two species first included by Lamarck, 1801).


The genus Hydrometra is characterized by the elongate thorax with its nonsulcate mesosternum, and in having the midcoxae closer to the forecoxae than to the hindcoxae. This is by far the largest genus in the family with about 100 species, of which 39 occur in the New World and nine in North America. Only two of these are reported from California, and one of them has not been found since the original collection was made.

The principle taxonomic works on the genus are Torre-Bueno (1926), Hungerford and Evans (1934) and Drake and Lauck (1959). Since Drake and Lauck published their checklist, Mychajliw (1961) described four new species, one of which occurs in the United States.

KEY TO CALIFORNIA SPECIES OF HYDROMETRA

Pleural lobes above fore and midcoxae each with one pit (fig. 39); sides of clypeus converging toward rounded apex; male sternum VII with a pair of short, transverse carinae basally whose ends are angular (fig. 40)............................................ australis Say Pleural lobes above fore and midcoxae with numerous pits (fig. 41); sides of clypeus slightly diverging toward truncate apex; male sternum VII with a pair of widely separated tubercles which are inclined outward ........................................... lillianis Torre-Bueno

Hydrometra australis Say
(Figs. 38-40)


The antennal differences used to separate H. australis and the common North American species H. martini seem to be clinal in a south to north direction and the latter species may prove to be a synonym of H. australis. The second antennal segment is usually about 2.5 times the length of the first in H. australis and most California specimens approach this ratio. The proportions in H. martini are about 2:1, and this species is typically a more northern form.

Geographic range. Transcontinental in the southern United States, southward into Mexico and the Caribbean islands.


Burdick (1968) recorded H. australis (as H. martini) from White's Bridge Slough, 33 mi. sw., Fresno, Fresno Co. At Snelling H. australis inhabited semipermanent pools of water that possessed some vegetation. In Death Valley it is found in a densely vegetated, permanent marsh formed by the warm outflow of Saratoga Spring.

Hydrometra lillianis Torre-Bueno
(Fig. 41)


Geographic range. California

California records. SANTA BARBARA CO.: Santa Barbara, "F'hill", VI-07 (KU, USNM).

Despite intensive searches in the Santa Barbara area by different collectors this species is known only from four type specimens. Torre-Bueno pointed out that in its general facies H. lillianis was different from all other western and southern U.S. species. This fact, plus the results of subsequent collectors, suggest that Torre-Bueno's material may have originated outside the U.S., but was mislabeled.
FAMILY MACROVELIIDAE

J. T. Polhemus and H. C. Chapman

These are slender bugs with an elongate head and spineless legs. The tarsi are three-segmented and the claws are apical. The unmodified legs and tarsi are better suited to walking than to rowing. The inner margins of the eyes are arcuate, but they do not converge anterad. In winged forms, the concealment of the scutellum by the pronotum, and the presence of six closed cells in the forewing are diagnostic. Ocelli are present except in wingless forms. Color varies from light brown to blackish gray. Winged forms have whitish hemelytral spots.

Macroveliids are closely related to the Mesoveliiidae and Veliidae. The parallel inner eye margins and spineless legs separate members of the family from Nearctic members of the Mesoveliiidae. The concealed scutellum in winged forms, and the absence of an ovipositor designed for piercing plant tissues also differentiate macroveliids from mesoveliiids. The single, median, metathoracic scent gland opening on the adult venter, commonly called the "omphalium," and the absence of fully developed lateral scent gland channels distinguish this family from the Veliidae.

We follow McKinstry (1942), Drake & Chapman (1963) and Štyš (1976) in recognizing the Macroveliiidae as a family. China and Usinger (1949b) treated the group as a subfamily of the Veliidae, and China and Miller (1959) transferred the subfamily to the Mesoveliidae on the advice of Usinger (footnote, p. 24 in China & Miller) who suggested this association because of similar nymphal morphology. Cobben (1968) said that on the basis of egg shell structure the Macroveliiidae is most closely related to the Veliidae.

The African genus Ocellovelia China & Usinger was included in the Macroveliiidae by Drake & Chapman (1963), but Štyš (1976) transferred the genus to the Veliidae, a move with which we concur. China (1963) suggested that another African genus, Heterocleptes Villiers, might be assigned to the Macroveliiidae but presently it is regarded as a hydrometrid. The Macroveliiidae consists of three monotypic New World genera: Macrovelia, Oravelia, and Chepuvelia China, the last known from Chile. Štyš (1976) keyed the genera.

California species inhabit spring or seep areas, usually where there is abundant vegetation, especially watercress and mosses. The bugs are normally found in the vegetation or on the nearby earth. Macroveliids are negatively phototropic and they tend to rest under overhanging rocks or on the vertical dark sides of stones. Oravelia occupied areas so dark that flashlights had to be used to find them (Drake and Chapman, 1963). Contrary to McKinstry's (1942) observations, Polhemus has repeatedly watched M. hornii Uhler cross spring water placed in an observation aquarium without difficulty. Some of the bugs spent protracted lengths of time on the water without breaking the surface film.

The feeding habits of Macrovelia and Oravelia are unknown, and no complete life history studies have been made. In aquarium studies Polhemus has observed copulation in Macrovelia. The male perches astride the female and grasps her with all of his legs. The female was able to move freely and the male did not drop off even when they were disturbed. Polhemus found that M. hornii females kept in an aquarium laid their eggs in moss on exposed rocks. The eggs are asymmetrically spindleshaped, flattened along one side (fig. 1), and are firmly glued to the substrate. The egg is 3.3 times as long as wide, and hatches in 10 to 13 days. Cobben (1968) described and figured eggs of all of the macroveliid genera. The egg of Oravelia is also spindleshaped and about three times as long as wide, and it has a nipplelike micropyle.

Adults of Macrovelia hornii overwinter and are active during warm periods in mid-January at Denver, Colorado. Macrovelia and Oravelia have been taken throughout the year in California.

Macrovelia hornii is parasitized by fungi (Laboulbeniales) which are location specific on bugs. Benjamin (1967) described Laboulbenia macroveliae from the legs and L. uhleri from the abdomen of M. hornii.
KEY TO NEARCTIC GENERA AND SPECIES OF MACROVELIIDAE

Ocelli absent; apterous; posterior margin of pronotum arcuate, scutellum exposed; antennal segments longer than head width across eyes; abdominal scent gland opening slightly beyond middle of tergum IV Oravellia pege Drake & Chapman

Ocelli present, well developed; macropterous or brachypterous; posterior margin of pronotum angular, concealing scutellum; antennal segments I-III shorter than head width across eyes; abdominal scent gland opening slightly before middle of tergum V .............. Macrovelia hornii Uhler

Genus Macrovelia Uhler


Macrovelia hornii Uhler (Figs. 42-43)


This is a much smaller bug (3.3-4.0 mm) than Oravellia pege. Wingless forms of hornii are unknown, but brachypterous bugs have been collected in the San Francisco Bay region and in northern California.

Geographic range. California, Oregon, and New Mexico to Nebraska and North Dakota; Baja California.

California records (map 12). Records span nearly the entire length and breadth of the state, and reach elevations of 9,000 feet. Specimens have been collected every month of the year although bugs taken in January were apparently hibernating under stones. The damp shores of permanent springs and streams in the low foothills are common habitats for M. hornii.

Genus Oravellia Drake & Chapman


Oravellia pege Drake & Chapman (Fig. 44)


This is a rather large bug (5.25-5.50 mm). All specimens known are completely wingless.

Geographic range. California.


This bug is known from one locality. It is found in cracks and crevices in the basal section of the face of a sheer, rocky cliff which is continuously moistened by water flowing from openings in the cliff. Specimens have also been found under rocks, leaves, and other moist debris on the ground at the foot of the cliff which borders an intermittent stream. Additional material has been taken in protected situations along the stream margin. The cliff site was in deep shade. Nymphs were seen on the moist walls of the cliff in April. Macrovelia hornii was occasionally taken with O. pege.

FIG. 44. *Oravelia pege*, apterous male (from Drake & Chapman, 1963).

FAMILY VELIIDAE/Small Water Striders, Water Crickets, Riffle Bugs

J. T. Polhemus and H. C. Chapman

Veliids are mostly small, oval, or elongate bugs. In comparison with the gerrids the legs are short. The antennae vary from moderately long to long, and are four-segmented. Ocelli are absent except in the Old World genus Ocellovelia China & Usinger. The middle pair of legs is located about midway between the front and hind pair except in the Rhagoveliinae and a few forms in other subfamilies. The claws are preapical except in the Old World genera Hebrovelia Lundblad and Velohydrobia Stys. The metathoracic scent gland ostioles are located on the sternum, and their secretions are disseminated through lateral channels that end on the pleuron in front of the hindcoxae. Usually a prominent tuft of setae surrounds the end of each channel. These bugs vary from yellowish brown to grey or black, with the dorsum often marked with yellowish, blue-grey, or silver spots. The body is covered with a velvety hydrofuge pile. Wing polymorphism is common in veliids, and taxonomy at the species level is based primarily on apterus forms because they are the most commonly encountered morphs.

The Veliidae are closely related to the Gerridae, and on a world basis the only apparent character that will distinguish the veliids is the membranous vesica of the aedeagus. However, all California veliids possess at least a weak, median, longitudinal groove or line on the frons. This head feature and the lateral metathoracic scent gland channels are absent in California gerrids. Further discussion of the difficulty in separating these two families can be found in the section on Gerridae.

As conceived by us, the Veliidae is divided into seven subfamilies containing about 30 genera and approximately 420 species. This classification differs from that of China & Usinger (1949b) in only two respects: we have recognized the Macroveliinae as a family, but we, like Stys (1976), have retained Ocellovelia, which China and Usinger considered a macroveliine, in the Veliidae. In their paper on the Macroveliidae, Drake and Chapman (1963) proposed the subfamily Ocelloveliinae for the single genus Ocellovelia. In our opinion the Ocelloveliinae belongs in the Veliidae because of the short, declivous head, the lateral metathoracic scent gland channels, the preapical claws, and the large parameres of the male genitalia. The Ocelloveliinae is similar to the Veliinae (tarsal formula 3:3:3 and general structure), but the presence of six closed cells in the forewing and presence of ocelli set Ocellovelia apart from this group and other veliids.

Four veliid subfamilies are restricted to the Old World: Ocelloveliinae, Perittopinae, Hebroveliinae, and Haloveliinae. The others, Microveliinae, Rhagoveliinae, and Veliinae, are cosmopolitan, but only the first two, with 10 species, are represented in California. The Veliinae occurs in Arizona. Smith and Polhemus (1978) published keys and checklists for all North American Veliidae. Stys’ (1976) subfamily treatment differs somewhat from ours.

Veliids inhabit an astonishing variety of habitats, but because of their small size and usually secretive habits they are not nearly as well known as the Gerridae. The genera Microvelia (Microveliinae) and Paravelia Bredin (Veliinae, = Velia of American authors, see Polhemus, 1976a) usually inhabit the banks and vegetation at the margins of streams, ponds, and springs, and venture onto open water only when disturbed. These bugs are at home on land, in contrast to the more specialized genus Rhagovelia (Rhagoveliinae) and related forms which live on the water surface. Most veliids are restricted to fresh water, but some genera have adapted to living on brackish or salt water. In southern Florida Husseyella Herring (Microveliinae) and Trochopus Carpenter (Rhagoveliinae) live among mangroves and the latter genus is even found on the open water of bays, usually close to shore.

Most Paravelia and many Microvelia prefer the recesses of overhanging banks of streams, the undersides of large stones or the tangles of tree roots near water, rock ledges, etc. Some veliids occupy special “container” habitats such as tree holes, bromeliads, and crab holes. A few wide-ranging open habitat species of Microvelia and Rhagovelia have also been found in caves.

The food of veliids is largely the same as that used
by other Gerromorpha, i.e., small arthropods that fall on the water surface, ostracods and *Daphnia* trapped in the surface film, and mosquitoes in various stages (Torre-Bueno, 1910; Hungerford, 1920; Bacon, 1956). *Microvelia* have been observed feeding on rafts of newly laid mosquito eggs (Laird, 1956), and Frick (1949) reared *M. capitata* Guérin-Méneville (apparently a synonym of *pulchella* Westwood) entirely on anopheline larvae. He concluded that these are their natural food. Miyamoto (1953) reared *M. diluta* Distant on *Drosophila*. Cheng and Fernando (1971) reared *Rhagovelia obesa* Uhler on commercial fish food consisting of insect parts, milk solids, and fish meal, and Kellen (1959) reared *Halovelia marianarum* Usinger on chironomid flies, collemбола, and leafhoppers.

Veliids apparently perceive their prey by a combination of visual and mechanical means. Meyer (1971) performed experiments on *Velia caprai* Tamanini with various kinds of visual stimuli, and concluded that this species locates prey by means of a visual "central flickering detector" in combination with a water surface vibration detector.

A number of life history studies are available for American veliids, but they are mostly for *Microvelia* and many of them are incomplete. Various *Microvelia* species have been studied by Torre-Bueno (1916, 1917a), Hoffmann (1925) and Frick (1949). The only American *Paravelia* that has been studied is *watsoni* (Drake), but Ekblom (1926) gave a good account of a European species of the related genus *Velia* Latreille, probably *V. caprai*. The only successful life history study in *Rhagovelia* was made by Cheng and Fernando (1971) on *R. obesa*, although Bacon (1956) made an attempt to rear *R. rivale* Torre-Bueno.

*Paravelia* and *Microvelia* lay their eggs on floating objects, moss, duckweed, stones, and living or dead leaves either just above or below the water surface. Eggs are laid singly or in clusters, and are attached with a gelatinous glue that covers much of the egg (Cobben, 1968). The eggs are white when laid but turn amber as development progresses, and they are often covered with sparse lines, cubical projections, or, in the case of *Microvelia gerhardi* Hussey and *M. americana* (Uhler), a honeycomb mesh structure. The eggs are oval, and usually slightly flattened lengthwise on one side. Torre-Bueno (1917a) found only two eggs at a time in *Microvelia pulchella* Westwood, but Miyamoto (1953) found that *M. diluta* laid an average of 7.4 eggs per day with three females laying a total of 375, and Frick (1949) noted that *M. pulchella* laid up to 505 eggs. Cheng and Fernando (1971) found only one to nine eggs per female of *Rhagovelia obesa* after dissection, and Brinkhurst (1959) found 16 eggs in a mature female of *Velia caprai*.

During maturation of the egg, the eyes and black egg burster become obvious, and finally the legs become visible. The egg burster splits the shell for 1/3 to 2/3 of its length. The embryonic cuticle is shed after the nymph has almost emerged from the split chorion (in *Microvelia*, Don, 1967). Successful hatching can occur above or below the water, and nymphs can remain submerged up to a day and still survive (in *Microvelia*, Miyamoto, 1953). Nymphal development time varies with temperature and other climatic factors. For example, the nymphal period for *Microvelia pulchella* in Panama averaged 20.7 days during a cool, humid, windless period, but 26.6 days in a hot, dry, windy environment (Frick, 1949). In experiments with *Microvelia macgregori* Kirkaldy, Don (1967) found the average nymphal period to be 13.8 days at 26° C. but 44.5 days at 15° C.

A number of nylpers have only four nymphal instars rather than the normal five. Torre-Bueno (1916, 1917a), Hoffmann (1925), Frick (1949), and Don (1967) have discussed this phenomenon for various *Microvelia* species, and Cheng and Fernando (1971) studied it in *Rhagovelia obesa*. Out of 110 separate rearings, Frick (1949) obtained only nine adults of *Microvelia pulchella* that had developed through four nymphal instars. However, some species apparently always have only four. Don reared 225 adults of *M. macgregori* from nymphs that were exposed to various depressed and elevated temperatures, and in each case there were four instars.

During copulation veliid males ride on the backs of the females. Many *Microvelia* males, for example, those of the Nearctic *M. australina* Torre-Bueno, ride more or less continuously, whether copulating or not. Miyamoto (1953) described this behavior in *M. diluta*, where not only adult males, but fourth and fifth instar nymphs rode on the backs of females. According to Miyamoto, the combs commonly found on the distal part of the foretibia, and sometimes other tibiae, of *Microvelia* species may be adaptations to help the male grasp the female while riding. In many tropical species the female prothorax, pleural region, and abdomen are modified also, and these modifications provide species characters which have seldom been used (Polhemus and Herring, 1970; Polhemus, 1974a).

Most temperate zone veliids overwinter as adults, although Cheng and Fernando (1971) concluded that *Rhagovelia obesa* overwinters in the egg stage. Temperate species of *Microvelia* and *Velia* are active during warm periods throughout the winter but become quiescent during cold periods (Ekblom, 1926; Southwood and Leston, 1959; Don, 1967). Polhemus has found *Microvelia torquata* Champion active in the gravels of a
seep area near Denver during a warm period (18°C) in January. One week earlier the temperature had been as low as -18°C.

Veliids are hosts for a number of parasites, such as cnidosporids, nematodes, and flagellates. Several hemipterous parasites are known from Velia eggs (Poison, 1957). Benjamin (1967, 1970) discussed the laboulbenial fungi known from veliids, and described a number of new species. Five species are known on Paravelia, four on Rhagovelia, and four on Microvelia, with one of the latter, L. microveliae Benjamin, described from California specimens of Microvelia beameri McKinstry. Laboulbeniales species exhibit remarkable specificity for host species, sex of host, and position on the host.

Stridulation is not recorded in the Veliidae, but some Paravelia species, and particularly those of the genus Stridulvelia Hungerford, have structures that have been interpreted as having a stridulatory function. In Stridulvelia there is a row of pegs on the paratergites and a file or roughened patch on the hindfemur. An undescribed species of Paravelia known to us has an arcuate row of pegs on the abdominal venter and a rasplike area on the hindtrochanter.

Microvelia and Paravelia walk readily on land and run on water, and all of their legs are subequal in length (rare exceptions). The rhagovelines, which also skate on the surface, have elongate, highly modified mid- and hindlegs. In Rhagovelia the last tarsal segment of the midleg is deeply cleft. The claws and a pair of plumelike structures are folded within the cleft. The plumes (fig. 10) can be extended down into the water fanlike to assist in propelling the bug when skating.

The posterior femur of many of these bugs is set with a row of long sharp spines that are used to clean the swimming plumes (Bacon, 1956). The specialized midlegs of Rhagovelia give these bugs great agility on the water surface and they often skate against strong currents for long periods, but on land the bugs are clumsy (Bacon, 1956). When disturbed, Rhagovelia sometimes dive under water where they swim with ease (Torre-Bueno, 1907). Husseyella and a few other extralimital genera have blade-like claws and arolia which are used like the plumes of Rhagovelia. An unusual method of water propulsion was found in some Old World Velia and noted by Polhemus for some Nearctic Microvelia, subgenus Kirkaldya, is the utilization of the contracting surface film to move forward at a rapid rate without moving the legs. Apparently the secretion of saliva by the bugs causes the film to contract (Linsenmair and Jander, 1963).

Evidently veliids are capable of extended flight. Several veliid genera have been taken at lights (Fernando, 1961, 1963, 1964b, Drake & Hussey, 1951), and Bacon (1956) found Rhagovelia distincta Champion in a water tank in Arizona that was 40 miles from the nearest water. Generally macropterous forms are uncommon in Nearctic veliids just as in gerrids, however, wing polymorphism in the Veliidae has not been studied as much as in the latter family. Don (1967) experimented with Microvelia macgregori, a polymorphic species found in New Zealand. He reared eggs and nymphs under controlled temperatures, but only apterous adults were obtained. In the field he noted that the percentage of alates increased as the habitat decreased. This, plus the negative results in his laboratory temperature experiments, suggest that changing microhabitat conditions may be one of the determining factors in the production of alates in multivoltine Microvelia species.

KEY TO NEARCTIC GENERA OF VELIIDAE

1. Last tarsal segment of midleg with a cleft that extends about three-fourths the length of the segment, two plumelike structures arising from base of cleft (fig. 10) .... 3

Rhogovelia

2. Last tarsal segment of midleg not deeply cleft, and without plumelike structures .... 3

Microvelia

3. Tarsal formula 1:2:2 (Rhagoveliinae) .......... 4

4. Claws and arolia of midleg blade-like; midcoxae much closer to hindcoxae; widespread (fig. 49) .......... Microvelia Westwood, p. 51

Subfamily Microveliinae

Members of the Microveliinae, of which only Microvelia is found in California, are characterized by the absence of ocelli, tarsal formula 1:2:2, claws preapical (at least in our forms), and hemelytra when present with four closed cells. See Styts (1976) for a discussion of the classification of this subfamily.

Genus Microvelia Westwood

Microvelia Westwood, 1834. Ann. Soc. Entomol. Fr. 3(2):pl. 6 & fig. 5.

Type-species: Microvelia pulchella Westwood, 1834, monotypic.


Microvelia is a cosmopolitan genus with about 200 species. Of the more than 70 New World forms, 19 occur in the continental United States. Usinger (1956) keyed nine species that were known from California or suspected to occur in the state. We can confirm the presence of eight of these and the ninth, *M. signata* Uhler, may be found eventually in southern California.

The taxonomy of *Microvelia* has been neglected, but the unpublished thesis of McKinstry (1933) contains much useful information. Smith and Polhemus (1978) published a key to the North American species and provided a checklist. Drake & Hussey (1955) discussed generic synonymy, the status of subgenera and thoracic morphology and gave a checklist of all New World species. Esaki and Miyamoto (1955) also treated thoracic morphology.

Drake and Hussey (1955) did not use subgenera for North American species of *Microvelia*. Polhemus (1970) restored *Kirkaldya* as a subgenus of *Microvelia* when it was discovered that the flat plane of the upward curving, leaflike arolium was horizontally oriented. In *Microvelia* s.s. and most Gerromorpha (see Cobben, 1968:365) both aroli are flattened and oriented in a vertical plane.

Some *Microvelia* are among the smallest of the semiaquatic bugs. Some specimens of *M. hinei* measure slightly more than a millimeter in length. Most of the smaller species are found around ponds or along the slow-moving portions of streams. Species of the subgenus *Kirkaldya* are most often found near cool streams and springs, as are *Microvelia* (*M.*) *cerifera* and (*M.*) *signata*: the latter species often secludes itself in small, dark recesses where it can rest on the rocks at the waters edge. Although *Microvelia* species usually stay close to the bank or on vegetation they often run rapidly over the water when disturbed.

Apterous forms are most often encountered and species taxonomy is largely based on them. Males offer the best characters and the following key is based solely on them. Females must be associated with males for identification.

### Places to Check

1. Mesonotum not concealed by pronotum; pronotum not attaining sublateral pits (fig. 45B), shorter than mesonotum as measured along midline (fig. 45B); length more than 2 mm; hindtibia straight... subgenus *Kirkaldya*...
2. Mesonotum concealed by pronotum; pronotum reaching to or beyond level of sublateral pits (fig. 45A), or if mesonotum exposed, then body length less than 2 mm and hindtibia curved... subgenus *Microvelia*...
3. Front femora black at middle and flattened on anterior or inner surface... *gerhardi* Hussey
4. Front femora not black at middle or flattened...
5. Pronotum short, mesonotum exposed; hindtibia curved... *pulchella* Westwood
6. Pronotum long, concealing mesonotum...
7. Venter of genital segment (VII) without conspicuous bristles or hair tufts (fig. 48A)... *torquatus* Champion
8. Pronotum extending only over mesonotum, sublateral pits (fig. 45A). shorter than mesonotum as measured along midline (fig. 45B): hindtibia shorter than thickness of tibia... *beameri* McKinstry
9. Genital segment with bristles arranged in a circular pattern ventrally (fig. 46A): hair of hindtibia much longer than thickness of tibia; very hairy species... *californiensis* McKinstry

#### Key to California Species of Microvelia

Based on apterous males

<table>
<thead>
<tr>
<th>Step</th>
<th>Character</th>
<th>Key</th>
<th>Species</th>
</tr>
</thead>
</table>
| 1    | Mesonotum not concealed by pronotum; pronotum not attaining sublateral pits (fig. 45B), shorter than mesonotum as measured along midline (fig. 45B); length more than 2 mm; hindtibia straight | subgenus *Kirkaldya* | *M. signata*
| 2    | Mesonotum concealed by pronotum; pronotum reaching to or beyond level of sublateral pits (fig. 45A), or if mesonotum exposed, then body length less than 2 mm and hindtibia curved | subgenus *Microvelia* | *M. hinei*, *M. beameri*, *M. cerifera*
| 3    | Front femora black at middle and flattened on anterior or inner surface | *gerhardi* Hussey | *M. hinei* *gerhardi*
| 4    | Front femora not black at middle or flattened |  |  |
| 5    | Pronotum short, mesonotum exposed; hindtibia curved | *pulchella* Westwood |  |
| 6    | Pronotum long, concealing mesonotum |  |  |
| 7    | Venter of genital segment (VII) without conspicuous bristles or hair tufts (fig. 48A) | *torquatus* Champion |  |
| 8    | Pronotum extending only over mesonotum, sublateral pits (fig. 45A). shorter than mesonotum as measured along midline (fig. 45B): hindtibia shorter than thickness of tibia | *beameri* McKinstry |  |
| 9    | Genital segment with bristles arranged in a circular pattern ventrally (fig. 46A): hair of hindtibia much longer than thickness of tibia; very hairy species | *californiensis* McKinstry |  |

#### FIG. 45. Thorax and base of abdomen in Microvelia: A and B, dorsal view, Microvelia hinei and beameri, respectively; C and D, left side of same species. Legend: P = pronotum, MS = mesonotum, MT = metanotum, SP = sublateral pit, T = dorsolateral triangles of abdominal segment I.
Microvelia (Microvelia) buenoi Drake


Geographic range. Northern half of U.S. to Alaska.

California records. SISKIYOU CO.: Lower Klamath Lake, VI-1-57 (Joe Schuh, JS). This is the first California record for buenoi.

Microvelia (Microvelia) cerifera McKinstry


The concealment of the meso- and metanotum by the pronotum in M. cerifera separates the species from other members of the subgenus. This species is also very pilose.

Geographic range. California, Colorado, Iowa, Kansas, Nebraska, New Mexico, and Utah.


Microvelia (Microvelia) hinei Drake

Microvelia hinei Drake, 1920, Ohio J. Sci. 20:207. Holotype, macropterus ♀: Columbus, Ohio (CJD).

The small size of M. hinei and the dark brown and pale markings of the abdomen are distinctive.

Geographic range. Canada, most of the United States, south to Argentina.

California records. FRESNO CO.: Friant, XI-3-61 (H. C. Chapman, HCC). Squaw Valley, VII-26-62 (W. R. Keilen, HCC). MADERA CO.: Fish camp, IX-21-52 (J. T. Polhemus, JTP). Oakhurst, X-9-52 (J. T. Polhemus, JTP). SHASTA CO.: Fall River Mills, IX-6-56 (D. R. Lauck, DRL). Millville, IX-7-62 (D. R. Lauck, DRL). Although M. pulchella was previously unrecorded from the state, we found it to be common in ponds in the foothills of the central Sierra Nevada.

Microvelia (Microvelia) pulchella Westwood

Microvelia (Microvelia) signata Uhler


Lectotype. macropterous ♂: San Esteban, Baja California, Mexico (CAS), designated by Polhemus, 1977.


This species has long, coarse pubescence, especially on the head and pronotum, and very long antennae. The foretarsal segment is not longer than the tarsal segments of the other legs.

Geographic range. Arizona, ? California, Colorado, New Mexico, Utah, and Mexico.

California records. Drake and Hussey (1955) list M. signata from California but we have been unable to confirm the presence of the species in the state. Because M. signata is widely distributed in Arizona and was described from Lower California, it may occur in California. M. signata should be looked for in cool, cryptic habitats such as under tangles of tree roots, or spring holes with overhanging rock ledges, particularly in desert areas.

Microvelia (Kirkaldya) beameri McKinstry

(Figs. 47, 49)


The twin ventral hair tufts of the genitalia are distinctive in the male (fig. 47A). The female of M. beameri was figured in Usinger’s (1956) book but it was mislabeled M. californiensis.

Geographic range. Arizona, California, Colorado, Nevada, New Mexico, Mexico, and Jamaica.

California records (map 13). M. beameri is one of the most common and widespread Microvelia in the state. It is found in slow streams, seep areas, and ponds of the coast ranges and foothills on the west side of the Sierra Nevada. It also occurs at various desert springs. Specimens were collected every month except December.

Microvelia (Kirkaldya) californiensis McKinstry

(Fig. 46)


This species was misidentified as M. paludicola Champion in the key to Microvelia in Usinger (1956). M. californiensis is a hirsute species and the last sterna and genitalia are diagnostic (fig. 46).

Geographic range. California, Oregon, and Baja California.

California records (map 14). This species is apparently most common in the coast ranges and surrounding areas, as well as in the western foothills of the Sierra Nevada. It has been taken at altitudes up to 5,000 feet. M. californiensis is absent from the deserts except for marginal incursions.

Microvelia (Kirkaldya) gerhardi Hussey


The black ringed and flattened forefemur is distinctive.

Geographic range. Arizona, California, Colorado, Nebraska, New Mexico, Utah, Wyoming, and Mexico.

California records. EL DORADO CO.: Lake Tahoe. VIII-8-37 (Drake and Andre, CJD).

Only three California specimens of M. gerhardi are known. In Colorado it is common along cool streams and springs; in the latter habitat it remains active during the warmer periods of the winter.

Microvelia (Kirkaldya) torquata Champion

(Fig. 48)

North American workers have long confounded this species with *M. paludicola* Champion, and most southwestern records under this name refer to *M. torquata*. The two are sympatric in Mexico and Central America, but in the United States *M. paludicola* occurs only in the southeast (Texas to Florida, Polhemus, 1977b). The absence of hair tufts on the male genitalia (fig. 48), and the presence of a few dark spines on the distal half of the hindfemur are distinctive features of both species. *M. torquata* differs from *M. paludicola* in that it usually has a glabrous, shiny, triangular area on the venter of the first genital segment. This area is setose and dull in *M. paludicola*. The abdominal venter of *M. torquata* is yellow brown and the vertex of the head is convex. The venter of *M. paludicola* is lead colored and the vertex is less convex.

**Geographic range.** Arizona, California, Colorado, Nevada, New Mexico, and Utah, south to Guatemala.

**California records.** RIVERSIDE CO.: Riverside. VIII-16-37 (Drake and Andre, CJD).

**Subfamily Rhagoviinae**

Members of this subfamily, of which only *Rhagovelia* is found in California, are characterized by the absence of ocelli; tarsal formula 3:3:3 or 2:2:2; claws preapical; last tarsal segment of midleg deeply cleft, the cleft containing a pair of plumelike structures; and hemelytra when present with up to four closed cells.

**Genus Rhagovelia Mayr**


*Kotovelia* Matsumura, 1913, Thousand Insects of Japan, Additamenta 1:98.


*Rhagovelia* is separated from other genera of the subfamily by the combination of three-segmented tarsi and the presence of plumelike structures only on the middle tarsus (fig. 10). Although China & Usinger (1949b) correctly recognized *Trochopus* as a valid genus because of its two-segmented tarsi, Bacon (1956) inexplicably treated the genus as a synonym of *Rhagovelia*, placing its two species, *R. plumbea* (Uhler) and *R. salina* Champion, in his *Rhagovelia angustipes* species group. Matsuda (1956) perpetuated the error in his supplement to Bacon's revision. Matsuda's paper dealt with
the comparatively uncommon winged forms which Bacon largely ignored. Matsuda established the subgenus Neorhagovelia for Bacon's R. angustipes and R. abrupta groups, both of which, after the removal of the two Trochopus species mentioned above, are Neotropical elements.

About 150 species of Rhagovelia are known and nearly 100 of these are New World forms. There are nine Nearctic species and three of these are recorded from California, but we have been unable to confirm the presence of one of these, R. rivale, in the state. Smith and Polhemus (1978) keyed the United States species and provided a checklist, but Bacon's (1956) revision remains the basic work on the genus, although over a dozen species have been described from the Americas since his paper appeared.

Rhagovelia species are inhabitants of streams and rivers, and most Nearctic forms occur in rather swift waters. Their common name, "riffle bugs," is derived from their habit of coursing in tight schools just out of the strong currents in the faster portions of streams. Although they are seldom still, their small size makes them inconspicuous. Macropterous specimens of Rhagovelia are rarely encountered in California, consequently the following key is based on apterous forms.

KEY TO CALIFORNIA SPECIES OF RHAGOVELIA

Based on apterous specimens

1. Middle femur of female transversely constricted at middle; abdominal terga without median, shining, black areas
   Middle femur of female dorsoventrally flattened for two-thirds of its length but not transversely constricted at middle; last abdominal tergum (and sometimes others) of male (and often female) with median, shining, black areas ....... 2

2. Female mesonotum not tumid, narrowly exposed or almost completely concealed by pronotum, hind margin sinuate*; all terga of male with prominent, median, shining black areas .................. R. distincta Champion
   Female mesonotum tumid, broadly exposed, hind margin almost straight; male with only traces or no median, shining black areas on terga 3 to 5 .......... R. rivale Torre-Bueno

Rhagovelia (Rhagovelia) choreutes Hussey


The transversely constricted femur of the female is distinctive.

6. In addition to the mesonotum and metanotum, there are seven visible abdominal terga of about equal length, although the suture between segments seven and eight is sometimes difficult to see.

Geographic range. California, Florida, Mississippi, New Mexico, Oklahoma, Texas, and Mexico.


Rhagovelia choreutes was misidentified as R. obesa Uhler by Usinger (1956). R. choreutes is restricted apparently to the southern part of the state. The San Diego record may be erroneous.

Rhagovelia (Rhagovelia) distincta Champion (Fig. 50)


MENKE: THE SEMIAQUATIC AND AQUATIC HEMIPTERA OF CALIFORNIA

(1931) proposed six varieties from the western United States and Mexico. Bacon (1956) decided that these were indistinguishable from the typical form. In the winged form, which is uncommon in California, the females have the apex of the pronotum prolonged backwards into a process varying from a short protuberance to a long bent process which is emarginate at the midline. There is a series from one locality in the Polhemus collection that contains all of these.

Geographical range. California to Texas and Wyoming, south to Honduras.

California records (map 15). This species has been collected in 23 counties scattered over the state, but R. distincta has not been taken from streams in the coast range. Habitats are fast flowing rivers, streams and creeks up to 2,000 ft. in elevation.

**Rhagovelia (Rhagovelia) rivale** Torre-Bueno


Geographic range. Colorado, Iowa, Kansas, Missouri, Nebraska, Oklahoma, and Texas.

California records. A male and female of *R. rivale* in the C. J. Drake Collection, Smithsonian Institution, bear the notation “California,” but the occurrence of this species in the state is doubtful.

The characters noted in the key will separate this species from the others. On account of its wide distribution and somewhat variable color and structures, Gould
Gerrids are elongate or oval-bodied bugs. The long antennae are four-segmented, and ocelli are absent. The front pair of legs is widely separated from the closely spaced middle and hindlegs, and the middle pair is longer than the others. The claws are usually preapical. Most gerrids have a single, median, metathoracic scent gland opening, the "omphalium," on the sternum (fig. 14), but among our forms it is absent in Trepobates and Metrobates. The body is covered with a velvety hydrofuge hairpile, and color ranges from black or grey to brown with the dorsum sometimes marked with light grey or yellow. Apterous forms are most commonly encountered.

The Gerridae contains about 56 genera and over 450 species. The extensive paper of Matsuda (1960) and the keys to genera and higher categories by Hungerford and Matsuda (1960) are the basic references for family classification. They recognized five subfamilies, but Andersen (1975) elevated to subfamily three tribes in the Gerrinae. Andersen's paper contains a key to the eight subfamilies, and an outline of the restructured Gerrinae. Six subfamilies occur in the New World of which three have California representatives (Gerrinae, Trepobatinae, and Halobatinae). There is disagreement among hemipterists over the family limits. For example, the peculiar Old World marine genus Hermatobates Carpenter was regarded as a gerrid by China (1957), but the Hermatobatinae was excluded from the family by Matsuda (1960) and Andersen and Polhemus (1976). Similarly, Halovelia Bergroth was referred to the Gerridae by Esaki (1924), and Poisson (1956) elevated the subfamily to family. China and Usinger (1949b), China (1957), and Andersen and Polhemus (1976) assigned the Haloveliinae to the Veliidae, and Kellen (1959) offered ethological evidence for this association.

The Gerridae and Veliidae are separated only with difficulty. Traditional external characters used to separate the two groups include (among others) differences in the metathoracic scent glands, leg spacing, and tarsal segmentation. The metathoracic scent glands of all Veliidae have paired, lateral, evaporative channels that end in front of the hindcoxae. These channels are absent in most gerrid genera. The scent gland openings are difficult to see in most veliids, but in gerrids, a single, common opening, the "omphalium," is usually easily recognizable (fig. 14), although it is absent in the Rhagadotarsinae and most Trepobatinae, including the California genera Trepobates and Metrobates. Some veliids in the Veliinae also have an omphalium. In gerrids the middle pair of legs is inserted closer to the hindlegs than to the front legs. In most veliids the middle pair is about equidistant from the front and hindlegs, but the typical gerrid arrangement is found in the Haloveliinae, Rhagoveliinae, and some Microveliinae (Husseyella Herring). The tarsi are two-segmented in all gerrids but segmentation varies from one to three in the Veliidae.

China (1957) concluded that the only reliable criteria for separating the families were internal characters of the male genitalia. He said that gerrids differ from veliids in possessing rudimentary parameres which are visible only by dissection, and also in having the vesica of the aedeagus sclerotized. However, only the latter of these is valid, because whole groups of gerrids (Ptilomerinae, Metrocorini) have well-developed, very visible parameres. Veliids have relatively large parameres which are visible externally and the vesica is membranous. Scudder (1959) has added female distinctions. The second gonocoxites are absent in female gerrids, but are present in veliids. In addition some veliids have feathery projections on the gonapophyses. Fortunately for students of the California fauna, our gerrids can be separated from veliids by the absence of a median, longitudinal groove on the frons, and the absence of metathoracic scent gland channels.

Water striders are a familiar sight on all kinds of

7. China (1957) was incorrect in saying that these channels are absent in the Haloveliinae, a group which we regard as part of the Veliidae.
water surfaces, and they are among the best known of the semiaquatic Hemiptera. Habitats range from tiny ponds to lakes, trickles to rivers, and even the open ocean. Some species tolerate a variety of habitats. For example, *Gerris remigis* Say, which prefers streams, is also found on the still water of stock tanks and ponds. The genus *Trepobates* occurs on the still to slow-moving portions of the Colorado River in California, but Floridian species occur in habitats ranging from ponds to swift, spring fed streams. *Metrobates* is typically a dweller of streams that have a moderate to swift flow, and individuals usually occur in great schools skating against the current for long periods without rest; but occasionally *Metrobates* occur on lakes. Most gerrid genera are restricted to fresh water, but the more widespread species, such as *Limnogonus franciscanus* Stål, may inhabit fresh or brackish water (Cobben, 1960). *Gerris buenoi* Kirkaldy is usually found on freshwater ponds, but it has been taken on saline lakes in British Columbia (Scudder, 1971b). Most species of *Rheumatobates* Bergroth inhabit fresh water, but some prefer brackish or saline coastal estuaries. *Halobates* is oceanic, and while some species are restricted to coastal waters, others are truly pelagic, occurring hundreds of miles from the nearest land. These are the only insects that have successfully invaded the open ocean.

Members of the genus *Gerris*, particularly *remigis*, commonly leave the water to rest on steeply sloping or vertical boards or rocks just above the water (Riley, 1921).

Gerrids are predaceous and their food consists mainly of insects and other organisms that fall on the water, as well as aquatic forms that come to the surface. Gerrids possess numerous sensillae on the trochanters and femora which enable them to perceive vibrations in the surface film caused by insects and other possible prey (Lawry, 1973; Weber, 1930), and to determine the angle from which these vibrations originate (Murphey, 1971). The front legs are used to hold prey and the mandibular styles have spines and teeth that anchor these structures in the prey (Cheng, 1967). The body contents of the prey are almost entirely dissolved by digestive enzymes before ingestion.

*Limnoporus canaliculatus* (Say) has been observed in nature feeding predominantly on various stages of mosquitoes (Penn and Goldsmith, 1950), but Herring (1950) found that the same species preferred beetle larvae over emerging mosquitoes. Torre-Bueno (1917b) observed *Gerris remigis* attacking a *Notonecta* in an aquarium. Riley (1918) stated that he observed *Gerris marginatus* Say and *G. remigis* feeding on floating fruits and berries in nature. The pelagic species of *Halobates* are apparently obligate feeders on coelenterates (Herring, 1961), while the near shore species have a more typical gerrid diet.

The Gerridae serve as food for few animals, possibly because the secretion from their metathoracic scent glands renders them distasteful. Riley (1925) summarized some earlier observations on predators which included frogs, fish, and beetles. Records of predation by vertebrates are rare, and in all of our field observations we have seen fish predation only once. In Kansas, hundreds of *Metrobates trux* (T-B) were found in the crops of wild ducks on the Republican River (Anderson, 1932). This genus also lacks an omphalium. Callahan (1974) reported that *Gerris* nymphs were eaten by trout in California. She also noted that *G. gillettei* Lethierry & Severin can dive beneath the surface film, Perhaps this is a means of escaping from predators.

More than 20 gerrid life histories are available in the literature, some species having been studied several times. Some of the earlier studies on *Gerris marginatus* and *G. remigis* were summarized by Hungerford (1920), and Hoffmann (1924a) provided information on *G. buenoi* and *Limnoporus dissortis* (Drake & Harris) (as *rufoscutellatus* Latreille). The American species of *Gerris* that have been observed lay their eggs singly just under the surface on floating sticks, vegetation, or other material. *Limnoporus canaliculatus* lays its eggs in rows (Herring, 1950). All of the eggs of American *Gerris* species that have been measured are about 1 mm by 0.33 mm, white when first laid, then turning amber. The incubation time for *Gerris remigis* is about 12 days, with nymphs reaching adulthood in about 28 days. Eggs of *Limnoporus dissortis* require 8-10 days for incubation, and an average of 19 days passes before nymphs reach adulthood.

The life history of the species of *Trepobates* found in California has not been studied, but both Hungerford (1920) and Hoffmann (1924a) studied *T. pictus* (Herrich-Schaeffer). This species lays 3 to 10 eggs at a time in solid masses of gelatinous material on the underside of leaves and sticks in the water. Each egg is 1 mm by 0.3 mm, elongate oval and spotted. The incubation time was noted as 5 days by Hungerford, but 12 days by Hoffmann. Each of the five nymphal instars lasted about 6 to 9 days (min. 5, max. 12), and an average of 39 days passed before the adults appeared. The life history of *Metrobates* has not been studied.

Although most gerrids lay their eggs on objects just beneath the surface film, there are a few exceptions. The pelagic forms of *Halobates* lay their eggs on many kinds of floating material, and have even laid numbers
of them on the tail feathers of a living sea bird, the Noddy (Anous stolidus (Linnaeus)) (Herring, 1961). Members of the subfamily Rhaagadotarsinae are unique among gerrids in that they have an ovipositor, and they insert their eggs in plant tissue (Silvey, 1931).

Gerrid embryos split the egg longitudinally at hatching by means of a sclerotized egg burster. The nymph then wriggles free from the egg, and swims to the surface which it easily breaks through if it is scum free. Nymphs may remain submerged for up to 2 hours and survive (Hungerford, 1920).

Developmental time from egg to adult is governed partially by temperature. For instance, the time from egg to adult for Limnopus canaliculates is shorter in the south, 21 days in Louisiana (Penn and Goldsmith, 1950) and 24 days in Florida (Herring, 1950) but extends to 34 days in Virginia (Bobb, 1951a).

All gerrids seem to have five nymphal instars. At ecdisis the nymphs are vulnerable to predation and cannibalism, with the first instars experiencing a particularly high mortality rate. The molting of Gerris nymphs is aided by a blood-filled vesicle which is extruded beneath the scutellum to split the skin (Wigglesworth, 1965).

During copulation, most gerrid males ride passively on the back of the female, with the genital organs twisted sideways and downward to engage the female (see figure in Hungerford, 1920, Plate 15). Copulation in Gerris ordinarily lasts from a few minutes to several hours, but Neogerris hesione (Kirkaldy) was observed in coitus for several days (Osborn and Drake, 1915).

The number of generations per year varies with the climate. In the tropics gerrids reproduce all year, but in colder regions there may be only one or two generations. Gerris remigis breeds throughout the summer in North America according to Hungerford (1920), but his observations were made at about the latitude of New York where there are three broods per season (Torre-Bueno, 1917b). In Ontario, Canada, there is probably one generation per season (Cheng and Fernando, 1970), and in Colorado there are two broods. Gerris incognitus Drake & Harris and G. gilletti are bivoltine in the San Francisco Bay area of California (Callahan, 1974).

Gerris hibernate as adults. Riley (1921) found G. remigis hibernating under piles of dead leaves, in holes in streambanks, under tree roots on land, and other sheltered places near the water. He found up to 250 individuals in hibernating clusters. Brinkhurst (1959) noted instances of alate gerrids hibernating far from their normal habitat.

A number of parasites and commensals are associated with the Gerridae, and Poisson (1957) has summarized much of this information. Wallace et al. (1960) described flagellate Protozoa from two North American Gerras. Hydrachnid water mite larvae are often abundant ectoparasites of gerrids. The mymarid wasp Potasson gerrisopagus (Doutt) has been reared from Gerris eggs in California (Usinger, 1956).

Death feigning in Gerris remigis has been described by Essenberg, (1915) and Riley (1921). The bug crosses its forelegs and becomes rigid. In this condition it can be handled and subjected to other physical stimuli without evidencing any signs of life. When left alone for 10 to 15 minutes, most bugs resume normal activity.

The degree of wing development, or alary polymorphism, varies greatly within gerrids, and is apparently related to dispersal and habitat stability. Day length and temperature have been identified as two environmental factors that influence the degree of wing development by acting on the genetic makeup of the bug (Brinkhurst, 1959; Vepsalainen, 1971a, b). Generally, apterism occurs only in species that live in open habitats such as rivers where wings are not required for dispersal. On the other hand, pond species require winged forms for dispersal to new habitats and hibernation sites. Callahan (1974) found that two bivoltine California species, Gerris incognitus and G. gilletti, were polymorphic in the San Francisco Bay area. The first generation is macropterous in both species. In the second generation females of G. incognitus are apterous, males macropterous; while 95% of the females and 50% of the males of G. gilletti are brachypterous.

Flight in temperate gerrids is not often observed, perhaps because it frequently occurs at night (Riley, 1925: Callahan, 1974). Many observations of flight in tropical species have been made.

The wings of macropterous forms in the Gerrinae do not extend beyond the end of the abdomen, but in Treopbatinae and Rhagadotarsinae, the hemelytra project beyond the abdominal apex. In the latter subfamilies, the hemelytra have a transverse suture or line of weakness where the wings can easily be broken off, as they commonly are, evidently to facilitate mating.

The rowing locomotion of Gerridae, the walking bug (Brinkhurst, 1960), Darnhofer-Demar (1969), Caponigrò & Eriksen (1976), and Andersen (1976) and their work is summarized in the Introduction to this bulletin.

KEY TO AMERICAN GENERA OF GERRIDAE
NORTH OF MEXICO

1. Inner margins of eyes sinuate or concave behind the middle; body comparatively long and narrow (fig. 63) .................. 2
   (Gerrinae) ................................................. 2

   Inner margins of eyes convex; body comparatively short and broad (figs. 64-66) ........................................ 5
2. Pronotum shining; head with longitudinal pale markings dorsally ........................................ 3
   Pronotum dull; head completely dark above (except for a transverse basal band or a pair of spots in some species) .................................................. 4
3. Fore lobe of pronotum with pair of long, pale lines ................................................................  Limnoporus Stål, p. 66
   Fore lobe of pronotum with single, median pale spot .............................................................. Neogerris Matsumura (h主one) (Kirkaldy)
4. Antennal segment I equal to or longer than combined lengths of II and III ............................. Gerris Fabricius, p. 61
   Antennal segment I less than combined lengths of II and III .................................................. Limnoporus Stål, p. 65
5. Tibia and first tarsal segment of middle leg with fringe of long hairs; always apterous; the meso- and metanotum fused, without trace of a dividing suture; marine forms ........................................... Halobates Eschscholtz, p. 66
   Tibia and first tarsal segment of middle leg without a fringe of long hairs; dimorphic, the meso- and metanotum of apterous forms with a distinct dividing suture ...................................................... 6
6. Third antennal segment with several stiff bristles which are at least as long as diameter of segment; abdomen as long as remainder of body; length of first antennal segment much shorter than remaining 3 taken together .................................................. (Rhagadotarsinae) Rheumatobates Bergroth
   Third antennal segment with fine pubescence or tuft of short, stiff bristles, but these not as long as diameter of segment; abdomen shorter than remainder of body, or if subequal then length of first antennal segment about equal to remaining three taken together ........................................... (Trepobatinae)
7. Length of first antennal segment subequal to remaining three taken together ................................ Metrobatobates Uhler, p. 67
   Length of first antennal segment much shorter than remaining three taken together .............. Trepobatobates Uhler, p. 68

Subfamily Gerrinae

Andersen (1975) recognizes two tribes in the Gerrinae, one of which, the Gerrini, is represented in North America. Three of the four North American genera, Limnoporus, Gerris, and Limnogonous, have been reported from California, but the presence of the last genus listed in the state remains to be verified.

Tribe Gerrini
Genus Gerris Fabricius

Gerris Fabricius, 1794, Entomol. Syst. 4:188. Type-species: Cimex Iacustris Linnaeus, 1758, designated by Lutreolent, 1810.
Aquarius Schellenberg, 1800, Das Geschlecht der Land und Wasserwanzen p. 25 (= subgenus).
Ures Distant, 1910, Fauna British India, Rhynchota 5:149.

Andersen (1975) narrowed the limits of this genus by elevating the subgenus Limnoporus to genus. The dull pronatal dorsum and antennal proportions mentioned in the key to genera separate Gerris from other elongate water striders. Members of this genus are the commonest and most widely distributed Gerridae in the world, and are the water striders most frequently noticed by laymen. In the New World, Gerris is most strongly represented in the Nearctic Region, which has 15 species. The genus is largely replaced in Central and South America by other genera. Seven species have been reported from California, but we have been able to confirm only five of these. One, G. marginatus Say, was listed from California by Drake and Harris (1934) and Kuitert (1942), but confusion with the closely related G. incurvatus probably explains these records. A second species, C. nyctalis Drake & Hottes, a high altitude lake dweller described from the Rocky Mountain region, was reported from Fresno, California, by Drake and Harris (1928), but we have been unable to confirm its presence in the state. We have been unable to consistently separate G. nyctalis from G. remigis, and we are not convinced that G. nyctalis is a valid species. The shorter body and antennae of G. nyctalis and purported differences in the male genital segments (see fig. 56) appear to be clinal variation due perhaps to environmental effects at high altitude, or these differences may be nothing more than generation morphs. Andersen (1975) says that measurements of appendages are subject to individual variation in gerrids, and that allometric growth compounds their unreliability in species discrimination.

Three subgenera are recognized in Gerris by Andersen (1975), two of which are found in the New World and California. The revision of Drake and Harris (1934) is the standard reference for the genus although somewhat out of date. Kuitert (1942) updated their key to species. Sprague (1967), Scudder and Jamieson (1972), and Calabrese (1974a) have provided keys to the nymphs of most North American Gerris species.

KEY TO CALIFORNIA SPECIES OF GERRIS

1. Large, robust species (length 11.5-16 mm) ................................................................. remigis Say
   Small species (length 11 mm or less) ...................................................................................... 2
2. Pronotum without a pale stripe behind eye; epimera of males strongly elevated .................... 3
   Pronotum with a pale stripe immediately behind eye; epimera of male scarcely elevated .... 4
3. Corners of mesal notch of male sternum VII broadly obtuse (fig. 61); lateral spines of female segment VII abruptly incurved, not reaching level of apex of segment VIII (fig. 51). ...................................................... incurvatus Drake & Hottes
   Corners of mesal notch of male sternum VII nearly rectangular (fig. 62); lateral spines of female segment VII not abruptly incurved, their apices reaching to apex of segment VIII (fig. 52) .......................................................... marginatus Say
4. Posterolateral angles of female abdominal segment VII
obliquely truncate in lateral view, not prolonged spinelike (fig. 53); male sternum VIII as broad as long; median notch at apex of male sternum VII broader than deep, sub-rectangular (fig. 60) ................. buenoi Kirkaldy

Posterolateral angles of female abdominal segment VII produced, spinelike in lateral view (fig. 54); male sternum VIII distinctly longer than broad, narrowed posteriorly; median notch at apex of male sternum VII about as broad as deep, evenly rounded .................... 5

5. Dorsal paratergites with silver spots at intersegmental sutures; male sternum VII with a pair of median, longitudinal troughlike depressions, VIII without conspicuous, long hairs laterally (fig. 58); female 9.5-11.5 mm long ........

gillettei Lethierry & Severin

Dorsal paratergites without silver spots at intersegmental sutures; male sternum VII without longitudinal depressions, VIII with conspicuous, long hairs laterally (fig. 59); female 8.75-10 mm long ........... incognitus Drake & Hottes

Gerris (Aquarius) remigis Say
(Figs. 56-57, 63)


NEW SYNONYMY.

Calabrese (1974b) considered G. remigis to be polytypic and proposed the subspecific name G. caloregon for the western form. We feel that her population sample was too small (apparently 40 western specimens) and we have not recognized subspecies. Furthermore, if future studies substantiate the recognition of subspecies in G. remigis, the name orba Stål will have to be used for Calabrese’s subspecies. We have studied a syntype of G. orba (Drake Collection) that was collected in the San Francisco area and it is G. remigis. It also bears a Calabrese caloregon determination label.

There is considerable variation in the length of the lateral spine on abdominal segment VII. We have illustrated two extremes (figs. 56-57). The shorter spine form is supposedly typical for G. nyctalis Drake & Hottes, a species that is possibly conspecific with G. remigis.

Geographic range. Reported from the 48 contiguous states, Canada, Mexico, and Guatemala. Michel (1962) found that specimens of “remigis” from Arizona, Texas, and Virginia represent a different species separable from true G. remigis on the basis of size, color, and phallic structure. Until the geographic limits of these two species are clarified the true distribution of G. remigis will not be known.

California records (map 16). Gerris remigis is by far the most common species in California. It occurs in almost every type of aquatic habitat from the marine zone to the high Sierra Nevada. It is particularly abundant in vernal pools and temporary ponds. It has a wide distribution and is found in virtually all climatic regions of the state. It is most common in the southern part of the state, where it is found in every county. In the north, it is found primarily in the coastal counties. It is also found in the Sierra Nevada, where it is found in the eastern and western slopes. It is found in the San Francisco Bay area, where it is found in the western counties. It is found in the Central Valley, where it is found in the eastern counties. It is found in the northwestern part of the state, where it is found in the western counties.

widely known semiaquatic insect in the United States, and we have seen this species from 43 counties that span the length and breadth of the state, and at elevations ranging up to 8,280 feet. However, the species appears to be absent from the Mojave and Colorado deserts. The specimens studied were collected in every month of the year. Chapman noted adults hibernating under stones in January in a foothill area near Fresno.

_Gerris (Gerris) buenoi_ Kirkaldy
(Figs. 53, 60)


The broad, subrectangular notch at the apex of the 7th male sternum, and the absence of spinelike lateral prolongations of female tergum VII coupled with the presence of a pale stripe along the anterolateral pronotal margins separate this species from most other California _Gerris_. It is also one of the smallest _Gerris_ in our region, ranging from 7 to 8.2 mm long.

_Geographic range._ Transcontinental in southern Canada and northern U.S.


This is the first valid record for the state.

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**_Gerris (Gerris) gillettei_ Lethierry & Severin**
(Fig. 58)


Among California _Gerris_ species the presence of conspicuous silver spots dorsally near the lateral margin of the abdomen is unique to _G. gillettei_. Apterous males of this species have a distinctive shape, the abdomen tapers rather evenly to the genital segments. Body length ranges from 8.5 to 11.5 mm. Females of _G. gillettei_ and _G. incognitus_ are similar, but according to Callahan (1974), those of _G. gillettei_ average larger than those of _G. incognitus_ (× 10.3 mm and 9.1 mm long, respectively). She also noted that the female venter of _G. gillettei_ is paler than in _G. incognitus_.


_California records_ (map 17). This species is primarily an inhabitant of mountain lakes in the Sierra Nevada. Specimens were captured from March to December.
**Gerris (Gerris) incognitus** Drake & Hottes
(Figs. 54, 59)


The characters in the key readily distinguish this small species (length 7-10 mm).

**Geographic range.** California, Colorado, Idaho, Montana, Nevada, Oregon, Washington, Wyoming; transcontinental in southern Canada.

**California records** (map 18). Specimens have been seen from 17 counties scattered over most of the state. Many records are from mountain areas. No material has been seen from the southeastern desert area. Specimens have been collected from February to December.

**Gerris (Gerris) incurvatus** Drake & Hottes
(Figs. 51, 61)


*Gerris incurvatus* is a relatively slender species with a length of about 8 mm.


**California records** (map 19). Specimens have been seen from 24 counties extending the length and breadth of the state and at elevations ranging up to 8,500 feet. We have not seen material from the deserts of southeastern California. Specimens were collected every month but January.

**Genus Limnoporus Stål**


*Limnoporus* was considered as a subgenus of *Gerris* until Andersen (1975) raised it to genus. Of the characters used by Andersen in his key to genera, we have found that only the proportions of the antennal segments hold up for generic separation of *Limnoporus* from *Gerris*.

The California species of *Limnoporus* is easily distinguished from *Gerris* by the combination of long antennae, reddish brown pronotum without a median dark stripe, and the very long posterolateral spines of abdominal segment VII. In the Americas this genus is represented by four species, all Nearctic in distribution. Three of the U. S. species, *L. canaliculatus* (Say), *L.

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**MAP 19.** California distribution of *Gerris incurvatus* Drake & Hottes.

**MAP 20.** California distribution of *Limnoporus notabilis* (Drake and Hottes).
dissortis (Drake & Harris), and L. notabilis (Drake & Hottes), are treated under the genus Gerris in the revision of Drake & Harris (1934). The last species is the only one in California. The fourth species, L. nearcticus (Kelton) was described from Alaska and the Yukon Territory by Kelton (1961).

**Limnoporus notabilis** (Drake & Hottes)  
(Fig. 55)


This is the largest gerrid in the state. Its long, slender body (15-20 mm long) and brownish pronotum are distinctive. Sternum VI of the male is not notched posteriorly (fig. 55). This plate is notched posteromedially in our other large gerrid, *Gerris remigis*. Wingless morphs are unknown in *L. notabilis*.

**Geographic range.** Arizona, California, Colorado, Idaho, Iowa, Oregon, Montana, South Dakota, Utah, Washington, Wyoming, and British Columbia.

California records (map 20). *L. notabilis* is known from 13 counties in northern and central California. The species is found at low to moderate elevations. Older western records of "*rufoscutellatus*" pertain to *notabilis*.

**Genus Limnogonus** Stål


The shiny thoracic dorsum with its pair of yellow spots anteriorly sets *Limnogonus* apart from *Gerris*, *Neogerris* and *Limnoporus*. Andersen (1975) recognizes two subgenera; all New World species belong in the subgenus *Limnogonus*. The reference for the genus in the New World is Drake and Harris (1934). There are about 26 species in the genus, 7 of which occur in the Western Hemisphere. The occurrence of *Limnogonus* in California is based on the probably erroneous record of one species, *L. franciscanus* (Stål) from the state. *Limnogonus* is a primarily tropical genus and it is largely replaced in temperate regions by *Gerris* and *Limnoporus*. All three genera occupy much the same habitats.

### BULLETIN OF THE CALIFORNIA INSECT SURVEY

**Limnogonus (Limnogonus) franciscanus** (Stål)


**Geographic range.** ♂ California, Florida and Texas to Peru, West Indies.

**California records.** Although Drake and Harris (1934) reported *L. franciscanus* from "California" (under the name guerini), the source of their record was not given and we have not seen this species in any material from the state. Drake and Harris (1935) examined Stål’s type of franciscanus and verified that guerini was a synonym, but they did not discuss the origin of his type material. The label on the type of franciscanus says "California." The "S:t Francisco" mentioned in Stål’s description refers to San Francisco, California according to Persson (1971), but a labelling error seems likely. Because *L. franciscanus* is primarily a neotropical species it seems more plausible that its type originated in South America, perhaps Peru (see data on the Eugenie Expedition in Persson). The closest record to California for *L. franciscanus* that we can authenticate is in northwestern Mexico (San Blas, Nayarit).

**Subfamily Halobatinae**

Matsuda (1960) recognizes two tribes in the Halobatinae, one of which, the Halobatini, consists of marine water striders. One genus, *Halobates*, is found in the waters around North America.

**Tribe Halobatini**

*Genus Halobates* Eschscholtz

*Halobates* Eschscholtz, 1822. Entomographien 1:106. Type-species: *Halobates micans* Eschscholtz, 1822, designated by Kirkaldy, 1901. Most authors attribute this type designation to Laporte (1832-1833), but there is no evidence in Laporte’s paper that he took such action.


Water striders of the genus *Halobates* are the only insects that have been able to adapt to a life on the open ocean. Some species are truly pelagic, spending their entire life cycle hundreds of miles from land. Eggs are laid on bits of flotsam, and the open ocean species feed on coelenterates, while the shore-colonizing species feed on other insects similar to inland gerrids. A splendid account of the life history and revision of the genus has been published by Herring (1961). For additional
discussion of habits and morphology accompanied by excellent figures and photographs see Andersen and Polhemus (1976). Only one species is known to occur off the California coast, although *Halobates sobrinus* White is found in the waters around Baja California.

*Halobates sericeus* Eschscholtz

(Fig. 64)


*Geographic range.* Pacific Ocean.

*California records.* The species has been collected about 250 miles off the California coast.

**Subfamily Trepobatinae**

Two of the 13 genera in this subfamily occur in North America and both are found in California.

**Genus Metrobates** Uhler


Water striders of the genus *Metrobates* have short, broad, flattened abdomens, and the second and third antennal segments of the male are swollen distally. The body is gray, but black markings are present. These characters separate the genus from its close relatives.

These bugs seem to prefer large rivers where there is a moderate current. They are rarely found on lakes.

*Metrobates* is a small genus of 14 species and four subspecies; five of the species occur in the United States with *M. trux* and its subspecies *infuscatus* occurring in California. The genus was last revised by both Anderson (1932) and Drake and Harris (1932b). A synonymic species checklist was published by Drake (1954).

**KEY TO CALIFORNIA SUBSPECIES OF *METROBATES TRUX***

Second antennal segment pale, at least basally; apterous specimens predominately pale; Colorado River ........... *trux trux* (Torre-Bueno)

Second antennal segment uniformly dark; apterous specimens predominately dark; central and northern California ....... *trux infuscatus* Usinger

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**FIG. 64. Halobates sericeus**, male (from Zimmerman, 1948).

*Metrobates trux trux* (Torre-Bueno)


*Geographic range.* Arizona, California, Colorado, Idaho, Kansas, New Mexico, Texas.


*Metrobates trux* s.s. is known only from the Colorado River in California. This predominantly pale subspecies is often common on the river near Blythe although difficult to capture because the schools are often some distance from shore.
MAP 21. California distribution of Metrobates trux trux (Torre-Bueno), circles; and M. t. infuscatus Usinger, squares.

Metrobates trux infuscatus Usinger  
(Fig. 65)

Metrobates trux infuscatus Usinger, 1953, Pan-Pac. Entomol. 29:178.  
Holotype ♀: Davis, California (CAS).

The uniformly dark second antennal segment and more extensive dark markings separate M. infuscatus from trux trux.


This subspecies occurs in the northern half of the state, primarily in large streams flowing into the Central Valley.

Genus Trepobates Uhler


Trepobates becki Drake & Harris  
(Fig. 66)

FIG. 66. Trepobates becki, apterous female (from Usinger, 1956).

**Geographic range.** Arizona, California, and Mexico.


Usinger (1956) first reported this species from extreme southeastern California along the Colorado River, and it is still known only from that area.
FAMILY NEPIDAE/Water Scorpions

A. S. Menke

These bugs are brown, either dorsoventrally flattened, or, as in all the California species, cylindrical. The legs are long and slender or “sticklike” and serve the bugs poorly when swimming. The anterior pair are raptorial, and all tarsi are one-segmented. Nepids do not have ocelli, and the antennae are short, usually three-segmented, and are concealed in pockets on the underside of the head. Water scorpions derive their name from the distinctive, long, slender, taillike, non-retractile, respiratory siphon on the end of the abdomen. This siphon can be freely rotated, and a flexible region at its base allows it to be held at a sharp angle to the rest of the body. In the adult, the siphon is a tube, formed by two channellike filaments held tightly together. In nymphs the filaments do not form a tube; instead the siphon has a ventral longitudinal channel. The respiratory siphon is derived from the eighth abdominal tergum and has two spiracles at its base.

The Nepidae contains nearly 200 species. The classification of the family has been treated by Menke and Stange (1964), De Carlo (1967, 1968), and Lansbury (1974). The last author recognizes 12 genera but the status of several Old World generic taxa remains unclear. Only three genera are known in North America, Nepa, Curicta, and Ranatra. Nepa is found in the eastern half of the country, and Curicta is primarily a Neotropical group that infiltrates Texas, Louisiana, and Arizona. Ranatra occurs throughout the United States and is the only genus represented in California. Two subfamilies are recognized by Menke and Stange, and by Lansbury: the Nepinae, including the broad, flat types such as Nepa and Curicta, and the Ranatrinae, including the long cylindrical Ranatra, and other rather narrow, elongate genera. Some authors have regarded these subfamilies as families (De Carlo, 1967, for example), but the discovery in Australia of two genera intermediate between the Nepinae and Ranatrinae (see Lansbury, 1974; Menke and Stange, 1964) has made arguments for their recognition as families untenable. De Carlo disagreed with the Menke-Stange assignment of genera in the two groups, but Lansbury’s refined Menke-Stange scheme is much more firmly based than that of De Carlo.

Nepids prefer still water habitats. Members of the genus Ranatra are usually found in tangled plant growth or debris where they are difficult to detect because of their sticklike appearance. Nepa and Curicta are more frequently found in shallow, muddy pools or slow-moving streams with little vegetation. Being awkward swimmers, nepids prefer to perch on some object in the water and wait for an organism to come within their reach rather than make an active search for food. In this “resting-questing” attitude (Radinovsky, 1964) the body is oriented obliquely to the water surface with the respiratory siphon at the surface film. The bug is motionless, and the grasping front legs are held outstretched in front of the head. Ranatra is lightning quick with its front legs and will grasp at anything that comes near. Cloarec (1976) demonstrated that prey perception in Ranatra is both visual and mechanical. The forefemoral tooth bears a group of sensillae which detect vibrations from potential prey. In the capture posture the femoral teeth are directed forward. Nepids are reported to feed on a variety of aquatic organisms, but mosquito larvae and tadpoles are among the most frequently mentioned. The East Asian ranatrine genus Cercotmetus Amyot & Serville, which feeds almost exclusively on mosquito larvae, is listed by Laird (1956) as one of the most potentially useful aquatic hemipterans known.

Nepid eggs are unique in possessing two or more slender respiratory horns on their anterior pole. Female water scorpions usually lay their eggs with the respiratory horns out of the water so that normally the eggs are essentially terrestrial in respiration. Hinton (1961) found that the respiratory horns have a peripheral plastron meshwork which is connected through an inner gas-containing meshwork with the air-filled meshwork of the inner shell wall of the egg. The plastron of the respiratory horn thus ensures respiration even when an
egg is totally submerged, as is frequently the case because of flooding or rain. Radinovsky (1964) kept Ranatra eggs under water up to four days without harming them. The respiratory horns also minimize water loss during respiration because the impervious surface of the egg is much greater in extent than the plastron area of the horns (Hinton, 1970). Hinton (1961) also explained the mechanism whereby nepid eggs increase in size during development. The posterior pole of the egg has a specialized area, or hydropyle, which admits water. This water uptake during development may increase the length of the egg by one-third.

The number of respiratory horns per egg is of taxonomic significance at both the subfamilial and generic levels (Hinton, 1962; Lansbury, 1974). The eggs of the Ranatrinae possess only two horns (fig. 2), while the number of horns in the Nepinae varies from four to 26 per egg and they are arranged in a rosette. The eggs of Ranatra are long and slender, with respiratory horns as long as or longer than the egg body. The eggs of the Nepinae are shorter and stouter, and the respiratory horns are usually shorter than the egg body.

Ranatra, and presumably other Ranatrinae, usually insert their eggs in slits cut in floating vegetation, although Hoffmann (1930) stated that the oriental R. chinensis Mayr oviposited in the mud bank of a pond. The subgenital plate in the Ranatrinae is swordlike and well designed for making the incision into which the egg is inserted. Usually, the egg is oriented so that the egg body is in the water, with the respiratory horns exposed to the air.

In those genera of Nepinae for which there is information (Nepa, Curicta, Laccotrephes Stål), the eggs are most commonly deposited out of water in the mud along the shore. However, some authors have seen Nepa laying eggs in decaying plant material in the water. Nepine females do not have sharply pointed, keeled, subgenital plates like those of the Ranatrinae. Instead, the plate is flattened and rather blunt and not well suited for making incisions in plant fibers.

The life history of the North American Ranatra fusca Palisot de Beauvois has been studied by Torre-Bueno (1906a, as R. quadridentata Stål) and by Radinovsky (1964). Radinovsky's paper contains excellent photographs which illustrate various aspects of development and behavior. The egg of R. fusca is about 3.5 mm long, and the respiratory horns are about 4 mm long. Radinovsky reported that a single female may lay up to 50 eggs at a time, placing them in rows. She may return later to the same location and lay additional eggs. Radinovsky found that first instar nymphs needed some vegetation or other suitable support near the surface to survive. Without such objects, they had great difficulty replenishing their air supply and usually drowned. Total developmental time (egg to adult) in R. fusca is about two months.

Both Ranatra and Nepa are known to fly, but flight has rarely been observed (Larsén, 1949b, Torre-Bueno, 1906a). Larsén gave excellent figures and an interesting description of how Ranatra prepares for flight and its attitude during flight. As in many other aquatic bugs, brachyptery and flight muscle degeneration occur in the Nepidae.

When handled, water scorpions often make a squeaking sound by rubbing the base of the anterior coxa against the inside edge of the flaring coxal cavity. Holmes (1906), Severin and Severin (1911) and Larsén (1949a) described in detail the "death feint" assumed by nepids on removal from water. As in the Belostomatidae, death feigning probably serves as a means of escaping detection by predators.

Water scorpions breathe air from an airstore concealed beneath the wings. To replenish the subhemelytra airstore, the bug breaks through the surface film with its siphon. In adults, air is carried down through the siphon, through the eighth abdominal spiracles at its base, and into the longitudinal tracheal trunks, thence to and through the first pair of abdominal spiracles, which are dorsal in position and open into the subhemelytra airstore (Parsons, 1972b). Apparently, the intermediate spiracles are non-functional in respiration, and an exposed ventral airstore is absent, at least in Ranatra and Nepa. The airstore in nepid nymphs is located on the abdominal venter and all the abdominal spiracles are functional and ventral in position. The abdominal terga of nymphs have lateral paratergites (Hamilton, 1931) which are folded under so that they cover the lateral spiralce bearing plates of the venter (fig. 67). The paratergites and the sircle bearing plates are covered with long hairs and form two lateral longitudinal airstores which are replenished with air through the siphon.

Another interesting feature of nepids is the "static sense organs." These distinctive, oval structures are closely associated with the fourth, fifth, and sixth abdominal spiracles (fig. 68). Baunacke (1912) and Thorpe and Crisp (1947) have demonstrated experimentally that these organs keep the bug correctly oriented in the water by detecting differences in water pressure among the three pairs of spiracles. Thorpe and Crisp's experiments proved that the static sense organs are not depth perceptrons. However, Miller (1961) suggested that an "extensible organ" in the thorax is a depth perceptor.
Fig. 67, Ventral view of part of nymphal abdomen in Ranatra; 68, abdominal venter of adult Ranatra showing static sense organs (SSO).

KEY TO NEARCTIC GENERA OF NEPIDAE

Nymphs and adults

1. Anterior lobe of pronotum not wider than head; body long, slender, cylindrical; abdominal sterna of adult undivided (fig. 69); adult female subgenital plate laterally compressed, keel-like... (Ranatrinae) Ranatra Fabricius, p. 72
   Anterior lobe of pronotum wider than head; body flattened; abdominal sterna of adult divided longitudinally into median and parasternites (figs. 70-71); adult female subgenital plate broad, flattened... (Nepinae) ......... 2

2. Median length of fifth visible sternum twice median length of fourth (fig. 71)... (Nepini) ............... Nepa Linnaeus
   Median length of fifth visible sternum about equal to length of fourth (fig. 70)... (Curictini) ............... Curicta Stål

Subfamily Ranatrinae

This subfamily contains Ranatra, which is cosmopolitan and Cercotmetus, which is oriental.

Genus Ranatra Fabricius


Ranatra is characterized by the long, narrow, cylindrical body and nearly contiguous middle and hind coxae.

This genus is nearly cosmopolitan in distribution and contains probably more than 120 species, of which about half occur in the New World, primarily in the tropics. Hungerford (1922), in his revision, recognized nine species in the United States. Since that work, three additional species have been described and one eli-
nated as a North American species. The total now stands at 11 North American Ranatra. De Carlo (1964a) published descriptions of most of the species of Ranatra from the Western Hemisphere, and although illustrated no key was provided. More recently De Carlo (1973) keyed all of the known New World species except one described by Polhemus (1976a). The problems I have encountered while attempting to determine some of the California Ranatra indicate that the genus in North America is still in need of a modern taxonomic review. Lansbury's (1972) revision of the oriental Ranatra provides an excellent model for such a study.

Three species are known from California, and Pierce (1948) described two fossil Ranatra from the McKittrick asphalt pits in Kern County.

KEY TO RANATRA OF CALIFORNIA

1. Closing face of forefemur with a rather narrow, subapical, semicircular notch which is defined basally by a strong tooth (fig. 74); Coachella and Imperial Valleys, Colorado River. .................. Ranatra brevicollis Stål

Closing face of forefemur broadly excavated near apex, never with a semicircular notch, excavation may or may not be defined basally by a tooth (figs. 72-73).......................... 2

2. Metasternal process nearly attaining base of abdomen (fig. 76); last sternum of female slender, gradually tapering to apex (in lateral view), keel more or less a straight line for most of its length (fig. 78); excavation of forefemur broad and shallow, without a basal tooth (fig. 72); length of basal section of forefemur usually less than length of apical section, average ratio = 0.92 in male, 0.95 in female. . . . southern California north to about 40° ........................ Ranatra fusca Montandon

Metasternal process short, ending at about one-half the length of the metacoxa (fig. 75); last female sternum broad, basal one-third of uniform height (in lateral view), keel broadly arched from base to apex (fig. 77); excavation of forefemur defined basally by a sharp angle, the angle occasionally forming a small tooth or prominence (fig. 73); length of basal section of forefemur more than length of apical section, average ratio = 1.08 in male, 1.14 in female; northern California south to about 36°; widespread in northern United States .......................... Ranatra fusca Palisot de Beauvois

3. Metasternal process short, ending at about one-half the length of the metacoxa (fig. 75); last female sternum broad, basal one-third of uniform height (in lateral view), keel broadly arched from base to apex (fig. 77); excavation of forefemur defined basally by a sharp angle, the angle occasionally forming a small tooth or prominence (fig. 73); length of basal section of forefemur more than length of apical section, average ratio = 1.08 in male, 1.14 in female; northern California south to about 36°; widespread in northern United States .......................... Ranatra fusca Palisot de Beauvois

4. Metasternal process short, ending at about one-half the length of the metacoxa (fig. 75); last female sternum broad, basal one-third of uniform height (in lateral view), keel broadly arched from base to apex (fig. 77); excavation of forefemur defined basally by a sharp angle, the angle occasionally forming a small tooth or prominence (fig. 73); length of basal section of forefemur more than length of apical section, average ratio = 1.08 in male, 1.14 in female; northern California south to about 36°; widespread in northern United States .......................... Ranatra fusca Palisot de Beauvois

Geographic range. California from 40° south to northern Baja California.

California records (map 22). Ranatra brevicollis occurs from southern Humboldt County to San Diego, inhabiting low elevation streams on both drainage sides of the Coast Ranges, and the foothills of the Sierra Nevada. It is found at moderate elevations in the mountains of southern California and occurs along desert margins. Adults have been collected almost throughout the year, from early February to the end of December, but most commonly from late March to mid-October.

Ranatra fusca Palisot de Beauvois
(Figs. 73, 75, 77)


Specimens of Ranatra fusca from the eastern United States (presumably the most typical R. fusca because the species was probably based on eastern specimens) are recognizable by their narrow, elongate form, short
metasternal process and the sharp angle or tooth on the basal side of the femoral excavation. Often, however, these characteristics are not as well developed in specimens from the far west, especially those from central California. Occasionally specimens from this part of the state are shorter and stouter, and the tooth on the front femur is often poorly developed, especially in males. These specimens are difficult to identify because of their close resemblance to *R. brevicollis* in one or more characters.

A few specimens, all females, have been seen from the Central Valley of California (Davis, Yolo Co.; Modesto and Newman, Stanislaus Co.; Lindsay, Tulare Co.). They appear to be *R. fusca*, but the front femur is suggestive of *R. brevicollis*. Furthermore, in these specimens the subgenital plate is shorter and stouter than is usual for *R. fusca*. More collecting is needed in the Central Valley before the significance of this variation can be ascertained.

**Geographic range.** Transcontinental in southern Canada and the United States, not definitely known from the southwest or Mexico.


*Ranatra quadridensata* Stål
(Fig. 74)

The narrow semicircular notch near the apex of the closing face of the front femur is distinctive in *R. quadridentata*. As I indicated earlier (Menke, 1964), there is some question as to whether the California and Arizona "quadridentata" are true *R. quadridentata*.

**Geographic range.** Southern California to Texas and Mexico.


This is primarily a Sonoran species which extends into the Coachella and Imperial Valleys of southern California.
FAMILY BELOSTOMATIDAE

Giant Water Bugs,
Electric Light Bugs, Toe Biters

A. S. Menke

Members of this family are brown, dorsoventrally flattened bugs. The strong, thick, front legs are used for grasping. The middle and hind legs are broad, flat, and fringed with swimming hairs. The tarsi are two or three-segmented. Belostomatids lack ocelli and the usually four-segmented antennae are concealed in pockets beneath the head. The most distinctive adult belostomatid feature is a pair of retractable, straplike appendages at the abdominal apex which are used to obtain air. These “airstraps” are homologous with the respiratory siphon of the related family Nepidae, being derived from the eighth abdominal tergum. Each strap bears a spiracle basally.

Seven genera of belostomatids, in three subfamilies, were recognized by Lauck and Menke (1961). De Carlo (1966) described an additional genus from South America. Approximately 150 species are known in the family. Two of the subfamilies are represented in California, the Belostomatinae, with Belostoma and Abedus, and the Lethocerinae, with Lethocerus. The third subfamily Horvathiniinae is restricted to South America and includes one genus, Horvathinia Montandon. Morphological terminology used here follows Menke (1958, 1960, 1963), Lauck (1962), and Lauck and Menke (1961).

Belostoma and Lethocerus prefer standing water habitats, but Abedus are almost invariably found in streams, especially under rocks in riffle areas or clinging to aquatic plants. Although belostomatids are strong swimmers, most are sedentary hunters. They seem to prefer to perch on submerged vegetation or other support and wait for prey to swim by. The raptorial front legs are held out in readiness, and the bugs are quick to seize any moving object that passes near. The stimulus that triggers the strike reaction is primarily visual in Lethocerus, according to Cullen (1969), although he does not rule out prey detection by water movement.

The diet of belostomatids is varied, and it is probable that these bugs will suck dry anything that they can subdue. One notable exception is found in the African genus Limnogeton Mayr whose species do not possess the broad grasping front legs found in other belostomatid genera. Voelker (1966, 1968) has found that L. fieberi Mayr is an obligatory feeder on freshwater snails. Cullen (1969) suggests that some Belostoma may prefer a snail diet also. Lethocerus feeds on a variety of aquatic organisms (tadpoles, small frogs, dytiscid beetles, etc.), and there are reports of them attacking prey much larger than themselves. Matheson (1907) gave an account of a bug clinging to a woodpecker, and Wilson (1958) described an incident in which L. uhleri (Montandon) fed on a twelve-inch banded water snake. Harvey (1907a, b) reported Abedus indentatus (Halde-man) killing a three-inch trout, and giant water bugs are sometimes important pests in fish hatcheries (Dimmock, 1886, 1887; Wilson, 1958).

The ability to make successful attacks on such large prey is due in part to the strength and tenacity of these bugs. However, Picado (1937, 1939) and De Carlo (1959) demonstrated that the paralyzing effect of the toxin injected by belostomatids must play a big role in subduing prey. Picado’s studies on the salivary secretions of Lethocerus delpontei De Carlo show that these fluids hasten coagulation of normal noncitrated blood of both man and rabbits. Hemolysis of red cells in rabbits is greater than that resulting from any snake poison, and the effects could not be neutralized by any serum except Crotalus terrificus antivenin. De Carlo performed experiments with L. annulipes (Herrich-Schaeffer) using frogs as prey. He found that the bites of Lethocerus ultimately resulted in partial or complete paralysis of the frog and eventual death, even in experiments in which the bug was allowed only a few seconds feeding on the frog. Necrosis of the tissue at the site of the wound and general swelling in the surrounding area usually accompanied the attack. Death from bites usually occurred within three to five hours, although in one experiment, a frog lived for three days. Rees and Offord
(1969) found that the salivary secretion of Lethocerus fakir (Gistel) (as cordofanus) contains a potent mixture of hydrolytic enzymes (proteases), and that in 10 to 15 minutes after a bug had injected a frog, the insides of the victim were liquefied. Ewing (1928) described the reaction of a man to the bite of Lethocerus (Benacus) griseus (Say). A bite on the hand of a few seconds duration produced an immediate burning sensation which lasted several hours. This was accompanied by swelling of the area and reddening around the puncture site.

The life histories of several New World Lethocerus have been studied by Hoffmann (1924b), Hungerford (1925), Rankin (1935), J. M. De Carlo (1962), and Cullen (1969). Lethocerus lay their eggs on emergent vegetation or other objects out of water. In this genus, the eggs have dark brown stripes extending downward from the free end (fig. 9). Lethocerus eggs are glued in contiguous rows forming batches which average about 70 eggs in L. americanus (Leidy) according to Rankin. De Carlo reported 15 to 43 eggs per mass for L. mazzai. De Carlo, an Argentine species, whereas L. maximus, studied by Cullen, laid 86 to 257 eggs. Incubation in Lethocerus takes one to two weeks, and hatching is accomplished by breaking open the apical end of the shell. The cap remains attached to the rest of the egg. The average time of development for L. americanus was given by Rankin as 33 days in nature and 59 days in the laboratory. According to De Carlo, L. mazzai takes 72 days to develop from egg to adult.

Females of Abedus and Belostoma, as well as other genera of the Belostomatinae, glue their eggs on the dorsum of males, who carry and care for them until they hatch (fig. 8). These are the only known examples of sex role reversal in insects (Smith, 1976a). Eggless males spend much time hanging vertically from submerged vegetation, but those with eggs float horizontally at the water surface. Male bugs encumbered with eggs engage in a variety of brooding behaviors that include keeping the eggs wet, frequently exposing them to atmospheric air, and maintaining an intermittent flow of water over them by stroking them with the hindlegs while below the surface (Smith, 1976b). Abedus herberti Hidalgo also employs brood pumping (rocking up and down on the longitudinal body axis) (Smith, 1976a). Brood pumping and stroking presumably provide for efficient embryonic gas exchange and enhance egg survival and development. Eggs fail to develop if kept submerged (inadequate gas exchange) or are left in open air (desiccation).

Counts of eggs laid on the backs of Belostoma flu-mineum Say males have varied from 65 to 159. Abedus females deposit a similar number of eggs. Generally, all of the eggs on the back of one male are laid by a single female, but there are exceptions. Torre-Bueno (1906b) and Hungerford (1920) indicate that incubation of B. flumineum eggs takes 6 to 12 days and that the total time for development from egg to adult is 42 to 54 days. Harvey (1907a, b) stated that Abedus indentatus eggs lasted 10 to 12 days. This agrees closely with incubation times published for most belostomatids, but in the laboratory incubation in A. dilatatus (Say) took 33 to 35 days (Menke, 1960), and eggs of A. herber thi Hidalgo took 21 to 23 days to hatch (Smith, 1974). The longer incubation times for these last two species probably reflect nonoptimal laboratory water temperatures. Smith (1974) found that total development time in A. herberti was about two months.

Belostomatid eggs increase in size and weight during incubation. According to Madhavan (1974) these changes are due to water uptake through the micropyle. Yolk protein is the chief metabolite during embryonic development and water is required in increasing amounts for protein hydrolysis. Of course, enlargement of the developing embryo accounts for some egg enlargement near the end of incubation.

Belostomatids often spend the winter buried a few inches down in the bottom ooze of ponds. Irwin (1962) reported Belostoma overwintering in cracks in a log on the bank of a pond beneath leaf litter. The bugs were caked with mud, and, when placed in aquaria, were sluggish for about an hour. For nearly a week the bugs attempted to get out of the water by climbing upon floating objects.

Severin and Severin (1911) studied the peculiar habit in Belostoma of holding the legs rigidly against the body when taken from the water. They found that increasing dryness shortened the duration of the rigid posture. This same attitude is assumed by Belostoma that are found overwintering under logs and debris near water (Irwin, 1962). Thus it would seem that this habit is correlated with removal from the normal aquatic medium, with loss of water contact probably triggering the rigid posture. This immobile habit makes the bugs difficult to detect amongst leaf litter on the shore, and, therefore, is of survival value.

When handled, most belostomatids eject a foul-smelling fluid from the anus. Both Abedus (Harvey, 1907a, b) and Lethocerus can squirt this fluid three or four feet, and this capability probably serves as a defense mechanism. Species of Lethocerus possess metasternal scent glands. These glands are well developed in the male but are small in the female, according to Staddon (1971). Their function is unknown, but males are said to have a strong odor, and the glands may secrete a sex pheromone. Staddon found that these glands are absent in the Belostomatinae.
Members of the genus *Lethocerus*, commonly called "Giant Water Bugs," frequently are attracted to lights in large numbers, especially in the eastern United States. This habit has also earned them the name "Electric Light Bugs." *Belostoma* often swarm around lights in the tropics, but in the United States this habit seems infrequent. Nearctic species of *Abedus*, referred to as "toe biters," have not been recorded in flight, but two Mexican species, *A. vicinus* Mayr, and *A. parkeri* Menke, have been taken at black light (Menke & Truxal, 1966; Menke, 1966, 1977). According to Cullen (1969) some belostomatids display lunar periodicity in their flight patterns, with most bugs flying at full moon. He hypothesizes that the maximum moonlight facilitates recognition of topography, especially water. In South America heavy rains may induce great flight activity regardless of lunar periodicity (Nieser, 1975).

Flight muscle degeneration often occurs in belostomatids after dispersal flights (Cullen, 1969). In *Belostoma*, muscle degeneration occurs in both sexes, but in females it is associated with the development of eggs.

The belostomatid airstrips are used in obtaining air for the subhemelytral airstore, but because they are flat and lie side by side, the airstrips do not form a tube. Instead, an air channel is formed by long, marginal hairs which converge mesad ventrally. According to Miller (1961) and Parsons (1972), air traveling down the channel goes directly under the wings into the subhemelytral airstore rather than into the tracheae by way of the eighth abdominal spiracles as in nepids. In belostomatids the fairly large airstrap spiracles are largely exhalant according to Parsons (1973). Gas exchange between the subhemelytral airstore and the tracheal system occurs primarily through the eighth abdominal spiracles. The smaller, ventrally located second through seventh spiracles are recessed and less permeable, but they also have a respiratory role. These spiracles are surrounded by, or are adjacent to, broad mats of hair which hold a thin film of air. This ventral abdominal "hairpile" functions in supplying air taken from the subhemelytral airstore to the spiracles. The ventral hairpile is continuous with the dorsal hairpile (associated with the dorsal airstore) at one or more of the following points (the number depends on the genus): (1) along the lateral margins of the third and fourth abdominal segments, (2) at a cleft between the sixth and seventh abdominal segments, and (3) at the interface between the lateral margin of the subgenital plate and the adjacent ventral paratergite. The exposed ventral airstore may act as a physical gill.

The nymphal airstore is confined to the abdominal venter, and because airstrips are not developed, the tip of the abdomen is used to break the surface film. All spiracles are functional in immatures. The metapleural episterna are prolonged posteriorly around the hindcoxae in nymphs (fig. 80). These large plates cover the first and second abdominal sterna and presumably function in protecting the basal spiracles and airstore. Tawfik (1970) found experimentally that these plates are necessary for the survival of the bug. They apparently aid in spreading the airstore over the spiracles. The problem of respiration during molting has been discussed by Smith (1975). Members of the family float at the surface during ecdysis.

Möller (1921) studied the tracheal system of *Lethocerus uhleri* Montandon and described "static sense organs" (or pressure receptors) similar in structure to, though smaller and not as complex as, those found in the Nepidae. These organs are associated with the spiracles of the first to sixth visible ventral abdominal segments. Their function is not known, but Möller suggested that they are used in underwater orientation.

**KEY TO NEARCTIC GENERA OF**
**BELOSTOMATIDAE**

**Adults**

1. Tibia and tarsus of hindleg strongly compressed, thin, much broader than middle tibia and tarsus (fig. 84): basal segment of beak about half length of second; length 40 mm or more ... (Lethocerininae) ....... *Lethocerus* Mayr, p. 79

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![FIG. 80. Ventral view of nymphal metathorax and abdomen, genus *Abedus*, showing expanded episterna around hindcoxae.](image-url)
Tibia and tarsus of middle and hind leg similar (figs. 95, 109); basal segment of beak subequal to second; length 37 mm or less... (Belostomatinae). .............. 2
2. Membrane of hemelytron reduced (fig. 109); length 27 mm or more... ........... Abedus Stål, p. 83
Membrane of hemelytron not reduced (fig. 95); length 26 mm or less........ Belostoma Latreille, p. 80

**Nymphs**

1. Foreleg with two equally developed claws...... Lethocerus Mayr
   Foreleg with one long claw.......................... 2
2. Interocular with narrow, linear depression closely paralleling inner orbit, convexity of interocular uniform, not interrupted by transverse swelling at posterior end of depression
   Interocular with a broad linear depression distantly paralleling inner orbit, convexity of interocular interrupted by transverse swelling at end of depression... Abedus Stål

**Subfamily Lethocerinae**

This subfamily contains the single, cosmopolitan genus Lethocerus.

**Genus Lethocerus Mayr**

*Iliastus* Gistel, [1847], in Gistel and Bromme, Handbuch Naturgeschichte aller drei Reich p. 490.


**Amorgiuris** Stål, 1866, Hemiptera Africana 3:179.

**Montandonista** Kirkaldy, 1901, Entomologist 34:6.


This genus is characterized by the broad, thin, flat hind tibiae and tarsi and by the division of the abdominal sternum into median and parasternites. Other diagnostic features are the two projections on the fourth antennal segment and the stout beak. The first segment of the beak is about half the length of the second. The front tarsus is three-segmented and terminates in one large claw; the other claw is much reduced.

**Lethocerus** has a worldwide distribution but reaches its greatest development in the Western Hemisphere, especially the Neotropical Region. The North and Central American species were revised by Menke (1963) and De Carlo (1964b) presented a synopsis of the entire genus. Two of the five species recorded for the United States occur in California. The subgenus *Benacus* is not represented in the state.

A petition has been submitted to the International Commission on Zoological Nomenclature (Menke, in press) asking for conservation of the name Lethocerus which was discovered recently to be a junior synonym of *Iliastus* Gistel (Menke, 1976).

**KEY TO UNITED STATES SPECIES OF LETHOCERUS**

1. Closing face of forefemur without grooves; U.S. east of 100th meridian... (subgenus *Benacus*) ........ *griseus* (Say)
   Closing face of forefemur with two grooves for reception of tibia... (subgenus *Lethocerus*) .............. 2
2. Distal, inner, ventral process of hindtibia sharp (fig. 82);
   Death Valley, California; Ash Meadows, Nevada .......... *angustipes* (Mayr)
   Distal inner, ventral process of hindtibia rounded (fig. 81)...... 3
3. Outer margin of hindtibia broadly curved (fig. 83); width of hindtarsal segment 1 (excluding marginal setae) greater than least interocular distance; Arizona to Texas .......... *medius* (Guérin-Méneville)
   Outer margin of hindtibia nearly straight (fig. 81); width of hindtarsal segment 1 less than or at most equal to least interocular distance .......... 4
4. Appressed pubescence of first visible ventral paratergite extending to epimeron; transcontinental in northern two-thirds of U.S. .......... *americanus* (Leidy)
   Appressed pubescence covering only one-half to two-thirds of first visible ventral paratergite, not attaining epimeron; U.S. east of 100th meridian... *uhleri* (Montandon)

**Lethocerus (Lethocerus) americanus** (Leidy)

(Fig. 84)


**Geographic range.** Transcontinental in southern Canada and the United States (mainly north of the 35th parallel).

**California records** (map 24). *Lethocerus americanus* is most abundant in the northern half of the state where it occurs from nearly sea level to 8,000 feet. The species is also known as far south as Orange and Riverside Counties, but not in the Mojave and Colorado Deserts. I have not seen any recent records of *L. americanus* from southern California, the trend toward decreasing rainfall in this area and resultant drying of suitable habitats being the probable explanation. Clear water ponds with much aquatic vegetation are the favorite habitat of this species. There are records during every month except December but most are from March to September. *L. americanus* is known from the Pleistocene La Brea Tar Pits in Los Angeles, California (Menke, 1963)

**Lethocerus (Lethocerus) angustipes** (Mayr)

(Fig. 82)

Mexican specimens have a light brown venter, but material from the Amargosa River system in California (Saratoga Spring) and Nevada (Ash Meadows) have brownish black venters.

Geographic range. Primarily Mexican but an isolated population exists in the Amargosa drainage of Nevada and California.

California records (map 24). INYO CO.: Saratoga Spring, Death Valley, VI-19-54 (W. McDonald, RLU); XII-1-54 (R. W. Sabbott.

Subfamily Belostomatinae

This group contains five genera, two of which occur in North America.

Genus Belostoma Latreille


subspecies *fusciventer* (Stål), 1854, was published in 1852. Hence it has priority over Stål's name. Lauck (1959) described the new species *B. thomasi* for a form that had long been known under the name *B. fusciventre* (see list of references in Lauck, 1964:117-118). Dufour (1863) described *fusciventre* from specimens bearing this Stål manuscript name, and Mayr (1871) redescribed and keyed Dufour's species after seeing the types. Mayr's key clearly identifies *fusciventre* as identical with *thomasi*, and I am synonymizing the latter (NEW SYNONMY). The species called *B. ellipticum* Latreille by Lauck (1959, 1962) is probably misidentified. Latreille's 1817 (not 1833) original description was unavailable to Lauck but I have examined it. The body dimensions given by Latreille for *B. ellipticum* (26 by 14 mm) are significantly less than the range for Lauck's "*ellipticum*” (31.5-41.5 mm long, 14-19.5 mm wide). I have maintained Lauck's usage of *B. ellipticum* here, but the status of the name needs investigation.

### KEY TO UNITED STATES SPECIES OF *BELOSTOMA*

1. Appressed hair of ventral paratergites IV-VI reaching margin of adjacent sterna or separated from them by a hairless zone that is much narrower than outer glabrous area (figs. 91-92) ................................................................. 2
2. Appressed hair of ventral paratergites IV-VI separated from sterna by a hairless zone that is about as broad or broader than outer glabrous area (figs. 89-90) .................................................. 5
3. Anteoculus length equal to or slightly less than eye length in lateral profile (fig. 93); lateral margins of pronotum usually concave (fig. 85) ................................................................. *flumineum* Say
   Anteoculus length two-thirds to three-fourths eye length in lateral profile (fig. 94); lateral margins of pronotum usually straight (fig. 86) ........................................ 4
4. Airstrap long, slender (fig. 88); legs pale brown with darker spots; Louisiana to California and north to Washington .......... *bakeri* Montandon
   Airstrip shorter and broader (fig. 87); legs chocolate brown; Death Valley, California ........................................... *saracotaque* Menke
5. Body 29 mm long or more; southern Texas .............................................. 6
   Body less than 25 mm long; widespread ........................................ 7
6. Anteoculus longer than interoculus length ....... *ellipticum* Latreille
   Anteoculus equal to or less than interoculus length ........ *subspinosum* ssp. *bifoveatum* (Haldeman)
7. Body twice as long as wide or less; coastal states from eastern Texas to New York ........................................... *festacorum* (Leidy)
   Body more than twice as long as wide; Texas, Arizona, Louisiana ................................................................. 8
8. Interoculus smoothly convex from eye to eye; glabrous outer margin of ventral paratergites uniformly pale brown; s.

Belostoma bakeri Montandon
(Figs. 86, 88, 92, 94, 95)

Belostoma flumineum Say
(Figs. 85, 92-93)


Belostoma flumineum can usually be recognized by


The rather straight lateral pronotal margins usually distinguish Belostoma bakeri from B. flumineum. The two species seldom occur together, and B. bakeri is more widespread in the state. Belostoma bakeri is similar to B. saratogae, but the airstraps of the latter are shorter and broader (compare figures 87-88). Usinger's (1956) figure 7:16a was mislabelled B. flumineum Say.

Geographic range. Washington to northern Baja California, eastward to Louisiana, south to Durango, Mexico.

California records (map 25). This is the commonest and widest ranging species of Belostoma in the state, but it seems to be largely absent from the Central Valley south of Sacramento where it is replaced by B. flumineum. Except for marginal incursions, B. bakeri is absent from the Mojave and Colorado deserts. Specimens have been collected every month of the year in the southern part of the state.

Belostoma flumineum Say
(Figs. 85, 92-93)


Belostoma flumineum can usually be recognized by
Belostoma Men*.

FIG. 95. Belostoma bakeri, dorsal view (from Usinger, 1956).

the concave lateral margins of the pronotum and elliptical body.

Geographic range. Transcontinental in southern Canada and the U.S., south into northern Mexico.


Belostoma flumineum is found principally in the Central Valley and in the Coachella and Imperial Valleys.

Belostoma saratogae Menke (Fig. 87)


The short, broad airstraps (fig. 87) separate Belostoma saratogae from the closely related B. bakeri.

Geographic range. Death Valley, California.

California records (map 26). INYO CO.: Saratoga Spring, Death Valley, type series (Menke. 1958); same locality: XI-28-58 (A. Menke. ASM); IV-3-59 (A. Menke and L. Stange. ASM); weed choked channel between spring pool and lake, II-21-64 (J. T. Polhemus. JTP); X-5-64 (J. T. Polhemus. JTP).

Belostoma saratogae is known only from the same hot spring pool and outlet channel described under Lethocerus angustipes. Adults have been collected near every month of the year.

Genus Abedus Stål


Deinostoma Kirkaldy, 1897. Entomologist 30:258 (= subgenus).


Abedus shares many characteristics with Belostoma and differs primarily in the reduction of the membrane of the forewing. Unlike the simple airstraps of Belos-
toma, these organs in most species of Abedus bear specialized setose structures dorsally, which in the male are diagnostic for each species (figs. 102-103, 105, 107). De Carlo (1969) relegated Abedus to a subgenus of Belostoma, but the wing difference coupled with the nearly universal specialized airstrap separates them. Furthermore, the two genera usually occupy different habitats, Abedus in streams, Belostoma in ponds. Abedus is divided into four subgenera; the single California species belongs in the subgenus Deinostoma.

Twelve species are now recognized in Abedus (Menke, 1977). Keys for their identification are found in Menke (1960, 1966). The genus is restricted to Central America, Mexico, and the southern United States (principally the southwest). One of the six U.S. species, A. immaculatus, occurs in the southeast, but its placement in Abedus is problematical.

KEY TO UNITED STATES SPECIES OF ABEDUS

1. Abdominal sternum II-VII completely covered with long, appressed, silky hair (fig. 96).............. (subgenus Deinostoma) .............................. 2
   Abdominal sternum VII (subgenital plate) glabrous, other sternum glabrous or at least IV-VI with hairless zone along midline (figs. 97-99).................................................. 3

9. Many specimens become greasy and this pubescence may be matted down and obscure.
10. The sterna and paratergite II may be covered with spicules which do not, however, obscure the integument.

2. Airstrip with narrow, oblique, sinuate band of long hair basad of which is a large, velvet-like mat of short setae (fig. 102) in both sexes; California .............. indentatus (Haldeman)
Airstrip with subapical, roughly triangular patch of long hair basad of which is a small patch of velvet-like setae in female (fig. 104), and a large circular depression usually containing one or more longitudinal folds in male (fig. 103); Arizona, Utah, New Mexico ....... herberti Hidalgo s.l.

3. Ventral paratergite II without long silky hair at least on outer half (fig. 97); airstrips slender, similar in both sexes, evenly covered with long hair dorsally (figs. 100-101) .......................................................... 4
Ventral paratergite II covered with appressed silky hair similar to that of III-VII (figs. 98-99); airstrips broad, sexually dimorphic, widest in male, dorsal pubescence in distinctive transverse patterns (figs. 105-108) ...... (subgenus Abedus) .......................................................... 5

4. Metasternum keel-like nearly to apex; sternum III-VI with long, appressed silky hair laterally (fig. 97); segments II-III of antenna each bearing long, lateral process; southeastern Arizona (Cochise Co.) ...... vicinus sonorensis Menke
Metasternum broadly swollen, somewhat keel-like at base; sternum without long, silky hair; segment II of antenna simple, III with short process; se. U.S. ...... (subgenus Microabedus) ...................... immaculatus (Say) .............................. 6

5. Airstrip with subapical, dorsal sac (figs. 107-108); southeastern Arizona (Cochise Co.) .......... ovatus Stål
Airstrip without dorsal sac or folds (figs. 105-106) ...................... 7

6. Hemelytral membrane narrow, cells short or poorly defined, largest wider than long or at most square (some females), combined width of membrane and translucent margin about equal to median length of posterior lobe of promo-

Abedus (Deinostoma) indentatus (Haldeman)  
(Figs. 96, 102, 109)


11. In some female A. breviceps the combined width of membrane and translucent margin may be greater than the width of the posterior lobe of the pronotum, but in these specimens the translucent margin is broader than the row of cells in the membrane. In A. parkeri females the translucent margin is narrower than the row of cells in the membrane.

De Carlo (1963) refuted my synonymizing Abedus hungerfordi De Carlo and A. mayri De Carlo with A. indentatus (Menke, 1960). In view of the variation found in A. indentatus, I am able to recognize only one species of Abedus in California. Usinger’s (1956) figure 7:16b was labelled A. hungerfordi De Carlo, prior to the synonymy.

Geographic range. California from about the 39th parallel south into northern Baja California.

California records (map 27). Abedus indentatus is found in most streams in the southern two-thirds of the state. The species has been taken at several isolated desert localities such as Hanaupah Canyon and Saratoga Spring in Death Valley; Surprise Canyon in Panamint Valley; San Felipe Creek, 5 miles W. of Kane Spring, Imperial Co.; and Palm Springs and Indio, Riverside Co. Low temperature may be the factor which is responsible for the scarcity of A. indentatus north of the 39th parallel. Most specimens from mountainous localities have been taken at lower elevations although I have seen several examples that supposedly were collected at Lake Tahoe and Truckee, Nevada Co. Both of these places are at an elevation of about 6,000 feet and confirmation of the presence of A. indentatus in the general area is desirable.

Watercress and other plants are favorite haunts of A. indentatus in many streams but in those lacking much aquatic vegetation, this bug usually is found clinging to submerged rocks.
MAP 27. California distribution of *Abedus indentatus* (Haldeman).
With about 500 species, the Corixidae is the largest family of aquatic Hemiptera. Water boatmen possess a number of unusual features among which the triangular head with its short, broad, triangular, unsegmented labium is unique and diagnostic. All other families in the Nepomorpha have a three- or four-segmented, beak-like labium. The corixid labium is broadly fused with the rest of the head and its exterior surface usually has a number of distinctive, transverse grooves and a median, longitudinal channel which houses the stylets (fig. 110). Other peculiar family characters include the one-segmented front tarsus termed the "pala" which is flattened and scooped like (in some corixids the tarsus and tibia are fused), the concealed scutellum (except in the Australian genus Diaprepocoris Kirkaldy), and the asymmetry of the male abdominal segments. In most genera tergum VI of the male bears a filelike plate called the "strigil" which is a misnomer because it apparently has nothing to do with stridulation. Ocelli are absent except in Diaprepocoris which has two. The antennae are short, concealed, and consist of three or four segments. The wing membrane is without veins. Unique scent glands are found on abdominal terga 111-V of the nymph, and adults have metathoracic scent glands that open near the midcoxae. A distinctive family trait is the pattern of alternating dark and light transverse banding of the dorsum which is common to most genera. Parsons (1977) gave other family characteristics and her paper, as well as Poisson's (1935), should be consulted for additional morphological details.

Each pair of legs is adapted to a special function in this family. The front legs are used in food gathering. The midlegs are used for clinging to the bottom or other substrate while feeding or resting. They are slender and usually terminate with a one-segmented tarsus and two long claws. Unlike the notonectids, water boatmen swim with their dorsum up. They are propelled through the water by their long, flattened, oarlike hindlegs which are fringed with long swimming setae. The hindlegs are also used in cleaning the body and ventilating the airstore (Griffith, 1945; Popham, 1960; Parsons, 1970).

Hungerford (1948a) divided the approximately 30 genera in the Corixidae among six subfamilies. Only the Coricininae, which contains the majority of the family members, is represented in California. Hungerford's classification has been refined by Leston (1955), but some workers prefer a more conservative approach to the recognition of genera (Walton, 1943; Macan, 1955), or subfamilies (Popov, 1971). This controversy will probably not be resolved until world studies are made. Seven genera and 25 species are known in California. These vary from the minute Trichocorixa, less than 2.8 mm long, to the rather robust Hesperocorixa, which may attain a length of 13 mm.

Corixids have successfully invaded a wide range of habitats. They occur below sea level in the saline waters of Death Valley and the Salton Sea of California, and reach elevations as high as 15,000 feet in the Himalayas. They inhabit frigid subarctic waters beneath ice (Sailer, 1952), hot spring water with a temperature of 35°C (Sailer, 1948), and some, such as Trichocorixa reticulata (Guérin-Méneville) and T. verticalis (Fieber), are halobions, living exclusively in saline or brackish waters. Hutchinson (1931) and Polhemus (1974b) recorded live specimens of the former species from the ocean (Delaware Bay) and the Gulf of California, respectively. According to Usinger (1956) T. reticulata occurs in the brine pools of the Leslie Salt Company on the south shore of San Francisco Bay which is also inhabited by brine shrimp, Artemia salina Leach, and the brine fly, Ephydra cinerea Jones. Gunter and Christmas (1959) found T. verticalis off the coast of Louisiana and Mississippi. Hungerford (1939) reported collections of Sigara lineata (Forster) from Lake Erie at depths down to 35 feet. Data in Applegate and Kieckhefer (1977) suggest that corixids are not uncommon at such depths.

Except for the Trichocorixa species mentioned above and two Corisella that sometimes inhabit saline or alkaline waters, California corixids prefer freshwater. Most
species are pond dwellers but individuals frequent the shallows of larger lakes and reservoirs, or the quiet pools of streams. A few species such as *Graptocorixa californica* (Hungerford) and *Sigara vandykei* Hungerford are exclusively associated with running water. *Graptocorixa californica* prefers the pools of small streams, while *Sigara vandykei* is found along the margins of rivers mixed with the more scattered individuals of typical pond species. *Trichocorixa* and *Corisella* each have two species that occur in saline waters and these pairs often share the same habitat, two closely related species of a single genus living together under what appear to be identical conditions. Certain corixids may reach extremely high population levels. For example, along the shallows of the Klamath River densities of *Sigara vandykei* and *S. mckinstyi* Hungerford reach several hundred per square foot of water. During the late summer when many individuals are molting, the bottom of these shallows appear as pink undulating carpets when the corixids are disturbed.

Water boatmen commonly forage on the bottom ooze, and the flat, scoolike palae which are fringed with long rake setae are rotated around each other like twirling thumbs forcing ooze past the bottom of the head. The palae excavate a small trench beneath the feeding bug. Algae, Protozoa, and various microscopic Metazoa are ingested through the long, vertical stylet groove on the face of the labium. According to Hungerford (1948a) some corixids feed on the cell contents of multicellular algae such as *Spirogyra* by piercing the cell walls with their stylets. Because corixids are primary converters of plant material they play an important role in aquatic communities, but water boatmen also serve as an early link in the animal food chain. The diet of some species also includes larger organisms such as mosquito and chaoborid larvae, and sometimes such a diet is apparently preferred as in some Alaskan *Callicorixa* (Sailer and Lienk, 1954). In this situation the prey is held against the labium by the forelegs and the stylets are used to pierce the victim. Sailer and Lienk suggested that these corixids may play an important role in keeping down populations of mosquitoes. Clearly, as Jansson and Scudder (1972) pointed out, corixids should no longer be regarded as strictly plant feeders. Because corixids ingest particulate matter as well as fluids, they have evolved a powerful, complex, bipartite food pump which includes tooth-like epipharyngeal grinders (Parsons, 1966a). The latter breaks up small ingested organisms. A strainer in the pump blocks passage of the larger particles.

Corixids are a preferred food of many fish. Popham (1942) demonstrated that corixids prefer to live on a background with which their own color harmonizes, and that fish easily spot and eat first those bugs that contrast with the bottom. The disruptive dorsal color patterns of corixids make them difficult to detect when they are sitting on the bottom. It is not known to what extent the bugs are rendered unpalatable by their scent glands.

All stages of corixids, particularly in *Ahuautla mexicana* de la Llave (formerly *Krizousacorixa femorata* Guérin-Méneville), *Corisella mercenaria* (Say) and related species, are used as human food in Mexico. The practice probably goes back many centuries since travelers noted this use of corixids as early as 1625 (Ancona, 1933). The eggs, which are often laid in enormous numbers, are gathered by placing reeds in the water and returning later to harvest them. The eggs, locally called “ahuautle,” are mixed with meal and made into cakes. Tons of nymphs and adults are collected, dried, and shipped abroad for use in bird, fish, and turtle pet food.

The eggs of water boatmen were reviewed by Hungerford (1948b) and more recently by Cobben (1968). Corixid eggs are attached to the substrate by a stack or buttonlike pedestal in most genera (fig.3), however the eggs of the Old World genus *Micronecta* Kirkaldy and the primitive Australian genus *Diaprepocoris* are laid on their sides. In general eggs are ovoid but not symmetrical, being more convex on one side than the other, and the surface is hexagonally reticulate. The micropylar end usually has a nipplelike formation. Eggs are usually laid on any available submerged surface, but the North American species *Ramphocorixa acuminata* (Uhler) displays a preference for laying its eggs on cray-fish, usually *Orconectes immunis* (Hagen) and *Procambarus simulans* (Faxon) (Griffith, 1945).

The life histories of a few New World species have been studied (Hungerford, 1917b; Griffith, 1945; Bobb, 1953; Peters and Spurgeon, 1971; and Dodson, 1975). Eggs hatch in one to two weeks and there are five nymphal instars, each lasting about a week to 10 days. The nymphal instars can be identified by the progressive development of the wing pads. First instars show no prolongation of the posterolateral margins of the mesothorax; in second instars the hindmargin is sinuate sublaterally; in third instars the hemelytral pads are half as long as the entire thorax; in fourth instars the wing pads attain the level of the first abdominal segment; and in fifth instars they reach the middle of the third segment. Most corixids pass the winter as adults and in the north they may be found swimming under ice; Hussey (1922) even found bugs completely enclosed in air pockets in ice.
Several species fly to lights and most of the records of *Trichocorixa* from the southwestern part of the state are based on material collected at lights. In the Central Valley, especially in areas with rice fields, *Corisella decolor* (Uhler) sometimes piles in mounds beneath lights on warm nights.

According to Young (1966) there are two types of migratory flights in Corixidae. The first is an obligatory early spring migration which occurs just before ovarian development in females. Young feels that this dispersal flight is the primary one in water boatmen. Secondary, facultative flights occur in early summer and fall, and environmental stimuli are responsible for them. Popham and Lansbury (1960) indicate that oxygen deficiency brought on by shrinking of the habitat and increasing water temperature is a strong stimulus for summer and fall migrations.

Many species of Corixidae are polymorphic with respect to flight musculature or development of flight wings, although the latter (brachyptery) is not as common as flight muscle polymorphism. Young (1965a, b) has found that during the teneral period of the adult, which may last from one to four weeks, the flight muscles do not enlarge in a percentage of the individuals of a population, and thus the bugs are incapable of flight. Usually the venter of the thorax and the anterior part of the mesonotum are paler in these bugs than in those capable of flight. The flightless morphs are most common in late spring populations according to Young (1965b). He hypothesized that the loss of flight capability confers an advantage to the species through the greater efficiency of flightless bugs in the habitat. Flightless bugs can often swim faster than those capable of flight (Young, 1969), and in laboratory experiments Young (1965b) found that flightless bugs live longer, when starved and at the same time laid a significantly greater number of eggs, and started ovarian development earlier. Young feels that there is a tendency for all species to be largely flightless but that this is expressed only in populations living in stable, permanent habitats. Obviously, in temporary habitats survival depends on the existence of flying forms. Food shortage and rising temperature are factors that probably trigger development of bugs capable of flight in these situations.

The asymmetry of the male abdomen has been explained by Peters (1962) as primarily providing a means of tightly grasping the female during copulation. There is a deep, lateral, V-shaped emargination between segments five and six on the side of asymmetry. This cleft clamps over the lateral edge of the female abdomen. The abdominal strigil aids in grasping the female during copulation according to Larsén (1938), and the special pegs found on the pala of the male probably have a similar function. Abdominal asymmetry is usually constant within a genus, either dextral or sinistral, but in some species occasional specimens occur in which the asymmetry is reversed ("situs inversus" of Peters, 1962). *Situs inversus* has no detrimental effect on the individual, he simply clamps the female on the opposite side of her abdomen during mating.

Popham (1960) suggested that asymmetry also plays a role in respiration. Because corixids obtain air in the thoracic area rather than at the apex of the abdomen, replenishing the airstore during copulation is a problem for the female who is beneath the male. According to Popham, mating bugs roll over on the asymmetric side and both bugs are thus able to break the surface film with the opposite side of their bodies.

Stridulation is well known in the Corixidae. Sound is usually produced only by males, but females also stridulate (Southwood and Leston, 1959; Jansson, 1972b, 1973, 1976). The mechanism for sound production consists of a group of setae on the base of the fore femur which are rubbed against the rather sharp, lateral edge of the head (Hungerford, 1948b; Jansson, 1972b). However, the lack of well-developed femoral stridulatory pegs does not necessarily mean that a species is unable to produce sound (Jansson, 1972b). Apparently most corixid species produce only one song but a few have two (Jansson, 1976). Songs are species and sex specific, and stridulation is correlated with sexual maturity. Females in *Cenocorixa* stridulate only when receptive to males, and when stimulated by conspecific male calls (Jansson, 1974). Corixid songs are used to form aggregations, to attract females, and to space out male individuals within a population (Jansson, 1973, 1976). Stridulation has been documented for 20 North American corixids in six genera (Jansson, 1973, 1976). The California genera that have the capability for sound production are *Callicorixa, Cenocorixa, Corisella, Hesperocorixa, Sigara,* and *Trichocorixa*.

Corixids are less directly dependent upon atmospheric oxygen than most aquatic Hemiptera and hence remain submerged for longer periods. This is possible because they carry considerable amounts of air on their bodies, and their airstore acts as a physical gill which extracts dissolved oxygen from the water. In corixids, as far as known, atmospheric air enters dorsally through spaces between the head and prothorax when the bugs break the surface film (Parsons, 1977). According to Popham (1960) the rastrate dorsal surface found on many corixids accelerates exposure to the pronotal-hemelytral area and retards the return of water when airstore replenishment is completed. The exposed air-
store is found primarily on the venter including the bases of the legs, but there is also a partial supra-alar airstore (Parsons, 1970). The high respiratory efficiency in water boatmen is enhanced by the frequent rowing movements of the hindlegs over the body. This activity causes fresh currents of water to flow over the airstore, an action which presumably increases the rate of oxygen uptake (Parsons, 1970). Part of the corixid airstore is concealed in the space between the head and prothorax, between the pro- and mesothorax and beneath the wings. Popham (1960) has shown that the longitudinal, abdominal, tracheal trunks are greatly reduced in diameter and that gaseous exchange occurs mainly in the thoracic tracheae. According to him, inspiration is primarily through the first pair of abdominal spiracles, but Parsons (1970) feels that the mesothoracic spiracles probably also have an important role in inspiration.

In most cases identification of male corixids is rather easy and there are numerous characters for differentiating species. However, a few sibling species are most positively identified only by the shape of the right clasper of the male genitalia. Females are often more difficult to recognize and I have been unable to differentiate the females of certain species. The more important characters used for identifying the forms treated in this paper are discussed below. General morphology is shown in figures 110-111.

**Abdominal strigil.** The size and shape of the strigil (on tergum VI) helps to characterize certain genera and species. It is present in all our genera except *Calli- corixa* and is on the right side of the dorsum (fig. 111) except in *Trichocorixa* (fig. 144).

**Abdominal asymmetry.** The term dextral is used when the strigil is on the right side as seen dorsally (fig. 111). Sinistral refers to location of the strigil on the left side (fig. 144).

**Abdominal terga of the male.** The shape of the asymmetrical terga, especially those of the seventh abdominal segment, are often characteristic for the species.

*Clavopruina.* A narrow, white frosted area along the anterior lateral margin of the clavus (fig. 114). The length of the clavopruina, especially in comparison to the length of the postnodal pruina, is diagnostic for some species.

*Coriopruina.* A white frosted area between the anterior apex of the corium and the clavopruina (fig. 114). The width and length of this pruinose area helps to characterize the species of *Corisella*, especially in females.

**Hemelytron.** Both the texture and the pattern of the hemelytra are useful characters in differentiating genera, and, in the case of the latter, species. The texture may be smooth, rugose, rastrate (with parallel scratches), or both rugose and rastrate, and the hemelytra may or may not have long setae. Various textures of the hemelytra are shown in fig. 115. The pruinose areas (clavopruina, coriopruina, and postnodal pruina) of the hemelytron are discussed separately.

**Infraoculus.** A narrow sclerite extending laterally along the posterior margin of the compound eyes and the rim of the head. This sclerite is divided by the hypocular suture which extends from the eye to the rim. In *Graptocorixa* the width of the infraoculus (fig. 123) at the hypocular suture is compared to the width of the pronotal lobe.

**Interocular width.** Although frequently used by students of corixids, the interocular width receives only occasional mention here. The interocular width is the shortest distance between the eyes and it is usually compared with the width of the eye (measured along its posterior margin).

**Length.** Since there is a considerable range in the size of various species of corixids, the total length helps to distinguish both genera and species. In several cases, the range in length may overlap for two different species, but the lengths of the females and males taken separately do not overlap.

**Male right clasper.** One of the most important characters in distinguishing corixids is the shape of the male right clasper or paramere. This clasper is attached to the male capsule (fig. 112) and must be removed or extended from the abdomen. With a little practice, a number one or finer insect pin with a hooked tip may be inserted between the relaxed eighth abdominal lobes; after hooking the capsule, it is withdrawn or extended from the abdomen. All male specimens should have the capsule extended before mounting. The shape of the male right clasper is the most reliable character to distinguish most species of corixids, and the right claspers of all species, except members of *Trichochorixa*, have been figured.

**Mesepimeron.** This mesothoracic sclerite (fig. 110), which has a ventral position in bugs, is useful in characterizing species. The posterior suture or margin of the mesepimeron runs mesad from the lateral margin and then curves posterad, sometimes rather abruptly, delimiting a slender, tapering posterior process of the sclerite. The curve is known as the *lateral bend* (fig. 110). The metathoracic scent gland ostiole is located somewhere along the margin of the posterior process of the mesepimeron. The position of the ostiole (fig. 110) relative to the lateral bend and apex of the process, as well as the shape of the mesepimeron, are distinctive in some species of *Sigara*.

**Metasternum.** The shield-shaped sternite between the
FIGS. 110-111. Ventral and dorsal aspect, respectively, of Corisella decolor showing major taxonomic characters; 112, male genital capsule showing position of right clasper; 113, male front leg of Cenocorixa blaisdelli showing major taxonomic characters; 114, enlarged portion of hemelytron of Corisella edulis showing pruinose areas.
hindlegs of corixids is usually called the metaxyphus by corixid taxonomists (fig. 110). Although the metasternum has frequently been used by students of corixids as a distinguishing character, it has not been found especially useful in characterizing the California species.

Pala. The shape of the pala (fig. 113), especially in the males, is characteristic for several genera, and the chaetotaxy of the male pala is often used in differentiating species. Special attention is given to the palar pegs of males.

Palar pegs. Across the inner face of the male pala is a row of short, stout pegs (fig. 113). They vary in number and arrangement in various species, and the species of Corisella are characterized by having two rows of palar pegs.

Postnodal pruina. A white frosted area along the lateral border of the corium posterior to the nodal furrow (fig. 111). The length of this pruinose area in relation to the clavopruina is diagnostic for certain species.

Pronotal disk. The texture of the pronotal disk (fig. 111) is important in characterizing the genera, while the number and width of the dark bands are useful in distinguishing certain species.

Prothoracic lobe. The prothoracic lobe (figs. 110, 123-126) is lateral to the forecoxae and it extends caudad from beneath the head. Its shape and size are diagnostic for a few species.

**Width.** Although body width is usually not as diagnostic as length, it does help to distinguish some species. Width here means the maximum distance across the head. This measurement is more constant than the width across the hemelytra, even though the latter is usually wider.

Since the position of the foreleg may need to be changed to examine the palar pegs, the hemelytra lifted from the abdomen, or the capsule removed from the abdomen, I have found storage in 75% ethyl alcohol advantageous. In alcohol-preserved specimens these structures may be easily manipulated without damage. Preservation in alcohol is less time consuming and large quantities may be stored cheaply in small spaces. If specimens are mounted, the foreleg should be extended to show the inner surface of the pala, the hemelytra parted with the right wing moved to show the strigil of males (the left wing in the case of Trichocorixa), and the genital capsule extended in the case of some males.

**KEY TO CALIFORNIA GENERA OF CORIXIDAE**

**Adults**

1. Pala slender, more than 5 times as long as median width (figs. 116-118); palar claw much stouter than setae of lower palar row (fig. 119).

   *Graptocorixa* Hungerford, p. 93

   Pala less than 3 times as long as median width (figs. 164, 184); palar claw setiform, similar to setae of lower palar row (Corisini) ............................................... 2

2. Large, broad species, more than 9 mm long (fig. 193); prothoracic lobe quadrate or trapezoidal, broader than long ....

   *Hesperocorixia* Kirkaldy, p. 110

   Small to medium sized, less than 9 mm long; prothoracic lobe elongate, longer than broad .................................. 3

3. Clavi of hemelytra smooth and shiny, at most only slightly rugulose (fig. 115B, C) .................................................. 4

   Clavi of hemelytra rough, either rastrate, rugose or both (fig. 115D-G) .......................................................... 5

4. Males with sinistral asymmetry (fig. 144) and single row of pegs on pala; females with apices of clavi not exceeding a line drawn through the nodal furrows (fig. 147); pronotum smooth and shiny ....

   *Trichocorixa* Kirkaldy, p. 98

   Males with dextral asymmetry (fig. 111); females with apices of clavi exceeding a line drawn through the nodal furrows (fig. 157); pronotum rugulose, .... *Corisella* Lundblad, p. 103

5. Clavus primarily rugose (fig. 115F), corium only shiny ........

   *Cenocorixia* Hungerford, p. 112

   Clavus and corium strongly rastrate (fig. 115D, G) ................ 6

6. Clavopruina not exceeding half the length of the clavopruina (fig. 177); males without abdominal strigil ....

   *Sigara* Fabricius, p. 117

   Clavopruina extending half the length of the clavopruina or more (fig. 218); males with abdominal strigil (fig. 233) ....

   *Callicorixa* White, p. 109

   ...
116 abdominellis  117 uhleri  118 uhleroides

FIGS. 116-118. Male pala, tibia, and femur in Graptocorixa.

KEY TO CALIFORNIA GENERA BASED ON FIFTH INSTAR NYMPHS

1. Dorsal abdominal scent gland openings very small and widely separated, the middle pair separated by about 10 times the diameter of one opening. (Middle claws less than two-thirds as long as tarsus; face with a dense mat of hairs; 3 tufts of long bristles at base of forefemur) .... (californica Hungerford) .................................................. Graptocorixa-

Scent gland openings larger, the middle pair less than 5 times as far apart as diameter of a single opening. (Middle claws subequal or longer than tarsus; face with scattered hairs but not with a dense mat of hairs; front femora without 3 tufts of long bristles near base) ........................................ 2

2. Mesonotum entirely covered with long, shaggy hairs; middle claws subequal to tarsal length ... (laevigata Uhler) ..... Hesperocorixa

Mesonotum bare on either side of middle posteriorly; middle claws longer than tarsus ........................................ 3

3. Metanotum at middle, and abdomen clothed with short, sparse, backward directed bristles (inscripta Uhler, decolor Uhler) ................................................. Corisella

Metanotum at middle and abdominal terga bare .................. 4

4. Abdomen with 6 longitudinal stripes above ... (mekinunryi Hungerford) ................................................. Sigara

Abdomen without longitudinal stripes .......................... 5

5. Scent gland openings large, the space between middle pair about twice the diameter of a single opening; middle of mesonotum bare except at anterior third and narrowly along a median-longitudinal carina ... (reticulata Guérin-Méneville) ........................................ Trichocorixa

Scent gland openings small, the middle pair about 5 times as far apart as diameter of a single opening; middle of mesonotum broadly pubescent, the lateral bare areas confined to hind margin near inner angles of hemelytral pads ... (wileyae Hungerford) ................................................. Cenocorixa

Tribe Graptocorixini

Two genera belong in this tribe but only one, Grapto- corixa, is represented in California. Members of the tribe are characterized by having a well-developed apical claw on the narrow pala (figs. 116-118), and they usually have a dense mat of hairs on the frons.

Genus Graptocorixa Hungerford

Graptocorixa Hungerford, 1930. Pan-Pac. Entomol. 7:22. Type-species: Corixa abdominalis Say, 1832, original designation.

All species of Graptocorixa occurring in California have exceptionally narrow palae, about ten times as long as broad. The hemelytra (fig. 115a) are deeply rastrate. Our species are large (7.9 to 11.0 mm long), comparable to Hesperocorixa, but a relatively small form, G. serrulata, occurs in Arizona, Nevada, and Oregon and it may eventually be found in California. Except for the females of G. californica and G. uhleroides, the four California species are easily separated.

KEY TO GRAPTOCORIXA OF CALIFORNIA

1. Less than 7.5 mm (6.1-6.7 mm) long [not recorded from California but has been collected close to the California border in Oregon, Nevada, and Arizona] ................ serratula (Uhler) More than 7.5 mm (7.9-11.0 mm) long ........................................ 2

2. Prothoracic lobe rounded at apex (fig. 123), its dorsal edge longer than apical width; apical width of prothoracic lobe subequal to or less than the infraocular width at the hypop- ular suture (fig. 123) ........................................... abdominalis (Say)

Apex of prothoracic lobe more quadrate (figs. 124-125), dorsal edge slightly less than or subequal to the apical width; apical width of prothoracic lobe equal to about one and a half to twice the infraocular width at the hypopular suture (fig. 124) ................................................. 3

3. Dark bands of pronotum (fig. 128) and hemelytra (fig. 120) narrower than intervening light bands; males 7.9-8.3 mm long, females 8.0-9.0 mm long ... uhleri (Hungerford) Dark bands of pronotum (fig. 129) and hemelytra (figs. 121-122) about same width as intervening light bands; males 8.6-10.4 mm long, females 9.9-11.0 mm long ............ 4

4. Right clasper of male gradually tapering to a point (fig. 136) ..... uhleroides Hungerford

Right clasper of male broadest near distal end, apex bluntly rounded (fig. 137) ............................................. californica (Hungerford)

12. From Usinger (1956). Callicorixa is not included. The mesonotal wing pads reach the middle of the third abdominal segment in fifth instar.
FIGS. 119-122, Female hemelytron in *Graptocorixa*; 123-126, lateral aspect of head and prothoracic lobe in *Graptocorixa* (hs = hypocular suture).
Graptocorixa abdominalis (Say) (Figs. 116, 119, 123, 127, 130, 134)


Graptocorixa abdominalis, although similar in size to G. californica and G. uhlerioides, has many distinctive characters in addition to those given in the key. The inner base of the forefemur (fig. 116) is greatly expanded, and the male pala has about a dozen sparsely spaced pegs followed by about five closely set apical pegs. This is the only California species of Graptocorixa with a small strigil (fig. 130). The male right clasper (fig. 134) is shorter and broader than those of other California species of Graptocorixa and its apex is beak-like. Females are 9.5-10.9 mm long, 3.2-3.7 mm wide, males 8.6-10.8 mm long, 2.8-3.7 mm wide.

Geographic range. California and Nevada to Mexico and Oklahoma.

California records. I have not seen this species from California, but have examined several series taken from northern Baja California. Hungerford (1948a) records abdominalis from Palo Verde, Imperial Co. and Monterey. The Palo Verde record seems quite plausible since there are numerous records from bordering Arizona. The record of three females from Monterey needs to be confirmed, but the specimens could not be located in the National Museum of Natural History. Hungerford also lists two females from Washoe Co., Nevada, which borders California.

Graptocorixa californica (Hungerford) (Figs. 122, 125, 129, 133, 137, 139)


This species most closely resembles Graptocorixa uhlerioides, but the latter is most commonly found in the southern part of California while G. californica is found in the northern two-thirds of the state. Where the ranges of the two overlap, the only reliable character for identification is the shape of the male right clasper. The clasper of G. californica (fig. 137) is bluntly rounded at the apex and narrowed in the middle, while the clasper of G. uhlerioides (fig. 136) gradually tapers to a sharp point. I have been unable to separate the females of these two species. Although Hungerford (1948a) gave characters for separating them, he left some females in collections labelled “Graptocorixa sp. need ọọ.” Graptocorixa californica differs from G. abdominalis in that the infraocular is narrower than the prothoracic lobe (fig. 125), in having the inner base of the forefemur not as conspicuously produced (fig. 118), and by the shape of the male right clasper (fig. 137). Graptocorixa californica is larger than G. serrulata and G. uhleri. Females are 9.9-10.8 mm long, 3.1-3.2 mm wide, males 8.0-10.4 mm long, 2.5-3.1 mm wide.

Geographic range. Northern California, Oregon.

California records (map 28). This species, which is found over a wide range of elevations in the northern two-thirds of the state, occurs primarily in pools of small streams.

Graptocorixa serrulata (Uhler) (Figs. 126, 138)


Graptocorixa serrulata is easily distinguished from all Graptocorixa occurring in California by its smaller size, 6.1-6.7 mm long (Hungerford, 1948a), and by the elongate prothoracic lobe (fig. 126). The shape of the male right clasper (fig. 138) differentiates this species from all other members of the genus.
Geographic range. Arizona, Nevada, New Mexico, Oregon, Texas, and Mexico.

California records. This species has not been recorded from California, but it is included here because individuals have been collected near the border in all three adjacent states.

Graptocorixa uhleri (Hungerford)
(Figs. 117, 120, 124, 128, 131, 135)

Arctocorixa uhleri Hungerford, 1925, Bull. Brooklyn Entomol. Soc. 20:19. Holotype ♀: “California” (USNM). Contrary to Hungerford’s original description, the type of uhleri does not bear a label citing “San Bernardino, Calif.” as the locality. “California” is the only geographic label data on the specimen.

In Graptocorixa uhleri the dark bands of the pronotum and hemelytra are narrower than the intervening light bands (figs. 120, 128), whereas they are about the same width in other California species. The male right clasper (fig. 135) is distinct from that of G. californica, but nearly identical to that of G. uhleroidea. The outer curve of the clasper is flattened in the middle and has a more acutely pointed apex in the latter (fig. 136). The abdominal terga (fig. 131) are similar to those of G. uhleroidea. Graptocorixa uhleri has about 23 pegs on the male pala (fig. 117) while both G. californica and G. uhleroidea have about 30 pegs (figs. 116, 118). This species differs from G. abdominatis by the narrower infraocular space, more truncate prothoracic lobe, larger abdominal strigil and the shape of the male right clasper. Graptocorixa uhleri is intermediate in size between the smaller G. serrulata and the larger G. californica and G. uhleroidea. Females are 8.0-9.0 mm long, 2.6-2.9 mm wide, males 7.9-8.3 mm long, 2.4-2.6 mm wide.

Geographic range. California and western Nevada.


The few records indicate that in California uhleri is restricted to the coast ranges and surrounding areas from about Monterey Bay to San Diego County.

Graptocorixa uhleroidea Hungerford
(Figs. 118, 121, 132, 136)


Graptocorixa uhleroidea is similar to G. californica and positive identification of these two species depends upon the shape of the male right clasper (compare figs. 136 and 137). The seventh male abdominal tergum
Tribe Corixini

Twenty genera are placed in this tribe, six of which occur in California. The pala is not narrow and the tarsal claw is setiform, resembling the other fringing setae of the tarsus. The frons is often bare or at least the setae do not form a mat.

Genus Trichocorixa Kirkaldy

Trichocorixa Kirkaldy, 1908, Can. Entomol. 40:118. Type-species: Corisa pygmaea Fieber, 1851 (= Corisa verticalis Fieber, 1851), original designation.

This is the only genus in California in which the males have sinistral asymmetry (fig. 144), and the apices of the clav do not exceed a line drawn through the nodal furrows of females (fig. 141). Trichocorixa species are small, varying in size from some males of T. reticulata which may be only 2.8 mm long, to females of T. verticalis ssp. californica which may attain a length of 5.8 mm. The pala is broad, triangular, and it has a single row of pegs in the male. Both the pronotum and hemelytra (fig. 115B) are smooth and shiny and the hemelytral pattern is usually reticulate.

A number of species of Trichocorixa prefer saline or alkaline waters. Four species, one of which has two subspecies in California, occur in the state.

KEY TO TRICHOCORIXA OF CALIFORNIA

1. Males: abdominal segments asymmetrical (fig. 152); pala with pegs; frons flattened ........................................ 2
   Females: abdominal segments symmetrical (fig. 153); pala without pegs; frons not flattened ................................ 6

2. Abdominal strigil curved (figs. 145-146) .................. 3
   Abdominal strigil straight (figs. 144, 152) ................. 4

3. Strigil long, very slender, with small indistinct combs (fig. 145) ............................................... calva (Say)
   Strigil shorter, broader, with larger more distinct combs (fig. 146) .................................................. uhleri Sailer

4. Left lobe of seventh abdominal tergum prominent, much longer than right lobe (fig. 144); postnodal pruina short (fig. 140), less than two-thirds length of clavopruina ...... reticulata (Guérin-Méneville)
   Left lobe of seventh abdominal tergum about as long as right lobe (fig. 152); postnodal pruina longer (fig. 148), more than two-thirds length of clavopruina ...... verticalis (Fieber) ........................................ 5

5. Head more than three times as wide as median length (fig. 154); vertex not prominently projecting, following dorsal curvature of eyes in lateral view (fig. 150) ....................... verticalis californica Sailer
   Head less than three times as wide as median length (fig. 155); vertex prominently projecting, not following dorsal curvature of the eyes in lateral view (fig. 151) ...................... verticalis sultoni Sailer
FIGS. 140-143. Hemelytron in *Trichocorixa*: 140 = male, 141-143 = female; 144-146, Dorsal aspect of male abdomen in *Trichocorixa*. 
FIGS. 147-155. Various structures in subspecies of *Trichocorix verticalis*: Hemelytron, 147-148 = females, 149 = male; 150-151, lateral view of male head; dorsal aspect of abdomen, 152 = male, 153 = female; 154-155, dorsal view of male head.
6. Hemelytra without a distinct postnodal pruina (fig. 141) .............................................
   
   Trichocorixa reticulata (Guérin-Méneville) ...............................

7. Embolium indented at about one-third the distance between its base and nodal furrow (fig. 142) ......................................

8. Embolium indented at about half the distance between base and nodal furrow (figs. 143, 147) ............................................................

9. Embolium indented at about two-thirds the distance between base and nodal furrow (fig. 147) ...........................................
   Trichocorixa saltoni Sailer

   Trichocorixa calva (Say)

   (Figs. 142, 145)


   The extremely long, narrow, male abdominal strigil with its indistinct combs (fig. 145) distinguishes T. calva from all other Trichocorixa. The embolium is indented from one-third to nearly one-half the distance from its base to the nodal furrow (fig. 142). Since this indentation sometimes nearly reaches the halfway point this character is not always valid for separating T. calva from T. uhleri. The interocular space of T. calva is less than the width of an eye but in uhleri it is equal to the width of an eye. This species is also larger than T. uhleri. Females are 4.2-4.6 mm long, 1.3-1.4 mm wide, males 3.8-4.2 mm long and 1.2-1.4 mm wide.

   Geographic range. Eastern and midwestern U.S. to Arizona and California.

   California records (map 31). IMPERIAL CO.: Heber (OSU). Imperial (OSU). Lake Houghtlen, near Bard (RLU). RIVERSIDE CO.: (no locality) (UCD). SAN BERNARDINO CO.: Earp (RLU). Colorado River, near Needles (DRL). In California Trichocorixa calva occurs in the Imperial Valley and along the Colorado River. Although the range of this species is similar to T. verticalis ssp. saltoni, the two probably do not occur in the same habitat because T. calva occupies fresh water while the latter is found in saline and alkaline waters.

   Trichocorixa reticulata (Guérin-Méneville)

   (Figs. 140-141, 144, 156)


   California records. (map 32). ALAMEDA CO.: Berkeley (CAS.

This halophilous species occurs in great abundance in tide pools and salt marshes along the entire coast, and individuals are sometimes associated with *T. verticalis* ssp. *californica*. In the arid regions of southeastern California *T. reticulata* is common in saline or alkaline pools. Specimens have also been taken in fresh waters such as Clear Lake, Lake Co.: Hidden Lake, Los Angeles Co.: and Lake Tahoe, El Dorado Co.

MAP 32. California distribution of *Trichocorixa reticulata* (Guérin-Méneville).

FIG. 156. *Trichocorixa reticulata*, dorsal view.

*Trichocorixa uhleri* Sailer (Figs. 143, 146)


The male abdominal strigil (fig. 146) of *Trichocorixa uhleri* is curved, but shorter and thicker than that of *T. calva* and it has distinct combs. The remaining species, *T. reticulata* and *T. verticalis*, have strigils of similar size but they are straight. Females resemble *T. calva* in that the indentation of the embolium is about mid-way between its base and the nodal furrow (fig. 143), while the indentation is closer to the nodal furrow in the two subspecies of *T. verticalis*. Females are easily separated from *T. reticulata* by the presence of the postnodal pruina. Sailer (1948) states that the length for males is 3.6-3.8 mm; females 3.6-4.0 mm.

**Geographic range.** Arizona, California, Colorado, New Mexico, and Texas.

**California records** (map 31). The first and only state record for this species is a specimen from Panamint Springs, Inyo Co. (UCD).
Trichocorixa verticalis (Fieber)


Sailer (1948) divided this widespread, variable species into five subspecies. Although two of these occur in California the nominate form is restricted to the eastern U.S., the West Indies, and Central America.

Trichocorixa verticalis californica Sailer
(Figs. 147, 150, 152-154)


Trichocorixa verticalis californica is usually more yellowish and larger than T. reticulata. The embolium of the female is indented about two-thirds the distance from its base to the nodal furrow (fig. 147), while the indentation of T. calva and T. uhleri is half or less the distance, and four-fifths the distance in the case of T. verticalis ssp. saltoni. The postnodal pruina is small but distinct. The abdominal strigil of the male (fig. 152) is similar to T. reticulata and T. verticalis ssp. saltoni; however, the left side of the abdominal tergum is not as long as that of T. reticulata and the vertex of T. verticalis ssp. californica is not as prominently produced as that of T. verticalis ssp. saltoni (figs. 150, 154).

Females of T. verticalis ssp. californica are 4.4-5.8 mm long, 1.4-1.7 mm wide, males 4.2-5.0 mm long, 1.3-1.5 mm wide.

Geographic range. Coastal California.

California records (map 33). ALAMEDA CO.: Albany (RLU). HUMBOLDT CO.: Arcata (DRL). CENTERVILLE (DRL). Fortuna (DRL). SAMOA (DRL). SAN LUIS OBISPO CO.: Cayucos (DRL). SAN MATEO CO.: Moss Beach (RLU). ORANGE CO.: Santa Cruz (RLU). Sailer (1948) reported this subspecies from the San Francisco area and the Humboldt Bay region. In the salt marshes of these two areas T. verticalis ssp. californica is relatively abundant and is found in nearly equal numbers with T. reticulata. A single female from Orange County in the Usinger Collection was thought to be mislabelled, but a rather thorough collecting trip for Trichocorixa from San Francisco southward netted an additional female from San Luis Obispo County. This single specimen was taken from the same tidal pool with over 500 T. reticulata.

Trichocorixa verticalis saltoni Sailer
(Figs. 148-149, 151, 155)


The embolium of the female is indented more posteriorly than in all other Trichocorixa, about four-fifths the distance from its base to the nodal furrow (fig. 148). The abdominal strigil (fig. 152) is straight and similar to those of T. reticulata and T. verticalis ssp. californica. The seventh tergum is not as long on the left side as that of T. reticulata. The male vertex (fig. 155) is more pronounced than the vertex of T. verticalis ssp. californica. Females are 4.1-5.6 mm long, 1.2-1.6 mm wide; males 3.9-5.1 mm long, 1.1-1.5 mm wide.

Geographic range. Arizona and southeastern California.


Genus Corisella Lundblad


Members of the genus Corisella are distinguished by their smooth, only faintly rugose, hemelytra (fig. 115C).
The hemelytra differ in texture from those of *Trichocorixa* in having shorter and more numerous hairs (fig. 115C). The dark bands of the clavus are effaced or narrowed at the inner basal angle (figs. 157-160), and the dark reticulations of the corium form irregular longitudinal rows. The male pala (fig. 165) has two rows of pegs (the upper row consists only of a single or double peg in the case of *tarsalis*), and the outer apex of the foretibia is produced over the base of the pala and has an apical, fleshy pad or protuberance.

Two of our species, *C. decolor* and *C. inscripta*, have a tolerance for saline waters, and Usinger (1956) found both of these in the sewage oxidation ponds at Concord, California.

**KEY TO CORISELLA OF CALIFORNIA**

1. Postnodal pruina shorter than the clavopruina (fig. 158) ........... 3
   *C. decolor* (Uhler)
   Postnodal pruina subequal to or longer than the clavopruina (fig. 157) ......................................................... 2

2. Hindtarsi brown; upper peg row of a male pala with only 1 or 2 conspicuous pegs (fig. 164) ......................... *tarsalis* (Fieber)
   Hindtarsi yellow; upper row of male pala with 8 or more pegs (figs. 166-167) .................................................. 3

3. Coriopruina of female broad (fig. 159), about twice as wide at midlength as corium; pegs of upper row of male pala contiguous (fig. 166), total length of row subequal to length of pegless basal area ............... *C. edulis* (Champion)
   Coriopruina of female narrow (fig. 160), at midlength about as wide as or less than width of corium; pegs in upper row of male pala more widely separated (fig. 167), total length of row about twice as long as pegless basal area .......... *C. inscripta* (Uhler)

**Corisella decolor** (Uhler)
(Figs. 158, 162, 165, 169, 172, 175)


*Corisella decolor* can be distinguished from the three other California species of the genus by the more prominent and broader dark bands on the pronotum (fig. 169). On the average there are 6 to 8 bands and they are rarely interrupted. The anterior part of the pronotum usually has a longitudinal median carina. The postnodal pruina (fig. 158) is shorter than the clavopruina in both sexes. The pegs of the upper row on the male pala are more widely spaced (fig. 165) than those of *C. inscripta* and *C. edulis*. In size and hemelytral pattern (fig. 158) *C. decolor* is similar to *Sigara omuni*, but the former is easily distinguished from the latter in that the hemelytra, especially the corium, are smooth rather than rastrate. This is the smallest species of *Corisella* in the state. The range in size overlaps that of *C. inscripta* but the size of the two sexes is distinct. Females are 4.6-6.6 mm long, 1.6-2.0 mm wide, males 4.1-5.6 mm long, 1.5-1.7 mm wide.

**Corisella edulis** (Champion)
(Figs. 159, 166, 173)


The large size of *Corisella edulis* separates it from all other species of the genus except *C. inscripta*. The markings of the hemelytra (fig. 159) and pronotum (fig. 170) of the two species are similar. Females of *C. edulis* differ from those of *C. inscripta* by the wider coriopruina (fig. 159) which extends to the end of the clavopruina. The pegs in the upper row of the male pala are contiguous (fig. 166), and the length of the upper row is subequal to the length of the basal pegless area. Females are 7.2-8.3 mm long, 2.3-2.6 mm wide, males 6.3-7.3 mm long, 1.9-2.4 mm wide.

**Corisella inscripta** (Uhler)
(Figs. 160, 163, 167, 170, 174)

*Corisella inscripta* Uhler, 1894, Proc. Calif. Acad. Sci. (2):4:294. Syntypes: "Cal." (= Cabo San Lucas, Baja California according to Uhler) (CAS, USNM). Hungerford’s (1948e) lectotype designation is invalid because two specimens (USNM) were chosen. Uhler, in the introduction to his paper, stated that the types were in the California Academy of Sciences. These were destroyed in the 1906 earthquake, but the USNM material still qualifies for lectotype designation.

*Corisella inscripta* is similar to *C. edulis*. Both are about the same size and have similar hemelytral pat-
FIGS. 157-163. Female hemelytron in *Corisella*. The wing illustrated in Fig. 160 is unusually dark and heavily banded. *C. inscripta* normally has banding intermediate between figs. 159-160; 161-163, dorsal aspect of male abdomen in *Corisella*. 
FIGS. 164-174. Various structures in *Corisella*: 164-167, Male pala, tibia and femur; 168-170, female pronotal disk; 171-174, right male clasper.
terns. Females of *C. inscripta* may be distinguished from those of *C. edulis* by the narrower coriopruina (fig. 160). Males differ in upper peg row detail and in the shape of the pala (fig. 167). In *C. inscripta* the pegs of the upper row are not contiguous, and the length of the row is about twice the length of the pegless basal area. The pronotum (fig. 170) has 10 to 15, irregular, usually broken, dark, transverse bands. Females are 6.8-8.8 mm long, 2.1-2.6 mm wide, males 6.0-7.5 mm long, 1.8-2.2 mm wide.

**Geographic range.** Arizona, California, Idaho, Oregon, Washington, Utah, and Baja California.

**California records** (map 35). This common pond species is found throughout the state at low to moderate elevations.

**Corisella tarsalis** (Fieber)
(Figs. 157, 161, 164, 168, 171)


This species is readily differentiated from other *Corisella* in California by the dark color of the hindtarsi and
FIGS. 176-185. Various structures of *Callicorixa*: 176-177, Female hemelytron; 178-179, female pronotal disk; 180-181, male right clasper; 182-183, dorsal aspect of male abdomen; 184-185, male pala, tibia and femur.
apex of the midtarsi. The upper peg row of the male pala has only one or two pegs (fig. 164). The pronotum (fig. 168) is crossed with 8 to 11 very narrow and often broken, dark, transverse bands. The dark reticulations of the hemelytra (fig. 157) are narrower and more broadly spaced than those of the other three species of *Corisella* in California. The female clavopruina is about equal in length to the postnodal pruina, but the clavopruina of males is shorter than the postnodal pruina. *Corisella tarsalis* is intermediate in size between *C. decolor* and *C. inscripta*. Females are 5.8-6.5 mm long, 1.8-2.1 mm wide, males 5.3-6.0 mm long, 1.5-1.8 mm wide.

**Geographic range.** Eastern California, Rocky Mountain region, Plains States to the northeastern U.S.

**California records.** This species was recorded from Mammoth Lakes, Mono Co., by Hungerford (1948a), and I have seen a single series of five females from Deep Springs, Inyo Co. (OSU).

**Genus Callicorixa** White


Two species of *Callicorixa* occur in California. They are moderately large forms, 6.3-8.3 mm long, comparable in size to species of *Cenocorixa* and the larger members of *Corisella*. Males are distinguished from all other California corixids by the absence of an abdominal strigil (fig. 182), and the break in the peg row of the pala (fig. 184). Both sexes differ from *Cenocorixa* and *Corisella* by the more rastrate clavus and corium of the hemelytra (fig. 115D). The banding of the hemelytra of *Callicorixa* is transverse (figs. 176-177, 186) and the bands are wider than those of *Cenocorixa* and *Corisella*, both of which tend to have longitudinal stripes. The hemelytra texture and pattern of *Callicorixa* is similar to that of *Sigara*, but all species of *Sigara* in California are smaller, less than 6.3 mm long. The coriopruina of *Callicorixa* does not extend along more than half the length of the clavopruina (fig. 177), while the coriopruina of *Sigara* extends along at least half the length of the clavopruina.

*Callicorixa* are predominately pond species and may occur in quiet water along the margins of streams and rivers, but are rarely as numerous as associated species of *Sigara*.

**KEY TO CALLICORIXA OF CALIFORNIA**

First tarsal segment of hindleg black or dark brown for a least part of its length ............... *vulnerata* (Uhler)
First tarsal segment of hindleg concolorous ...... *audeni* Hungerford

![FIG. 186. Callicorixo vulnerata, male, dorsal view (from Usinger, 1956).](image)

*Callicorixa ausdeni* Hungerford

(Figs. 177, 179, 181, 183, 185)


The dark bands of the pronotum (fig. 179) and hemelytra (fig. 177) are slightly narrower than those of *C. vulnerata*, and are usually narrower than the intervening light bands. The right male clasper although similar to that of *C. vulnerata* is not as abruptly bent (fig. 181). Females are 7.1-8.3 mm long, 2.2-2.7 mm wide, males 6.3-7.2 mm long, 2.1-2.3 mm wide.

**Geographic range.** Primarily boreal, but *C. ausdeni* extends southward through the Rocky Mountains, the Sierra Nevada, and the Coast Ranges.


This species is found in northern California and ranges southward through the Sierra Nevada and along the coast to San Diego County.

*Callicorixa vulnerata* (Uhler)  
(Figs. 176, 178, 180, 182, 184, 186)


The dark bands of the pronotum (fig. 178) and hemelytra (fig. 176) are slightly broader than those of *C. audeni*, and are about as wide as the intervening light bands. The right male clasper (fig. 180) is similar to that of *audeni* but it is slightly more bent midway toward the apex. Females are 6.9-7.9 mm long, 2.2-2.5 mm wide, males 6.8-7.4 mm long, 2.1-2.3 mm wide.


This species occurs from San Luis Obispo County northward along the coast and inland along the mountain ranges of northern and central California.

**Genus Hesperocorixa** Kirkaldy


The two species of *Hesperocorixa* found in California are large, robust insects, 8.8-11.7 mm long, and they resemble *Graptocorixa*. They differ from the species of *Graptocorixa* by the broader pala (fig. 189) in both sexes and the slightly more rastrate pronotum and hemelytra (fig. 115E).

**KEY TO HESPEROCORIXA OF CALIFORNIA**

Dark bands of hemelytra primarily transverse (fig. 187); male right clasper with a nearly ninety degree bend about midway to apex (fig. 191).

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**Callicorixa vulnerata Hungerford.**

**Hesperocorixa Kirkaldy**

**Anticorixa Iaczenski**

**Graptocorixa**
Various structures in *Hesperocorixa*: 187-188, Female hemelytron; 189-190, male pala, tibia and femur; 191-192, male right clasper.

Dark bands of hemelytra more reticulate, especially in the mid-region (fig. 188); male right clasper only slightly curved toward apex (fig. 192) ......... *laevigata* (Uhler)

**Hesperocorixa laevigata** (Uhler)

(Figs. 188, 190, 192)


The apex of the male pala (fig. 190) of *H. laevigata* is gradually rounded, while the apex of the pala of *H. vulgaris* is slightly oblique (fig. 189). The shape of the male right clasper of these two species is distinct (compare figs. 191 and 192). This is the largest corixid in California. Females are 9.8-11.7 mm long, 3.2-3.7 mm wide, males 8.8-10.6 mm long, 3.0-3.4 mm wide.

*Geographic range.* Transcontinental in Canada and the U.S., south to Mexico.

*California records* (map 38). *Hesperocorixa laevigata* is one of the commonest corixids in California. It occurs everywhere except in the Mojave and Colorado Deserts. Ponds and lakes with dense submerged vegetation are typical habitats. Usually *H. laevigata* is found in association with *Notonecta*.

MAP 38. California distribution of *Hesperocorixa laevigata* (Uhler).
Hesperocorixa vulgaris (Hungerford)
(Figs. 187, 189, 191, 193)

Hesperocorixa vulgaris differs from laevigata in that the apex of the male pala is obliquely angled (fig. 189). The male right clasper (fig. 191) is long and slender with a nearly right angle bend about halfway to the apex. Superficially the pattern and size of this species is similar to Graptocorixa but H. vulgaris is easily distinguished from members of that genus by the broader pala of both sexes (compare figs. 116, 189). Females measure 9.5-10.3 mm long, 3.1-3.4 mm wide, males 9.2-9.8 mm long, 3.0-3.2 mm wide.

Geographic range. Northeastern California, Oregon to the Plains States and northeastern U.S.


Genus Cenocorixa Hungerford


The Cenocorixa of California are moderate sized, varying from 6.0 to 8.3 mm in length. They are somewhat larger than the California species of Sigara. They differ from Callicorixa, which are comparable in size, by the presence of the abdominal strigil and by the narrower, more reticulate dark bands of the hemelytra (figs. 194 and 196), which tend to form longitudinal stripes. This longitudinal striping will also distinguish our Cenocorixa from all species of California Sigara except S. omani which usually has an effaced hemelytral pattern and in which the postnodal pruina is shorter than the clavopruina. The postnodal pruina of Cenocorixa is about the same length as the clavopruina. At high magnifications (100 X) the dark bands of the hemelytra are pebbly in appearance (fig. 115F), and with reflected light the pronotum and hemelytra are
rugose rather than rastrate as in Callicorixa and Sigara.

Three species of Cenocorixa have been found in California. Three others, C. andersonii, C. bifida, and C. utahensis, listed as occurring or possibly occurring in California by other authors, have been omitted from the following key; but a brief discussion of their status in California has been included.

Jansson (1972a) reviewed the genus.

**KEY TO CENOCCORICA OF CALIFORNIA**

1. Pronotum with 8-10 dark bands (fig. 198) which are equal to, or wider than intervening light areas; male right clasper (fig. 203) not bifurcate, bluntly pointed at apex .......... blaisdelli (Hungerford)

Pronotum with 10 or more dark bands (figs. 197, 199) which are narrower than intervening light areas; male right clasper (figs. 201, 204) either bifurcate or hooklike at apex .............. 2

2. Last segment of hindtarsus brown; peg row of male pala gradually arched (fig. 209); male right clasper bifurcate (fig. 201). ........................................... kuiterti Hungerford

Last segment of hindtarsus yellow, concolorous with first; peg row of male pala abruptly recurved (fig. 211); male right clasper hooklike at apex, not bifurcate (fig. 204). .............. wileyae (Hungerford)

*Cenocorixa andersonii* Hungerford

(Fig. 202)


*Cenocorixa andersonii* Hungerford was included in the key given by Usinger (1956) as possibly occurring in California. This species is found along the Pacific Coast in northern Oregon and Washington but has not been found in southern Oregon or in northern California despite extensive collecting. The distribution pattern of *C. andersonii* is similar to that of several other species of more northern Corixidae, and I do not anticipate finding it in California. However, the species may be distinguished from all other *Cenocorixa* occurring in the state by the male right clasper (fig. 202). The clasper is similar to that of *C. blaisdelli* but is not widened beyond the subapical bend and has more acutely pointed tip.

*Cenocorixa bifida* (Hungerford) (Fig. 200)


Hungerford (1948a) lists two California localities for *Cenocorixa bifida*. I have examined his Mt. Kaiser specimen, and as could be expected by the high altitude of this locality (9,000 feet), it has proven to be *C. kuiterti*, not *C. bifida*. Dr. Moore of the University of Michigan Museum of Zoology provided notes and illustrations of the male pala drawn from the Adobe Valley, Mono Co., series, and clearly these specimens are *C. wileyae*. I have not collected *C. bifida* in California, nor do I anticipate the occurrence of this species in the state. *Cenocorixa bifida* may be distinguished from other members of the genus by the shape of the bifurcate male clasper (fig. 200).

*Cenocorixa blaisdelli* (Hungerford) (Figs. 195, 198, 203, 207, 210)

*Arctocorixa blaisdelli* Hungerford, 1930, Pan-Pac. Entomol. 7:26.

Holotype ♀: Vine Hill, Calif. (CAS).


*Cenocorixa blaisdelli* usually has fewer pronotal bands (8-10) than *C. kuiterti* (10-12) and *C. wileyae* (12-15). The hemelytral pattern (fig. 195) is relatively dark with more prominent longitudinal banding than *C. wileyae*. Both the male pala (fig. 210) and abdominal dorsum (fig. 207) of *C. blaisdelli* are similar to *C. kuiterti*. The palar pegs form a continuous arch and the dorsal strigil is large in both species. The central expansion of the seventh abdominal tergum of *C. blaisdelli* is similar to that of *C. wileyae* and more triangular than the central expansion of *C. kuiterti*. The male right clasper (fig. 203) distinguishes *C. blaisdelli* from all other *Cenocorixa*. The apex is relatively blunt and the base is only slightly expanded. Females are 6.5-7.7 mm long, 2.1-2.4 mm wide, males 6.2-7.2 mm long, 1.9-2.3 mm wide.

**Geographic range**. California, Washington, and British Columbia.

FIGS. 194-205. Various structures in *Cenocorixa*: 194-196, Female hemelytron; 197-199, female pronotal disk; 200-205, male right clasper.
This species is limited to the coastal counties where it ranges from the northern border to Santa Barbara County.

*Cenocorixa kuiterti* Hungerford
(Figs. 194, 197, 201, 206, 209, 212)


*Cenocorixa kuiterti* can be distinguished from *C. blaisdelli* and *C. wileyae* by the brown last tarsal segment of the hindleg. This segment is yellow and concolorous with the first tarsal segment in the other two California species. The pronotal disk of *C. wileyae* is about 1.65 times as wide as long while the disk of *C. kuiterti* is about 1.8 times as wide as long. The dark bands on the hemelytra, especially those of the males, are usually lighter brown than those of *C. blaisdelli* and *C. wileyae*, and the bands (fig. 197) are broader than those of *C. wileyae*. The peg row of the male pala is arched (fig. 209) similar to that of *C. blaisdelli*. The abdominal strigil of *C. kuiterti* is large 13 and the central projection of the seventh tergum is more rounded (fig. 206) than that of *C. blaisdelli* and *C. wileyae*. The male right clasper is bifurcate (fig. 201) and has a prominent basal hump. Females are 6.0-8.1 mm long, 2.0-2.7 mm wide, males 7.0-7.5 mm long, 2.3-2.4 mm wide. This size range includes three unusually small females taken from 9,000 ft. in Yosemite National Park.

**Geographic range.** California.


13. Hungerford (1948b) reported that the strigil was small, but the paratypes from the same locality as the holotype and all the specimens listed above have large abdominal strigils.
MAP 40. California distribution of *Cenocorixa bluidelli* (Hungerford).

MAP 41. California distribution of *Cenocorixa kuiterti* Hungerford.


This species is found in high altitude ponds and lakes (7,000 to 10,500 feet) in the Sierra Nevada.

*Cenocorixa utahensis* (Hungerford)  
(Fig. 205)


This species was reported from two localities in California by Hungerford (1948a) because he misidentified his material. The specimens are *C. kuiterti*, a closely related species. Perhaps the basis for this error was due to the allegedly small strigil of *C. kuiterti* (see footnote under *C. kuiterti*). I have seen no specimens of *C. utahensis* from California nor do I believe that this species occurs in the state; thus, it is omitted from the key. However, if doubt should arise concerning this species, specimens may easily be distinguished from all other *Cenocorixa* by the shape of the male right clasper (fig. 205). Note that the bifurcate tip is C-shaped and the antiapical projection is not abruptly turned toward the base as in *C. kuiterti* (fig. 201).


Cenocorixa wileyae is a rather distinctive species. The pronotal disk is about 1.65 times as wide as long as compared to 1.7-1.8 times as wide as long for the other two California Cenocorixa. The dark bands of the pronotal disk are very narrow (fig. 199) and 12 and 15 in number. The hemelytral pattern (fig. 196) is more reticulate than that of C. blaisdelli and C. kuiteri. The abdominal strigil (fig. 208) is much smaller than that of C. blaisdelli and C. kuiteri. The male right clasper distinguishes this species from all other Cenocorixa (fig. 204). The apex is long and slightly hooked. Females are 7.1-8.3 mm long, 2.3-2.5 mm wide, males 6.6-7.5 mm long, 2.1-2.3 mm wide.

Geographic range. California and Washington to Colorado and New Mexico.

California records (map 42). This is a common pond corixid that occurs across the northern part of California and through the Sierra Nevada to Southern California. It extends south through the Coast Ranges to the San Francisco region but apparently is absent in the central coastal area and the southeastern deserts.

Genus Sigara Fabricius


Basilocorixu Kirkaldy, 1938, Entomologist 31:252.


MAP 42. California distribution of Cenocorixa wileyae (Hungerford).


Microsigara Poisson, 1957, Faune Fr. 61:95 (= subgenus).


The genus Sigara contains numerous, variable species which are usually grouped into several subgenera. Jaczewski (1962) expressed the opinion that subgenera are not warranted. Presently all those species occurring in California are placed in the subgenus Vernicorixa.
Walton of which Nasicorixa and Archicallicorixa are synonyms according to Jaczewski (1968).

All the California species are relatively small, 4.5-6.2 mm long. Species of Trichocorixa and Corisella of comparative size have smooth pronota and hemelytra, while the pronotum and hemelytra of Sigara are rastrate (fig. 115G). The hemelytral pattern of these two genera is either reticulate or longitudinally striped, while the Sigara in California, except S. omani, have distinct transverse banding on the hemelytra. Members of the genus Cenocorixa are larger and the hemelytra, especially the corium, are only moderately rugose. Calli-
corixa species also have rastrate hemelytra, but they are larger and the males lack an abdominal strigil.

Six species of Sigara are known in California. In addition, S. nevadensis (Walley) is found in Nevada near the border, and it may occur in the state. Although this species is not listed in the key, S. nevadensis may be distinguished from all the Sigara known from California by the male right clasper (fig. 231).

KEY TO SIGARA OF CALIFORNIA

1. Hemelytral pattern usually effaced, dark markings forming longitudinal stripes (fig. 218) .......... omani (Hungerford)
   Hemelytral pattern not effaced, dark markings primarily forming transverse bands (figs. 213-217) ................. 2

2. Metathoracic scent gland ostiole located near lateral bend of mesepimeron (at about one fourth distance from bend to apex of process, fig. 220) .......... grossolineata Hungerford
   Ostiole located about midway between lateral bend and apex of mesepimeral process (figs. 219, 221) or beyond (figs. 222-223) .................. 3

3. Ostiole located about midway between lateral bend and apex of mesepimeral process (figs. 219, 221) ................. 4
   Ostiole located closer to apex of mesepimeral process (figs. 222-223) .................. 5

4. Mesepimeral process nearly parallel or gradually widening from ostiole to lateral bend (fig. 221) .... mckinstryi Hungerford
   Mesepimeral process broadest just anterad of ostiole, then narrower and parallel sided to lateral bend (fig. 219) .... washingtonensis Hungerford

5. Lateral margin of female hemelytron protuberant where corium meets membrane (fig. 217); postmedian projection of seventh abdominal tergum of male triangular (fig. 236) .................. sandvikei Hungerford
   Lateral margin of hemelytron without a protuberance (fig. 216); projection of seventh abdominal tergum of male trapezoidal (fig. 235) .................. willis Lauck

Sigara (Vermicorixa)grossolineata Hungerford
(Figs. 214, 220, 226, 233)


The location of the metathoracic scent gland ostiole near the lateral bend of the mesepimeron distinguishes S. grossolineata from the other California species of Sigara. The size, shape, hemelytral pattern (fig. 214), and abdominal terga (fig. 233) are similar to S. washingtonensis. The male right clasper (fig. 226) is similar to the clasper of mckinstryi, but it is not as broadly expanded anteriorly to the fingerlike projection. Females
are 5.2-5.8 mm long, 1.7-1.9 mm wide, males 4.7-5.6 mm long, 1.6-1.7 mm wide.

**Geographic range.** Primarily the northeastern U.S. and Plains States, but also California and Utah.

*California records* (map 43). The occurrence of this species in California is quite surprising. I have examined part of the series from Mammoth Lakes, Mono County (KU), listed by Hungerford (1946a) and there is no question as to their identity. However, I have collected in this area on two occasions without finding additional specimens. An error in labelling is a possibility.

**Sigara (Vermicorixa) mckinstryi** Hungerford
(Figs. 215, 221, 227, 238)


The hemelytra (fig. 215) of *mckinstryi* have fewer and broader bands than the other California species of *Sigara*. The lateral bend of the mesepimeron (fig. 221) is more gradually rounded in *S. mckinstryi* and in *S. washingtonensis* which has a similar metathoracic scent gland ostiole location (fig. 219). *Sigara mckinstryi* has fewer palar pegs (28-31) than *S. vallis*, but a similar number are found in *S. washingtonensis*, *S. grossolineata*, and *S. vandykei*. The posteromedian projection of the seventh abdominal tergum of the male (fig. 234) is triangular but not as prominent as that of *S. grossolineata* and *S. vandykei*. The male right clasper (fig. 227) is similar to that of *S. vallis* but it is thickened more toward the apex in *S. mckinstryi*. This is a rather small species. Females are 4.7-5.6 mm long, 1.5-1.8 mm wide, males 4.5-5.3 mm long, 1.4-1.6 mm wide.

**Geographic range.** California.

*California records* (map 44). This species is the most common *Sigara* in California. Individuals frequent both ponds and the margins of streams and rivers. *Sigara mckinstryi* is found in the coastal counties as far south as Los Angeles. In the north it ranges across the state to the Nevada border.
**Sigara (Vermicorixa) omani** (Hungerford)  
(Figs. 218, 224, 230, 237)


*Sigara omani* is quite distinct from other species of *Sigara* found in California. The hemelytral pattern (fig. 218) is usually effaced and forms longitudinal rather than transverse striping. Because of its size and longitudinally striped hemelytral pattern, this species superficially resembles *Corisella decolor*, but it is easily distinguished from it by the rastrate pronotum and hemelytra. As in *S. vandykei*, the metathoracic scent gland ostiole (fig. 224) is near the apex of the mesepimeron. There are fewer palar pegs in the male (20-23) than in the other California *Sigara*. The right male clasper (fig. 230) is very slender and tapering, somewhat similar to that of *S. vandykei*. Females are 5.5-6.2 mm long, 1.8-2.1 mm wide, males 5.3-5.7 mm long, 1.7-1.9 mm wide.

**Geographic range.** Arizona, California, Nevada, Oregon, Washington, Wyoming, British Columbia.

*California records* (map 45). This species occurs across the northern part of the state and south along the coast and Coast Range into Lake and Mendocino Counties. However, *S. omani* extends much farther south in the Sierra Nevada. *S. omani* is primarily a pond species, but it may also be collected along the quiet margins of streams and rivers.

FIGS. 232-237. Dorsal aspect of male abdomen in *Sigara*. 

232 *washingtonensis*  
233 *grossolineata*  
234 *mckinstryi*  
235 *vallis*  
236 *vandykei*  
237 *omani*
FIG. 238. Sigara meckinstryi, male, dorsal view (from Usinger, 1956).

MAP 43. California distribution of Sigara meckinstryi Hungerford, circles; and S. grossolineata Hungerford, triangle.

MAP 44. California distribution of Sigara meckinstryi Hungerford.

Sigara (Vermicorixa) vallis Lauck
(Figs. 216, 222, 228, 235)


The hemelytral pattern (fig. 216) of S. vallis is similar to S. washingtonensis and S. vandykei, but it is slightly more reticulate. The metathoracic scent gland ostiole is located near the mesepimeral apex as in S. vandykei, but females of S. vallis lack the lateral protuberance of the hemelytra, and the two species have different male right claspers (compare figs. 228-229). The male clasper of S. vallis most closely resembles that of S. meckinstryi but the latter has fewer palar pegs (33 to 36 in S. vallis), and the posteromedian projection of the seventh abdominal tergum is different (compare figs. 234-235). The projection of the seventh abdominal tergum of S. vallis (fig. 235) is especially prominent and trapezoidal. The projection in S. washingtonensis is rounded apically. This is the largest species of Sigara in the state. Females are 5.6-6.2 mm long, 1.8-2.1 mm wide, males 5.3-6.0 mm long, 1.6-1.9 mm wide.

Geographic range. California.

This species is apparently restricted to the Central Valley, and is the only Sigara known in this region, except for a single record of S. mckinstryi from Yolo County.

**Sigara (Vermicorixa) vandykei** Hungerford
(Figs. 217, 223, 229, 236)


Males of *vandykei* are easily separated from all other *Sigara* found in California by the long slender male right clasper (fig. 229). Females are also distinct in having the lateral margin of the forewing slightly protuberant near the membrane (fig. 217). *Sigara vandykei* appears lighter in color than *S. mckinstryi* due to the narrower banding of the pronotum and hemelytra (fig. 217). In Oregon *S. vandykei* is frequently associated with *S. washingtonensis*. The hemelytral banding of *S. washingtonensis* (fig. 213) is similar to *S. vandykei*, but in addition to the characters given above, the metathoracic scent gland ostiole of *S. vandykei* (fig. 223) is located near the apex of the mesepimeral process, while in *S. washingtonensis* it is located about midway between the apex and lateral bend of the broader mesepimeron. The hemelytral pattern is distinct from *S. omani* and the pegs of the male pala are more numerous (27-31). Two other species from California, *S. grossolineata* and *S. vallis*, are not found within the range of *S. vandykei*. *Sigara vallis* has a hemelytral pattern similar to *S. vandykei*, but the male of *S. vallis* has more palar pegs (33-36), and a more prominent posteromedian projection on the seventh abdominal tergum (compare figs. 235-236), and the ostiole in both sexes is about two-fifths the distance from the apex to the lateral bend. The ostiole is almost at the lateral bend in *S. grossolineata*. *Sigara vandykei* is slightly larger than *S. mckinstryi*, the species with which it is almost always associated in California. Females are 4.9-5.6 mm long, 1.6-1.9 mm wide, males 4.5-5.3 mm long, 1.5-1.7 mm wide.

**Geographic range.** Coastal rivers from Sonoma, California, north into Washington.

MAP 47. California distribution of *Sigara vandykei* Hungerford.

*Sigara vandykei* was previously known only from the type localities, Van Duzen River, Humboldt Co., California, and Kalama River, Washington.

This is the most abundant corixid in the coastal streams and rivers of northern California; but, except for the Klamath and Eel River drainages, *S. vandykei* is restricted to the coast. This species is almost always associated with *S. mckinstryi*. In the lower drainages of rivers *S. vandykei* is always dominant, but *S. mckinstryi* becomes more abundant in the upper drainages of the Klamath and Eel Rivers.

Along the Klamath, in the more sluggish flows near the Oregon border, *S. vandykei* completely disappears from the corixid population, and it has not been found in the northern Klamath in Oregon even though the flow becomes more rapid again.

*Sigara (Vermicorixa) washingtonensis* Hungerford

(Figs. 213, 219, 225, 232)


This species differs from all other California *Sigara* by the location of metathoracic scent gland ostiole about midway between the apex and the lateral bend of the mesepimeron (fig. 219). The hemelytral pattern of *S. washingtonensis* (fig. 213) is similar to *S. vandykei* and *S. vallis*, but the dark bands are narrower than those of *S. mckinstryi*. The male palar pegs are more numerous (27-29) than those of *S. omami* and less numerous than those of *S. vallis*. The male right clasper (fig. 225) is similar to those of *S. grossolineata, S. mckinstryi* and *S. vallis*, but it tapers more toward the apex than in these species. Females are 5.4-6.1 mm long, 1.7-2.0 mm wide, males 5.1-5.5 mm long, 1.7-1.9 mm wide.

**Geographic range.** Rocky Mountain states northward to Alberta and British Columbia, west to northeastern California and to the coast in Oregon and Washington.


The distribution of this species in California has been confused by misidentification. All California specimens labelled "washingtonensis" that I examined proved to be *S. mckinstryi*. *Sigara washingtonensis* is found only on the eastern side of the Sierra Nevada in California.
These bugs are characterized by their 2:2:3 tarsal formula; the long, slender beak which reaches the hind coxae; the moderately short but exposed four-segmented antennae which are inserted beneath the eyes; the presence of two ocelli; the slender legs fitted for running (first pair not raptorial); and by their small size, oval form, and dark color with lighter spots. Superficially ochterids appear intermediate between the Gelastocoridae and the Saldidae. Although resembling Saldidae in body form, size, and in having exposed antennae, ochterids are structurally more closely allied with the Gelastocoridae as demonstrated by the asymmetrical genitalia and abdominal segments in the male, the four-segmented beak, and by the absence of trichobothria on the head. Parsons (1966a, 1967) detailed other similarities between the two families.

This small family contains about 32 species in three genera. Ochterus contains 30 species and is cosmopolitan. Jaczewski (1934) described Megochterus for an Australian species, and Drake and Gomez-Menor (1954) described Ocyochterus for a South American form. Kormilev (1971) recently summarized what is known about the family, and Rieger (1976) gave an excellent account of morphology. One species of Ochterus occurs in California. Pelogoniidae has been used as the name of the family by some workers, China and Miller (1955) for example, because it is the oldest group name; but in most of this century the family name Ochteridae has gained general acceptance and Article 40(a) of the Code permits continuance of this usage.

Ochterids are shore dwellers, and their cryptic coloration makes them nearly invisible, but they can run rapidly or jump when disturbed. They are capable of flight, but our species rarely flies. The biology of two ochterids has been studied. Takahashi (1923) reported on the Old World Ochterus marginatus formosanus (Matsumura), and Bobb (1951b) discussed the habits of the New World O. banksi Barber. The eggs are laid singly on sand grains and debris along the shore. The egg of O. banksi is 0.8 mm long and 0.47 mm wide, white, and has an irregularly marked surface. The nymphs are sluggish and cover their dorsum with sand grains, presumably for concealment. The clypeus is armed with spines for scooping up the grains. Takahashi and Bobb reported that older nymphs were occasionally found in water swimming awkwardly beneath the surface film. Prior to molting, nymphs dig cells in the sand leaving only a small hole at the top.

Ochterus marginatus formosanus completes its life cycle in about one month, but Bobb found that O. banksi overwinters in the fourth instar, at least in Virginia. Two weeks exposure to temperatures of less than 45 degrees F. were required before the overwintering fourth instar nymphs would molt. Total developmental time for O. banksi averaged 316 days with the overwintering fourth instar lasting an average of 214 days. Collembola, fly larvae and aphids are eaten by nymphs and adults of O. banksi according to Bobb.

Genus Ochterus Latreille

Type-species: Acanthia marginata Latreille, 1804. monotypic.
Ochterus Bergroth, 1890, Bull. Soc. Entomol. Fr. 1890:cxix. Unjustified new name for Ochterus Bergroth, 1890.

In Ochterus the front of the head is declivous, and antennal segments three and four are slender and long-
er than segments one and two. The membrane contains about seven cells.

Schell (1943) revised the New World species, and Drake (1952) gave an updated catalog. Five species are known from the United States. The single California species is found at the Colorado River.

The extensive, different, and unwarranted spellings of *Ochterus* represent a nomenclatorial comedy of errors of a magnitude seldom encountered.

*Ochterus barberi* Schell
(Fig. 239)


*Geographic range.* Arizona, California, New Mexico, and Orizaba, Mexico.


FIG. 239. *Ochterus barberi*, dorsal view (from Usinger, 1956).
FAMILY GELASTOCORIDAE / Toad Bugs

A. S. Menke

Gelastocorids are short, broad bugs with protruding eyes. They commonly hop or jump when disturbed, which, along with their warty appearance, has earned them the common name "toad bugs." Members of this family have stout, raptorial front legs; short four-segmented antennae which are concealed beneath the head; and a rather short beak. Ocelli are usually present. The abdominal sterna are asymmetrical in both sexes although most strongly so in the male. Parsons (1959, 1960) published detailed studies of the external and internal morphology of Gelastocoris.

There are two toad bug genera, the New World Gelastocoris and the cosmopolitan Nerthra, which are assigned to separate subfamilies. Todd (1955) revised the family and subsequently published (1961) a checklist. About a hundred species are currently recognized. Some authors have used the family name Galgulidae for this group because it is the oldest family group name, but Article 39 of the Code negates such usage. Similarly the subfamily Nerthrinae has been called the Mononychinae (China and Miller, 1955), but Article 40(a) permits conservation of the former which has now gained acceptance among contemporary workers.

Gelastocoris species are found along the banks of streams and ponds, and their mottled appearance usually makes them difficult to detect unless they move. Although some Nerthra species occupy littoral habitats similar to Gelastocoris, others are found far from water. Todd (1955) summarized reports of Nerthra having been found living in decomposing banana trunks, rotting logs, and in leaf litter on the forest floor. Lauck and Wheatcroft (1958) found Nerthra manni Todd in cow dung in Mexico, and in one instance no water was close by. Those species of Nerthra that are found on the banks of streams and ponds are usually secretive, hiding under stones or other objects near water, and often burrowing in the soil. Nerthra has also been found in water. La Rivers (1953a) found N. martini Todd crawling on plant stems under water in Cow Creek, Death Valley. He also observed this same species in Nevada clinging to the undersurface of wood floating in the water of a hot spring. At another Nevada locality La Rivers found N. martini under rocks in swiftly flowing water.

The biology of Gelastocoris has been documented by Hungerford (1922b) who studied G. oculatus (Fabricius). The eggs are white and are laid on the sand where they blend perfectly with their surroundings. A single female probably lays about 200 eggs during her lifetime, with 1-13 laid in a day. Incubation takes about two weeks, and total developmental time takes from 60 to 100 days according to Hungerford. Nerthra biology is poorly known. According to Usinger (1956) the eggs of N. martini Todd are laid in small holes in the mud beneath stones near water. Apparently the female remains with the eggs until they hatch since Usinger found the parent bug in a position above the nearly fully developed eggs. In Trinidad, Kevan (1942) reared last instar nymphs of N. nepaeformis (F.) to adults in two weeks. Hungerford and Kevan fed their gelastocorids a variety of small insects, and it is probable that members of this family normally feed on many different insects.

Wing and flight muscle polymorphism is common in the Gelastocoridae (Parsons, 1960). Although individuals with well-developed flight muscles and normal wings are apparently common, at least in Gelastocoris, there appears to be only one record of flight in this family (Gelastocoris, see Nieser, 1975). The trend toward flightlessness in the Gelastocoridae seems correlated with their burrowing habits (Todd, 1955). The extreme is reached in some Nerthra species that have the forewings immovably fused.

KEY TO NEARCTIC GENERA OF GELASTOCORIDAE
Nymphs and adults

Foretarsus articulating with tibia, 1 segmented with 2 claws in nymphs and adults; forefemur only moderately enlarged at base, twice as long as basal width, not subtriangular; closing face of forefemur flat and bordered by two rows of short spines; beak clearly arising at front of head, directed caudad, longitudinal axis essentially parallel to longitu-
Gelastocoris oculatus

Subfamily Gelastocorinae
Genus Gelastocoris Kirkaldy

Gelasrocoris Kirkaldy, 1897, Entomologist 30:258. New name for Galgulus Latreille.


Adult Gelastocoris are readily separable from Nerthra by the one-segmented foretarsus which bears two claws. Also, the beak arises from the apex of the head in Gelastocoris and is directed caudad. In contrast to the rather drab, uniform color of Nerthra, Gelastocoris species are usually colorful, with shades of brown, red or green predominating. The variation in color pattern from individual to individual, even within a small population, is often striking.

Todd (1955, 1961) considered the South American taxon, Montandonius Melin, as a synonym of Gelastocoris, but Nieser (1975) elevated it to genus. There are about a dozen species of Gelastocoris, only two of which occur in the United States and both are found in California.
KEY TO GELASTOCORIS OF CALIFORNIA

Lateral margin of pronotum abruptly sinuate, forming a strongly projecting posterolateral lobe (fig. 243); distributed throughout the state .................. oculatus (Fabricius)
Lateral margin of pronotum smoothly sinuate, posterolateral lobe less well defined (fig. 242); along Colorado River near Parker Dam .................. rotundatus Champion

Gelastocoris oculatus oculatus (Fabricius)
(Figs. 240, 243-244)


Geographic range. The nominate subspecies is common throughout most of the United States. The subspecies variatus (Guérin-Méneville) occurs from Texas to Panama.

California records (map 48). This common toad bug has been collected in nearly every county in the state, and over a wide range of elevations and life zones.

Gelastocoris rotundatus Champion
(Fig. 242)


Geographic range. California (Colorado River) to Texas and Honduras.

California records (map 48). San Bernardino Co.: Bennett Wash, 8 mi. SW. Parker Dam, II-24-51 (P. A. Adams and C. D. MacNeill, RLU, CIS). Wash 3.5 mi. N. Cross Roads, 1V-12-52 (J. D. Lattin, RLU).

The above data both refer to the same locality.

Subfamily Nerthrinae
Genus Nerthra Say


FIG. 244. Gelastocoris oculatus, dorsal view (from Usinger, 1956).
Nerthra is separated from Gelastocoris by the fused tarsus and tibia of the front leg. In addition the beak appears to rise from the back of the head and is directed ventrad. Our species of Nerthra are commonly found under stones near water.

Todd (1961) lists 85 species, four of which occur in the United States. Two of these are known from California.

Harris (1942) demonstrated that Laporte's work was published in 1833, but according to Direction 63 of the I.C.Z.N. (Opin. Decl. Rend. Int. Comm. Zool. Nomencl. 1E (3):21-60), the first 16 pages are to be considered as published in 1832. Following Article 21(b) (ii) of the Code, the 1832 portion of Laporte's paper must be dated Dec. 31 of that year. Say's 1832 paper undoubtedly appeared before then, since the first 8 pages were printed in 1831 according to Scudder (1899). Hence Nerthra has priority over Mononyx.

**KEY TO NERTHRA OF CALIFORNIA**

Apex of male clasper lanceolate (fig. 245); last female abdominal sternum with an angulate notch (fig. 247); southern half of the state.......................... *martini* Todd

Apex of male clasper broadly spatulate (fig. 246); last female abdominal sternum broadly, roundly emarginate (fig. 248); vicinity of Parker Dam on the Colorado River ......... *usingeri* Todd

*Nerthra martini* Todd

(Figs. 241, 245, 247, 249)


*Mononyx fuscipes* of authors, not Guérin-Méneville, 1843.

The aedeagus offers the best means of separating males of *N. martini* from *N. usingeri*. Females of *N. martini* have an angulate notch in the last sternum in contrast to the round notch found in *N. usingeri*.

**Geographic range.** Arizona, California, Nevada, Baja California, and Sonora, Mexico.


**FIGS. 245-246. Dorsal view of male genital clasper in Nerthra; 247-248, abdominal sternum in female Nerthra.**


This species is also known from Cow Creek in Death Valley (La Rivers, 1953).

*Nerthra usingeri* Todd
(Figs. 246, 248)

*Nerthra usingeri* Todd. 1954. Pan-Pac. Entomol. 30:116. Holotype \( \sigma \): near Parker Dam, California (CAS).

The aedeagus will identify males of *usingeri*. Females of this species differ from *martini* in having a broadly rounded emargination at the apex of the last abdominal sternum.

**Geographic range.** California; Jalisco, Mexico.


Both localities are the same place, and this is the only California record for *N. usingeri*. The series collected by Menke and Stange was found under stones along the margin of the stream that flows in the wash.

MAP 49. California distribution of *Nerthra martini* Todd, solid circles; and *N. usingeri* Todd, open circle.
FAMILY NAUCORIDAE/Creepping Water Bugs, Saucer Bugs

J. T. Polhemus

Naucorids are oval, flattened bugs with raptorial front legs. The middle and hindlegs are modified for swimming. The antennae are four-segmented and usually hidden. The beak is short in our forms, the ocelli are absent, and there are no veins in the hemelytral membrane. Naucorids lack the caudal, straplike abdominal appendages which are characteristic of the Belostomatidae. Nymphs possess a pair of abdominal scent glands with openings on the hind margin of tergum III. Although the openings are present in adults, Usinger (1947) could not locate any glands. Color varies from blackish brown to yellow brown, greenish or gray, and the dorsum is often mottled.

Following Usinger (1941a), the Naucoridae is divided into eight subfamilies containing 37 genera and about 300 species. Two of the subfamilies, Cheirochelinae and Aphelocheirinae, occur only in the Old World. Of the others, i.e., Potamocorinae, Laccocorinae, Cryphocricinae, Limnocorinae, Ambrysininae, and Naucorinae, only the last four are Nearctic and only the last two are represented in California, by Ambrysinus and Pelocoris, respectively. A third genus, Usingerina La Rivers (fig. 250), occurs in a southern Nevada hot spring (La Rivers, 1950). This monotypic genus is considered by De Carlo (1951) to be a synonym of Limnocoris Stål, a tropical genus which enters the Naucoridae. Of the Naucorinae, Ambrysininae, and Naucorinae, only one species is restricted to fast water where they cling to the stones and crawl about, while other species swim amongst the pebbles in slower waters.

Naucorids feed upon a variety of small organisms. Ambrysinus have been reported attacking corixids and other insects, and Pelocoris sometimes feed on mollusks and dragonfly larvae (Uhler, 1884). Hungerford (1927) fed Pelocoris mosquito and chironomid larvae, corixids, and Entomostraca in rearing experiments. Ambrysinus mormon is said to feed on various aquatic larvae (Usinger, 1946).

The painful bites of naucorids are well known, and members of the genus Pelocoris are especially noted for their ferocity (Uhler, 1884; Hungerford, 1927). Blatchley (1926) stated from personal experience that P. femoratus (Palisot de Beauvois) inflicts a wound more painful for a few seconds than that of a hornet. Ambrysinus buenoi Usinger is also known as an aggressive bug (La Rivers, 1953a).

The life history of Pelocoris femoratus has been studied in more detail than other Nearctic naucorids (Hungerford, 1927; Torre-Bueno, 1903). According to La Rivers (1948), Hungerford’s studies of P. carolinensis Torre-Bueno actually pertain to P. femoratus. The creamy white eggs are glued with white adhesive to the leaves and stems of aquatic plants such as Nitella. The

14. Because of its unique mode of respiration, long beak, etc., Aphelocheirus Westwood is considered by some workers (La Rivers, 1971; De Carlo, 1971; Parsons, 1969a, b, for example) as representing a separate family. Usinger (1956) and Popov (1970) maintain the genus in the Naucoridae. Since the status of this peculiar genus is still not settled, I have accepted the latter, more conservative viewpoint.
eggs enlarge about 20% as the embryo develops. One female laid 53 eggs in 14 days, and hatching time varied from 32 to 45 days (Hungerford, 1927). Torre-Bueno (1903) stated that hatching time varied from 22 to 27 days. After the eggs hatch, development to adult takes 50 to 62 days.

Usinger (1946) studied the biology of *Ambrysus mormon* in California. The creamy white eggs are glued to the surface of pebbles by overwintering females during the spring and early summer. After about a week the eggs turn gray and as development progresses the reddish eye spots can be seen through the chorion. Hatching occurred in 25 to 33 days at Davis, California, but took 47 to 52 days at Berkeley, where it was cooler. The egg burst in a crescent-shaped tear at the micropyle end during hatching. Subsequent development to adult took about 76 days.

Copulation of the Old World *Ilyocoris cimicoides* (Linnaeus) and *Aphelocheirus aestivalis* (Fabricius) was studied by Larsén (1938) who showed that the male typically is astride the back of the female with his genital segments strongly twisted and extended to engage the female. The Nearctic species *Ambrysus occidentalis* La Rivers copulates in a similar fashion (Constantz, 1974).

In Nearctic naucorids, hibernation is known only in *Pelocoris femoratus* from the eastern United States. This species retreats to the bottoms of pools and ponds where there is some depth of muck and especially where water plants remain rooted through the winter (Uhler, 1884). Other forms, including the *Pelocoris* found in California, inhabit warmer regions or hot springs for the most part, and generally hibernation is unnecessary.

Naucorids are parasitized by endo- and ectoparasites. Poisson (1957) lists as endoparasites the flagellate *Lep- tomonas naucoridis* Poisson in *Naucoris maculatus* Fabricius, and the chalcid wasp *Prestwichia aquatica* Lubbeck in *Aphelocheirus*. Water mites (hydrachnids) are common ectoparasites of naucorids.

Little is known of the dispersal mechanisms of naucorids. Many species possess fully developed flight wings, but flight has rarely been observed (Usinger, 1956). Naucorids have been found in habitats which had to be reached by flying, and some tropical species have been taken at lights.

Most naucorids breathe through the cuticle as nymphs, and through spiracles in contact with an airstore as adults. They replenish their subalar air bubble by breaking the surface film with the tip of the abdomen; this airstore is connected with an air bubble which appears as a silvery sheen on the pubescent venter. According to Parsons (1970), the most probable connections between the two airstores is the first abdominal spiracular chamber and the lateral edges of the second abdominal segment. The exposed ventral bubble, with its large surface, acts as a "physical gill" which transfers carbon dioxide out and oxygen in, thus using the dissolved oxygen in the water as a secondary air source (Thorpe, 1950). Certain naucorids, especially some *Limnocoris*, *Cheirochela Hope*, and *Cataactocoris* Usinger (all extralimital), typically occur in swift and hence well-oxygenated water where it seems unlikely that they surface for air except at rare intervals, apparently deriving sufficient oxygen through their physical gill.

Members of two naucorid genera, the Old World *Aphelocheirus* and the Neotropical *Cryptocricos* Signoret, are most commonly brachypterous and their respiration does not function as described above. The most studied of these is *Aphelocheirus* (Thorpe, 1950) which has reached the apex of an evolutionary trend, being able to survive under water without ever surfacing. This bug is largely covered by a very thin air layer or "plastron" which is held in place by an unwettable hair pile (2 million hairs per square mm) which provides a maximum water to air surface. This uncompressible, thin, permanent air layer acts as an external gill, which is connected to rosette-shaped ventral or basil spiracular openings consisting of a flat bag and numerous outgrowths. Normal spiracular openings would either become waterlogged or collapse under the water pressure. The respiratory mechanism of *Cryptocricos* is apparently the same as that of *Aphelocheirus* (Parsons and Hewson, 1975). Both genera possess a unique type of paired abdominal pressure receptors. In the Naucoridae, as in all Nepomorpha, the subalar airstore has at least one nonrespiratory function. Three pairs of scopophorous organs, presumably equilibrium sensors, lie in the air space under the forewings (Larsén, 1957).

**KEY TO GENERA OF NAUCORIDAE IN AMERICA NORTH OF MEXICO**

Based on adults

1. Anterior margin of pronotum straight or slightly concave behind interocular space (figs. 250-251) ................................................. 2
2. Anterior margin of pronotum deeply concave behind interocular space (fig. 266) ................................................................. 4
2. Inner margins of eyes diverging anteriorly (fig. 250); meso- and metasterna bearing prominent longitudinal carinae which are broad and foveate along middle; body broadly oval, subflattened ... (*Limnocorinae*) .................................................. 3
3. Inner margins of eyes covering anteriorly (fig. 251); meso- and metasterna without longitudinal carinae at middle; body strongly convex above, the embolium rounded ... (*Naucorinae*) .................................................. 2
4. Embolium produced outward and backward as an acute spine (fig. 250); Warm Springs, Nevada .................. 3

*Usingerina* La Rivers (naucoridis La Rivers)
Embolium more or less dilated but not produced into a spine; Guadalupe Riv., Texas ....... Limnocoris Stål (luti La Rivers)

4. Posterior part of prosternum covered by plate-like extensions of propleura which are nearly contiguous at midline; abdominal venter densely pubescent, except glabrous around spiracles; each spiracle also with a transverse row of small glabrous areas behind; macropterous ........ (Ambrysiniae) ....... Ambrysus Stål, p. 134
Prosternum completely exposed, separated from flattened pleura by simple sutures; abdominal venter bare and with a perforated disk-like area near each spiracle; dimorphic, the brachypterous forms with hemelytra truncate at apices, about half as long as abdomen; Rio Frio, Texas .. (Cryphocricinae) ........... Cryphocrocis Signoret (hungerfordi Usinger)

KEY TO GENERA OF NAUCORIDAE OF AMERICA NORTH OF MEXICO
Based on Fifth Instar Nymphs

1. Abdominal venter naked; front femur long, slender, with 1 ventral and 2 dorsal longitudinal ridges of granules ....... Cryphocrocis Signoret
Abdominal venter pubescent; front femur roundly inflated, without ventral and dorsal longitudinal ridges ........ 2
2. Inner margins of eyes convergent anterad and to some extent posterad; mesosternum without a foveate carina .......... 3
   Inner margins of eyes diverging anterad; mesosternum with a longitudinal carina which is foveate along the middle .... 4

3. Anterior margin or pronotum deeply concave behind interocular space (fig. 266) .............. Ambrysus Stål
   Anterior margin of pronotum scarcely concave behind interocular space (fig. 251) .......... Pelocoris Stål
4. Outer margin of wing bud protruding lateral about the width of an eye beyond outer margin of adjacent paratergite ....... Usingerina La Rivers
   Outer margin of wing bud extending little, if any, beyond outer margin of paratergite ........ Limnocoris Stål

Subfamily Naucorinae
Genus Pelocoris Stål (Fig. 251)


Pelocoris is distinguished from other Nearctic genera by the anteriorly convergent inner margins of the eyes, the straight anterior pronotal margin, and the absence of carinae on the meso-metasternum. The genus is restricted to the New World where it is widely distributed. There are about 20 species. The United States forms were keyed by La Rivers (1948). One polytypic species is found in the west. The nominate subspecies is found in the White River drainage in Nevada, and another subspecies occurs in the Amargosa River system of Cali-

FIG. 250. Usingerina moapensis, female, dorsal view (from Usinger, 1956).

FIG. 251. Pelocoris shoshone shoshone, female, dorsal view (from Usinger, 1956).
forinia and Nevada. The genus is widespread in western Mexico. Our species belongs in the subgenus *Pelocoris*.

*Pelocoris (Pelocoris) shoshone amagosus* La Rivers


This subspecies is larger and darker than *P. shoshone* s.s. The latter is known from a few hot springs in southern Nevada.

**Geographic range.** Endemic to the Amargosa River system of California and Nevada.


Subfamily Ambrysinae

**Genus Ambrysus Stål**


*Ambrysus* is distinguished by the deeply concave anterior pronotal margin, the propleura produced plate-like over the posterior part of the prosternum, and the densely pubescent venter. Of the nearly 70 species in this genus, 14 are known from the United States and 5 from California. Another species is known from Ash Meadows, Nevada, near the California border. La Rivers (1951) revised the United States species of *Ambrysus*, and subsequently (1953a, b) described two new U.S. species. Other important revisionary works are those of Montandon (1909), Usinger (1946), and De Carlo (1950). La Rivers (1964) discussed the subgeneric classification of *Ambrysus*. All our species except *A. funebris* belong in the subgenus *Ambrysus*.

The shape of the posterior margin of the female subgenital plate (figs. 260-265), and the shape of the hook-like or angular process (when present) of the right side of the hind margin of the fifth male tergum (figs. 254-259) provide specific diagnostic characters in this genus, but as the figures show, the outlines of surrounding terga also are useful in species identification. The overall sizes, colors, and contours of each species are distinctive but very difficult to describe.

**KEY TO SPECIES OF AMBRYUS IN CALIFORNIA AND ADJACENT STATES**

1. Lateral margins of first and second abdominal segments smooth, those of segments 3-5 minutely serrate (best seen from below); size small, 6-6.5 mm; hot springs in Ash Meadows, Nye County, Nevada. ........ amagosus La Rivers

   Lateral margins of all segments smooth; size usually larger ....... 2

2. Propleura not contiguous, separated by a small but distinct gap over middle of prosternum; hemelytra greenish or yellowish brown with ill-defined paler markings at base of embolium. *californicus* Montandon ............ 3

   Propleura contiguous over middle of prosternum; hemelytra black with distinct pale markings at lest at base of embolium and usually at inner apex of embolium and at middle of apical margin of corium ............ 4

3. Posterolateral angles of abdominal segments produced into small but distinct spines (fig. 253); northern California and streams in the coast ranges. *californicus bohartorum* Usinger

   Posterolateral angles scarcely produced, little more than right angles (fig. 252); southern California. ............ *californicus californicus* Montandon

4. Size small, 6-6.5 mm; male without dorsal genital process on abdominal tergum V (fig. 259); Death Valley, hot spring streams. .......... *funebris* La Rivers

**FIGS.** 252-253. Outline of abdominal terga, dorsal view of subspecies of *Ambrysus californicus*. 

252   253

c. californicus   c. bohartorum
254 amargosus
255 californicus
256 mormon
257 occidentalis
258 puncticollis
259 funebris
260 amargosus
261 californicus
262 mormon
263 occidentalis
264 puncticollis
265 funebris

FIGS. 254-259, Dorsal view of abdominal terga V-VI in male Ambrysus (arrow indicates genital process); 260-265, ventral view of female subgenital plate and associated sterna in Ambrysus.

Size larger, 8.15.5 mm; male with well-developed genital process on fifth abdominal tergum (figs. 256-258) ............. 5

5. Corium unicolorous; body 13 mm long or more; apex of female genital plate simply, shallowly concave (fig. 264); stream near Parker Dam, Colorado River .......... puncticollis Stål

Corium marked with pale areas; body 8-12.5 mm long; apex of female genital plate trimarginate (fig. 263), or with broad U-shaped emargination (fig. 262); widespread .......... 6

6. Width of head through eyes more than half greatest width of pronotum (ratio 7:13); corium with a large bilobed spot at inner apex of embolium, and a large crescent-shaped spot at middle of apical margin; male genital process as broad as long (fig. 257); apex of female genital plate trimarginate (fig. 263); southern California streams occidentalis La Rivers

Head slightly less than half width of pronotum; corium with small spot at inner apex of embolium, and at middle of apical margin or rarely without spots (fig. 256); male genital process much longer than wide (fig. 256); apex of female genital plate deeply concave at middle (fig. 262); northern and central California, streams and shallow margins of lakes .......... mormon Montandon

Ambrysus (Ambrysus) amargosus La Rivers (Figs. 254, 260)


Ambrysus amargosus is a small ovate species (6.0-6.5 mm long, 4.0-4.5 mm wide), with a strongly multicolored dorsum. The small male process (fig. 254), and the shape of the slightly asymmetrical female subgenital plate are diagnostic (fig. 260). This species is flightless, the hindwings being noticeably shortened, reaching only to the middle of the fourth tergum.

Geographic range. Nevada.

California records. None, but the type locality is less than six miles from the California border and it is part of the Amargosa River drainage which terminates in Death Valley. However, A. amargosus is known only from a single spring and this flightless species may have narrow ecological tolerances that prevent its dispersal through the Amargosa system. A. amargosus prefers the gravel bottom of the swift-flowing portions of the hot spring outlet where the water is a few inches deep. Specimens have not been found far below the spring.

Ambrysus (Ambrysus) californicus californicus Montandon (Figs. 252, 255, 261)


Ambrysus californicus is a small (7.5-8.5 mm long, 4.75-6.0 mm wide), unomitted species with a yellowish brown to greenish dorsum. The male process and female subgenital plate are diagnostic (figs. 255, 261). La Rivers (1951) recognized two subspecies of A. californicus which are separated by differences in the posterolateral angles of the abdominal terga. These angles are spineless in typical A. californicus (fig. 252).

Geographic range. Streams in the California Coast Ranges from Monterey County southward.
The size of *A. mormon* is quite variable; the bugs range from 9-12 mm long and 6-9 mm wide. Usually there is a pronounced mottling of the anterior portion of the hemelytra. The shape of the male process and female subgenital plate are diagnostic (figs. 256, 262). La Rivers (1971) recognized four subspecies of *A. mormon*, but only the typical form occurs in California.


**California records** (map 50). *Ambrysus (Ambrysus) mormon mormon* Montandon, open circles; and *A. c. bohartorum* Usinger, solid circles.

MAP 50. California distribution of *Amblysus californicus californicus* Montandon, open circles; and *A. c. bohartorum* Usinger, solid circles.

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The range of this subspecies overlaps that of *A. bohartorum* in the region between Monterey and San Luis Obispo counties.

**Ambrysus (Ambrysus) californicus bohartorum** Usinger
(Fig. 253)


**Holotype** 9: Austin Creek near Cazadero, Sonoma Co., Calif. (CAS).

The posterolateral angles of the abdominal segments are produced and spined in *A. bohartorum* (fig. 253).

**Geographic range.** Streams in the Coast Ranges of central and northern California.


**Ambrysus (Ambrysus) mormon mormon** Montandon
(Figs. 256, 262, 266)

Ambrysus (Ambrysus) occidentalis La Rivers
(Figs. 257, 263)


*Ambrysus occidentalis* is a median-sized species (10-12.5 mm long, 7-8.25 mm wide) with very strong mottling. The female subgenital plate and male process are diagnostic (figs. 257, 263). *A. occidentalis* is likely to be confused only with *A. mormon*.

**Geographic range.** Arizona, California, and western Mexico (Sonora and Baja California).


**MAP 51.** California distribution of *Ambrysus mormon* Montandon.

**MAP 52.** California distribution of *Ambrysus occidentalis* La Rivers, circles; *A. puncticollis* Stål, square; and *A. funebra* La Rivers, triangle.

**FIG. 266.** *Ambrysus mormon mormon*, female, dorsal view (from Usinger, 1946).

This is the common species in southern California. It is found in still pools of streams and is commonly taken by sweeping along undercut banks, but *ocidentialis* sometimes occurs in ponds such as those at Zzyza Springs.

*Ambrysus* (*Ambrysus*) *puncticollis* Stål
(Figs. 258, 264)


Being a large, elongate species (13-15.5 mm long, 7-9 mm wide), _puncticollis_ is easily recognizable. The female subgenital plate and male process are also diagnostic (figs. 258, 264).

**Geographic range.** Arizona, California, Texas, and Mexico.

_California records_ (map 52). SAN BERNARDINO CO.: Wash, 3.5 mi. N. Crossroads, IV-12-52 (R. L. Usinger, CIS); 10 mi. N. E. Earp, I-26-57 (Menke & Stange, LACM).

The two records above refer to the same stream. _A. puncticollis_ is found under rather large stones in riffle areas and will probably be discovered in other streams associated with the Colorado River.

*Ambrysus (Acyttarus) funebris* La Rivers
(Figs. 259, 265)


This species is by far the smallest naucorid occurring in California (6.0-6.5 mm long, 3.5 mm wide). The absence of a male genital process (fig. 259), and the shape of the female subgenital plate are also diagnostic (fig. 265), although _A. amargosus_ La Rivers from nearby Ash Meadows, Nevada, has a tiny male genital process. However, _A. funebris_ is elongate and _A. amargosus_ is ovate. Like the latter species, _A. funebris_ has short hindwings and is flightless.

La Rivers (1953a) discussed at length the morphological divergence of this species from the remainder of the genus, especially the loss of the costal cell in the reduced hindwing. He attributed this divergence to rapid speciation in thermal waters and isolation from other populations of naucorids. The monotypic subgenus _Acyttarus_ La Rivers (1964) is based on the absence of the costal cell.

**Geographic range.** Death Valley, California.


_Ambrysus funebris_ is known from the waters of several hot springs located within a few miles of each other but without direct connections except perhaps during periods of heavy flooding. Cow Creek is 36°C. These bugs prefer the swift flowing portions of the streams where they crawl in the gravel at the bottom.
The backswimmers differ from other aquatic insects (except Pleidae and Helotrephidae) in the habit of swimming on their backs. In general body form, they are long and slender, deep-bodied, flat ventrally, and convex dorsally. The eyes are large, reniform, and occupy most of the head. Ocelli are absent. The short antennae are three- or four-segmented and concealed from above. The rostrum or beak is short. The front and middle legs are adapted for grasping while the long oarlike hindlegs are flattened and heavily fringed for swimming. The tarsi in our species are two-segmented, but males of the Old World genus *Anisops* Spinola have one-segmented foretarsi. The tarsi possess two apical claws with those of the hindlegs greatly reduced and inconspicuous. The abdominal venter has a prominent longitudinal keel with long hairs which, together with the hairs along the sides of the venter, cover two longitudinal troughs forming air chambers.

The approximately 300 species of backswimmers are divided among nine genera. Two subfamilies are recognized, the Notonectinae and Anisopinae. To the former belong *Notonecta*, *Enithares* Spinola, *Aphelonecota* Lansbury, *Neonychia* Hungerford, *Nychia* Stål, and *Martarega* White. The remaining three genera, *Paranisops* Hale, *Anisops*, and *Buenoa* are placed in the Anisopinae. Lansbury (1965, 1968) and Poisson (1966) included keys to genera and higher categories. The Anisopinae possess a "pit" at the anterior end of the hemelytral commissure while this structure is absent in the Notonectinae. Poisson (1926) considered this structure a sensory organ, at least in *Anisops producta* Fieber. Staddon and Thorne (1974) suggested that another difference between the two subfamilies is the apparent absence in the Anisopinae of metathoracic scent glands. These are present in the Notonectinae. Only three genera of notonectids, *Notonecta*, *Buenoa* and *Martarega* are found in North America. *Notonecta* and *Buenoa* occur throughout the United States and are the only genera represented in California (with a total of 10 species). In the United States *Martarega* is confined to Arizona.

Notonectids are excellent swimmers and occur in a variety of freshwater habitats. For the most part they prefer the quiet waters of pools and lakes but a few are more frequently found in creeks. Streams and Newfield (1972) found that although several New England species of *Notonecta* occurred together in the same habitat that each species tended to occupy a different microhabitat (shallow vs. deep water, sunny vs. shady locations, cold vs. warm water, for example).

Adults may be found during every month of the year in California but are most abundant from midsummer through fall. All of our species fly and most have been collected at light traps. Several North American species of *Buenoa* and *Martarega*, however, are known primarily from brachypterous specimens, the macropterous forms being found infrequently. Among California notonectids *Buenoa scimitra*, *B. omani*, and *Notonecta shooteri* are frequently brachypterous.

All members of the family are predaceous, feeding generally on small aquatic arthropods but occasionally they overpower and feed on small fish and other aquatic vertebrates. Prey are grasped with the first and second pairs of legs. Predatory strategies differ among *Notonecta*, *Buenoa*, and *Martarega* (Gittelman, 1974b). The first two live in static water waiting for free-moving prey to come near. *Notonecta* species hang from the surface film with their hindlegs poised forward ready to dart after approaching prey or insects entangled in the surface film. *Buenoa* are also active predators but they hover in almost perfect equilibrium with the water, below the surface film. *Martarega* species, on the other hand, inhabit eddies of rivers where there is slight current, and swim constantly at or near the surface, maintaining their position in the current with little difficulty. Unlike the other two genera, *Martarega* is a sedentary predator and waits for the current to bring helpless prey, trapped by water, to it.

The biology of the Notonectidae was studied in detail by Hungerford (1920). McPherson (1965-1967) reported on the California species, *Notonecta hoflmani* Hungerford. Most species overwinter as adults although some
overwinter in the egg stage. Rice (1954) found that the *Notonecta* and *Buenoa* of the Douglas Lake area of Michigan vary considerably in the overwintering stages. Some overwinter as eggs only, some as adults only and the rest as both eggs and adults. Oviposition however, generally occurs during spring and early summer in the United States. In England, Walton (1936) found that four species of *Notonecta* generally oviposit during the winter and early spring. Usually eggs are laid in or on aquatic vegetation, but those of *Notonecta* are often found on the surface of rocks and submerged debris. *Notonecta* and *Buenoa* eggs are generally yellowish white when first deposited and elongate-oval in shape. The incubation period and number of generations per year vary with the species and climate. So far as known there are five nymphal instars.

During his early biological studies Hungerford (1922c) discovered hemoglobin in *Buenoa margaritacea* Torre-Bueno. His student Bare (1928) gave much more detail on this interesting subject. Miller (1964, 1966) presented evidence clearly indicating that the hemoglobin in *Buenoa* and its Old World counterpart *Anisops*, functions in enabling the insect to maintain approximate neutral buoyancy during much of its subsurface activity. As Miller pointed out, the Anisopinae have thus gained a significant evolutionary advantage in being able to exploit the midwater zone which is not readily available to other aquatic insects (except certain nematoceran larvae).

Hungerford (1924b) discovered that during courtship prior to mating in *Buenoa*, a high-pitched chirping sound is made by the male. Hungerford originally noted this for *B. limnocastoris* Hungerford. More recently it has been recorded for *B. scimitra* Bare by me (unpublished notes), and for several species by Wilcox (1969), and studied in detail by Wilcox for *B. macrotibialis* (1975). Three stridulatory mechanisms responsible for the production of sound by male *Buenoa* were proposed by Bare (1928): (1) tibial comb: rostral prong (2) femoral ridge: coxal peg (3) femoral apex: base of beak. Wilcox (1975) experimented with the first two mechanisms because of their obvious specializations as stridulatory structures. He found that *B. macrotibialis* males produced at least four acoustic signals during courtship (i.e., trills, chirps, dart-chirps and grasping-chirps) and three non-courtship behavior signals (i.e., disturbance-chirps, cleaning-chirps, and capture chirps). Wilcox noted that the precopulation signals of *Buenoa* are species specific and suggested that these signals function in sexual stimulation and reproductive isolation. The frequency spectrum of acoustic signals in, at least *B. macrotibialis*, is generated by resonation and not by rate of stridulation. During my revisionary stud-

KEY TO NEARCTIC GENERA OF NOTONECTIDAE

1. Hemelytral commissure with an elliptical pit at anterior end; antenna three segmented (fig. 277) .......................................................... (Anisopinae)

   *Buenoa* Kirkaldy, p. 145

2. Hemelytral commissure without a pit; antenna four segmented (Notonectinae) ..........................................................

KEY TO NYMPHS OF CALIFORNIA GENERA

(From Usinger, 1956)

Abdominal spiracles large, oval, about 1/4 as long as segments, located medially on ventral hair fringe; hindlegs without rows of conspicuous, stout spines .................................... *Buenoa* Kirkaldy

Abdominal spiracles small, round, less than 1/10 as long as segments; hindlegs with rows of short, stout, black spines. ....

*Notonecta* Linnaeus

Subfamily Notonectinae

Genus *Notonecta* Linnaeus


Type-species: *Notonecta glauca* Linnaeus, 1758, designated by Latreille, 1810.

Hungerford (1933) cites Lamarck (1801) as having designated the type species for *Notonecta*, however, there is no evidence in Lamarck’s paper of such action.

Members of this genus are robust in appearance and are readily separable from *Buenoa* in lacking the elliptical pit at the anterior end of the hemelytral commissure. The parameres (claspers) are symmetrical in *Notonecta*, but asymmetrical in *Buenoa*. The color patterns in *Notonecta* are often striking, but in many cases are quite variable within the species. Certain forms, *N. shooterii* for example, exhibit bichromatism within individuals of the same population.

*Notonecta* is cosmopolitan and contains approximately 65 species. Seven species (discounting a doubtful record for *N. ochrothoe* Kirkaldy) are known from California. Hungerford (1933) revised the genus. He recognized five subgenera, three of which occur in the state. The seven species of California *Notonecta* are distributed in these subgenera as follows: *Paranecta* with *kirbyi*, *undulata*, *indica*, *unifasciata*, *spinosa*; *Bichromonecta* with *shooterii*; *Erythronecta* with *hoffmani*.

**KEY TO NOTONECTA OF CALIFORNIA**

1. Keel of 4th abdominal sternum bare, hairs confined to sides
   - Keel of 4th abdominal sternum not bare.
   2. Head broad, 5/6 as wide as pronotum; eyes large, rear width of one eye as great as length of lateral margin of pronotum; scutellum 1/2 again as broad as long... *hoffmani* Hungerford
   - Head narrower, 2/3 as wide as pronotum; eyes smaller, rear width distinctly less than length of lateral margin of pronotum; scutellum less than 1/4 broader than long... *kirbyi* Hungerford

3. Pronotum longer than scutellum; males with a stout tubercle at angle of fore trochanter; bichromatic, one form dirty white, the other black, marked with white
   - *shooterii* Uhler
   - Pronotum shorter than scutellum; males without a tubercle on fore trochanter.

4. Trochanter of middle leg rounded or nearly so (fig. 269)
   - Trochanter of middle leg distinctly angulate or produced into a tooth or stout spinelike process (figs. 270-271)

5. Lateral margins of pronotum distinctly, though shallowly, concave; length 10-11 mm; last abdominal sternum of female scarcely or shallowly notched at tip, the notch wider than deep; anterior trochanter of male with large conspicuous hook... *indica* Linnaeus
   - Lateral margins of pronotum straight; length usually larger, 11-12 mm; last abdominal sternum of female with an apical notch which is deeper than wide; anterior trochanter of male with small to moderate size hook (fig. 268) (in an occasional specimen, hook is large)... *undulata* Say

16. Modified from Usinger (1956). Excludes *N. ochrothoe* Kirkaldy because California record is doubtful.
6. Middle trochanter angulate or produced into a short tooth at inner posterior angle (fig. 270). unifasciata Guérin-Méneville Middle trochanter produced into a long, spinose process (fig. 271). spinosa Hungerford

KEY TO FIFTH INSTAR NYMPHS OF CALIFORNIA NOTONECTA

1. Midventral carina of 4th abdominal segment largely bare. 
   carinal hairs confined mostly to the sides of the carina . . . . 2
   No bare area on carina, entire area covered with long or short 
   hairs ............................................................................. 5
2. Midfemur with at least six long setae (those on the most proximal 
   tubercle counted as one) ............................................. kirby
   Midfemur with less than six setae .................................. 3
3. Midfemur with only two setae; eyes prominent; dark, conspicu-
   ous striping on mid and hind femora and trochanters . . . . . . . hoffmani
   Midfemur with three large and two small setae; striping re-
   stricted to the hind femora if present ................................ 4
4. Anterior aspect of vertex flattened ..................................... indica
   Anterior aspect of vertex rounded .................................... unifasciata
5. Large, over 8 mm long; posterior angle of midtrotchanter 
   rounded ................................................................. shooterii
   Small, less than 8 mm long; midtrotchanter acutely rounded or 
   toothed .............................................................................. 6
6. Posterior end of midtrotchanter produced into tooth or stout 
   tubercle ............................................................................. spinosa
   Middrotchanter acutely rounded, but not toothed .............. unifasciata

Notonecta (Bichromonecta) shooterii Uhler

Syntypes (destroyed): near San Diego, California (originally CAS).

A single male specimen extant in the CAS and taken at San Jose del Cabo by G. Eisen was referred to by Uhler but not included in the type series.

Notonecta shooterii is a bichromatic species. One form is pale luteous while the other is black with white or pale luteous markings. The pale forms have the flight wings reduced accompanied by a reduction in the prominence of the humeri and in the size of the scutellum. These two forms are found within the same populations with the pale form usually predominating. The subgenus Bichromonecta was established by Hungerford (1933) as a taxon to incorporate the several species that exhibit bichromatism.

Geographic range. Coos County, Oregon, south through California to Baja California, Mexico.

California records (map 53). This species is common in and around the Coast Ranges from San Diego County to Marin County. I have seen records from as far north as Humboldt County and presumably the species occurs along the coast to Oregon. Notonecta shooterii is known from two isolated locations in the eastern side of the state:


BULLETIN OF THE CALIFORNIA INSECT SURVEY

Notonecta (Erythronecta) hoffmani Hungerford

Notonecta hoffmani Hungerford, 1925, Can. Entomol. 57:241. Syn-

types. Q, Q: Laguna Beach, California (KU).

Notonecta hoffmani Hungerford, 1933, Univ. Kans. Sci. Bull. 21: 
68. Invalid emendation (Art. 32(a)(ii.).

This species can be distinguished from others in California by its color pattern, which is relatively stable. The basic color is red-orange with a black scutellum and brown-black hemelytral membrane. The only other California species that approaches this color is kirbyi which has the distal half of the corium broken by two small light-colored spots. N. kirbyi is also more elongate.

Geographic range. California from Yolo County, south to northern Baja California and Arizona.

California records (map 54). Notonecta hoffmani is common in the southern coastal counties and it is also known from a few nearby desert localities. The species occurs in the Coast Ranges as far north as the San Francisco Bay region and in low elevation waters on both sides of the San Joaquin Valley. N. hoffmani has been collected every month of the year but most captures are between March and July, and during October. Females are most common during the winter months. The available ecological data indicate that N. hoffmani occurs from sea level to 9,000 feet.

Notonecta (Paranecta) indica Linnaeus


Notonecta americana Fabricius, 1775. Systema Entomologiac p. 690. 


This species is often confused with N. undulata. The color patterns of these two are so similarly variable, from pale luteous to nearly black (typically black and white), that color is not an aid in distinguishing them. N. indica can be separated from N. undulata by a large conspicuous hook on the anterior trochanter of males of the former, the shallow notch (wider than deep) on the last abdominal sternum of the female, and by the male genitalia.

Geographic range. Southern United States south of 35° latitude except east of Allegheny Mountains where it extends north to approximately 38°, south through Central America to Colombia and the West Indies.

California records (map 55). IMPERIAL CO.: nr. S. end' Salton
MAP 53. California distribution of Notonecta shooterii Uhler.

MAP 54. California distribution of Notonecta hoffmani Hungerford, solid circles; and N. spinosa Hungerford, open circles.

MAP 55. California distribution of Notonecta kirbyi Hungerford, solid circles; and N. indica Linnaeus, open circles.

Notonecta (Paranecta) kirbyi Hungerford


This is the largest notonectid in California, ranging from 13 to 16 mm in length. The only other California species with which it might be confused is N. hoffmani because of their similar color (see discussion under N. hoffmani). An eastern species, N. insulata Kirby, is frequently confused with N. kirbyi.

Geographic range. Western United States and Canada.


This is one of the few species of Notonecta common to both North and South America. In California, N. indica is restricted to the Imperial Valley and waters associated with the Colorado River.
and Colorado Deserts, although it is found in a few isolated desert waters.

**Notonecta (Paranecta) spinosa** Hungerford  
(Fig. 271)


This species is readily separated from all other species by the spinose mesotrochanter.

**Geographic range.** British Columbia, Canada, and western United States.


In California *N. spinosa* is known only from the Owens Valley, the Great Basin, and adjacent areas.

**Notonecta (Paranecta) undulata** Say  
(Figs. 268-269)

Notonecta undulata Say, 1832, Descriptions New Species Heteroptera North America, New Harmony, Indiana, p. 39 (Fitch reprint, 1858, Trans. N.Y. State Agric. Soc. 17:812). Types lost, "Missouri & Indiana." Hungerford (1933) designated a lectotype for *N. undulata* from material in the Harris Collection (now at MCZ) that was identified by Say, but the designation was invalid. The material in the Harris Collection was sent to Say for determination and did not contain Say types (see Weiss & Ziegler 1931 and Johnson, 1925).


This species is frequently confused with *N. indica* (see comments under *N. indica*), and other North American species with similar black and white patterns. The rounded mesotrochanter of *undulata* separates it from *unifasciata* and *spinosa*, which have angulate to spinose mesotrochanters. The small to moderate size of the hook on the anterior trochanter of the male (in occasional individuals the hook may be considered large) and the deep, narrow notch in the last abdominal sternum of the females separate it from *indica*.

**Geographic range.** Throughout North America and into northern Mexico.

*California records* (map 56). Notonecta undulata is widespread in California north of 37° latitude, but only two records are known for the southern part of the state: Calipatria (KU) and Moulton Ranch, east of Laguna Beach (LACM). The species has been collected from April to December, but most commonly in the summer. It has been taken at elevations ranging from near sea level to 8,000 feet.

Much has been written on the biology of this common backswimmer. Hungerford (1920) describes in detail the habitat, hibernation, mating, oviposition, incubation, hatching and behavior of newly hatched, food habits, and life history from egg to adult.

**Notonecta (Paranecta) unifasciata** Guérin-Méneville  
(Figs. 270, 272)


Notonecta indica of authors, not Guérin-Méneville.

*Notonecta unifasciata* superficially resembles three other California backswimmers, *N. spinosa*, *N. undulata*, and *N. indica*. The characters presented in the key (and notes under *N. undulata*) should serve to separate these species.

Hungerford (1933) divided this species into four sub-
species on the basis of variations in the shape of the male genital clasper, mesotrochanter, and the vertex. Usinger (1956) pointed out, that except for a series of typical *N. unifasciata* taken on Santa Catalina Island (Los Angeles Co.), California specimens pertain to *N. andersoni*.

**Geographic range.** Western Canada, western United States, and Mexico.

**California records** (map 57). *Notonecta unifasciata* is widespread in the state although no material from the northwestern counties has been seen. The species has been taken during every month of the year, but most captures are between April and October. *N. unifasciata* exhibits a wide range of tolerance to its aquatic medium. It has been collected in saline pools (Francis Lake near Tecopa and Saline Valley, Inyo Co.) as well as from hot springs and ponds with temperatures as high as 97.3°F.

**Subfamily Anisopinae**

**Genus Buenoa Kirkaldy**

*Buenoa Kirkaldy*, 1904, Wiener Entomol. Ztg. 23:120. Type-species: *Buenoa antiqua* (Kirkaldy), 1899, original designation.

Members of this genus are long and slender, and they are readily distinguished from *Notonecta* in possessing an elliptical pit at the anterior end of the hemelytral commissure, asymmetrical parameres, and stridulatory structures on the rostrum and front tibia of the male. Color patterns are of no great aid in distinguishing species, and bichromatism and brachyptery within species adds to the confusion. Generally, females, which lack the rostral prong and foretibial stridulatory apparatus found in the males, can only be identified by association with males.

*Buenoa* is a New World genus and is best developed in tropical South America where about 30 species are recorded. The genus embraces a total of 45 species. Although 15 species are recorded for the United States, including one described (Reichart, 1971) since my revision (Truxal, 1953), California has only four, one of which is doubtfully present.

**KEY TO BUENO A OF CALIFORNIA**

Based on Males

1. Forefemur with less than 5 (usually 4) sclerotized ridges in stridulatory area (fig. 273) ........................................ *omanii* Truxal
   Forefemur with 15 or more sclerotized ridges in stridulatory area (figs. 274-276) .................................................. 2

2. Forefemur with long, conspicuous, swordshaped stridulatory area consisting of approximately 60 fine sclerotized ridges (fig. 274) ........................................ *scimitra* Barel
   Forefemur with less than 30 (usually 15 to 25) sclerotized ridges in stridulatory area ........................................ ..... 3
Buenoa omani Truxal
(Fig. 273)


This is the only California species that can generally be recognized by its color. Usually B. omani is nigrovioletaceous and the scutellum is black except for a yellow to orange apex and lateral margins. Rarely, a pale, sordid white form is encountered. The other three California Buenoa are basically sordid white.

**Geographic range.** Southern California south to Chiaspas, Mexico.


In California, B. omani is found only in the Coast Ranges and environs from Monterey County to San Diego County. It is uncommonly collected and nothing is known of its biology.

**Buenoa scimitra Bare**
(Figs. 274, 277)


**Buenoa scimitra** superficially resembles two other California species, B. margaritacea and B. uhleri. It is readily distinguishable from these two by the large sword-shaped stridulatory area on the inner face of the male forefemur. This species varies considerably in size and color. In general facies it is sordid white to fuscus.

**Geographic range.** Widespread in the southern United States, also Mexico and the West Indies.

**California records (map 59).** Buenoa scimitra is the most common species of the genus in California, and it is found in the Coast Ranges and environs from Sonoma County to San Diego County. It also occurs around the Central Valley, including the Sierran foothills, and in the Imperial Valley and along the Colorado River. It has also been taken at isolated Sheep Creek Spring near the southern end of Death Valley.
Buena scimitra exhibits a considerable range of tolerance to extremes of temperature. It has been collected in Douglas County, Kansas, in ice-covered ponds during December where the air temperature was 30°F. and in the shallow outlet of Sheep Creek Spring, California, during July with air temperatures recorded at 131°F.

Buena uhleri Truxal
(Fig. 276)


Although this species superficially resembles B. margaritacea, the key characters should serve to identify it. In general it is more robust than other California Buena, particularly in the thoracic area.

Viewing the black abdominal terga through the transparent wings gives this species an over-all gray appearance.

Geographic range. Southern California, Texas, and Mexico.


Buena uhleri is primarily a Mexican species which extends into southern Texas and California. Perhaps the California record should be regarded as doubtful until the Needham localities can be absolutely confirmed. Further collecting should reveal its presence in Arizona and New Mexico if the species really exists in California.

FIG. 277. Buena scimitra, male, dorsal view (from Usinger, 1956).
Alayo, P.


Ancona, L.


Andersen, N. M.


Applegate, R. and R. Kieckhefer


Bacon, J. A.


Börner, C.


Brindley, M. D.


Brinkhurst, R. O.


Brown, E. S.

1948. The ecology of Saldidae inhabiting a salt marsh,


Burdick, D. J.


Butler, E. A.


Calabrese, D.


China, W. E. and R. L. Usinger


China, W. E., R. L. Usinger, and A. Villiers


Cloarec, A.


Cobben, R. H.


Constantza, G.


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Pierce, W. D.
Poisson, R.
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Polhemus, J. T. and J. L. Herring

Porter, T. W.


Radinovsky, S.

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Rees, A. and R. Offord

Reichart, C. V.

Reuter, O. M.


Rice, L. A.

Rigger, C.

Riley, C. F. C.


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Rimes, G. D.


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Truxal, F. S.

Uhler, P. R.

Usinger, R. L.

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Wilcox, R. S.


Wiley, G. O.

Williams, F. X.

Wilson, C. A.

Wroblewski, A.

Young, E.


Index

(Synonyms in italics, main page references in bold face)

Generic and subgeneric names

Abedus Stal, 4, 6, 83, 110
Acanthia Fabricius, 23
Aciyturus La Rivers, 134
Aepophilus Signoret, 16, 17, 18
Allosigara Hungerford, 117
Ambrymus Stal, 10, 134
Amorgius Stal, 79
Amphischizops Montandon, 72
Anchornella Poisson, 52
Anisops Spinola, 139, 140
Annulovelia Poisson, 52
Anticorixa Jaczewski, 110
Antisigara Jaczewski, 117
Aphelocheirus Westwood, 10, 13, 131, 132
Aphelonecta Lansbury, 139
Aphelosigara Hungerford, 117
Aquarius Schellenberg, 61
Arcicallicorixa Soos, 117
Arctosigara Hungerford, 117
Baecula Stal, 55
Basileocorixa Kirkaldy, 117
Belostoma Latreille, 4, 80, 83
Belostomum Burmeister, 80
Benacus Stal, 79
Bichromonecuta Hungerford, 141, 142
Buenos Kirkaldy, 141, 145
Calacanthia Reuter, 18, 19, 21
Callicorixa White, 109, 112
Catacarctopus Usinger, 132
Cenocorixa Hungerford, 8, 109, 112
Cercotmetus Amyot & Serville, 4, 70
Charalamptra Torre-Bueno, 33
Cheirochela Hope, 132
Chepuvelia China, 46
Chiloanthus Reuter, 19, 20
Corallocoris Cobben, 16
Corisella Lundblad, 7, 103, 109, 118
Cryphocricos Signoret, 10, 132, 133
Curicta Stal, 72
Deinostoma Kirkaldy, 83
Diaprepocoris Kirkaldy, 87, 88
Dyocytalus La Rivers, 133
Enallopsal Polyphemus, 19, 20
Enithares Spinola, 139
Enitharonecta Hungerford, 140
Eremocorixa Jaczewski, 117
Erythronecta Hungerford, 141
Euratus Distant, 66
Fabatus Distant, 66
Fieberia Jakowleff, 40
Galgulus Brisson, 127
Galgulus Latreille, 127
Gelastocoris Kirkaldy, 127, 129
Gerriselloides Hungerford & Matsuda, 61
Gerris Fabricius, 7, 9, 61, 65, 66
Glossoapis Blanchley, 128
Graptoecorixa Hungerford, 93, 110, 112
Halicorixa Walton, 117
Halobates Eschscholtz, 7, 66, 68
Halovelia Bergroth, 58
Hebrovelia Lundblad, 49
Hebrus Curtis, 35, 37
Hebrusella Poisson, 35
Hermatobates Carpenter, 58
Hesperocorixa Kirkaldy, 93, 110
Heterocleptes Villiers, 43, 46
Hilliella China, 66
Horvathinia Montandon, 76
Husseyella Herring, 15, 51, 58
Hydrosa Burmeister, 51
Hydrometra Latreille, 45
Hygrotrichus Stal, 61
Iliastus Gistel, 79
Joscytus Reuter, 21, 22
Kallistometra Kirkaldy, 68
Kirkaldya Torre-Bueno, 51, 52
Kirkaldya Montandon, 79
Kotovelia Matsumura, 55
Lacotropheps Stal, 71
Lampracanthia Reuter, 18, 19, 21
Lamprotrichus Reuter, 66
Lasiosigara Hungerford, 117
Leptosalda Cobben, 16
Lethocerus Mayr, 4, 7, 8, 79
Limnobates Burmeister, 45
Limnabatoides Hussey, 43
Limnecoris Stal, 131, 132, 133
Limnogeton Mayr, 4, 76
Limnognoides Poisson, 66
Limnogonoides Poisson, 66
Limnogonus Stal, 61, 66
Limnotrochus Stal, 61
Lipogomphus Berg, 37
Macrosaldula Southwood & Leston, 23, 24
Macrovelia Uhler, 46, 47
Madevelia Poisson, 39
Martaega White, 140
Matina Stal, 128
Megaecherus Jaczewski, 124
Merragata White, 37
Mesovelidae Multus & Ray, 6, 7, 40
Mesoveloeidea Hungerford, 39
Metrobates Uhler, 67, 68
Micractanthis Reuter, 21, 22
Mieroabedus Hussey & Herring, 83
Micronecta Kirkaldy, 88
Microsigara Poisson, 117
Microvelia Westwood, 4, 8, 9, 51
Monomyx Laporte, 128, 129
Montandonista Kirkaldy, 79
Montandonius Melin, 127
Naegeus Laporte, 35
Nasicorixa Stichel, 117
Neogerris Matsumura, 61, 66
Neonychia Hungerford, 139
Neorhagovelia Matsumura, 55, 56
Neovelia White, 55
Nepa Linnaeus, 72
Nerthra Say, 127, 128
Notonecta Linnaeus, 4, 140, 145
Nyctia Stal, 139
Ocellovelia China & Usinger, 46, 49
Ochterus Latreille, 124
Ochterus Agassiz, 124
Ochterus Bergroth, 124
Ochterus Bergroth, 124
Ochterus Bergroth, 124
Ocyochterus Drake & Gomez-Menor, 124
Omania Horvath, 16
Oravelia Drake & Chapman, 7, 46, 47
Parabedus De Carlo, 83
Paracorixa Stichel, 117
Paralosa!da Polhemus & Evans, 20
Paranecta Hutchinson, 141
Paranisos Hale, 139
Paraphrynoveniia Poisson, 39
Parasgara Poisson, 117
Paratismasiellus Poisson, 35
Paratismaius Poisson, 35
Paravelia Breddin, 51
Pedinocoris Mayr, 83
Pediosigara Hungerford, 117
Pelachoris Drake, 20
Pelocoris Stal, 133
Peleogonous Laterreille, 124
Peltoperus, Guerin-Meneville, 128
Pentacora Reuter, 20
Pervelia Poisson, 52
Perthostoma Leidy, 81
Phaeosigara Hungerford, 117
Phintius Stal, 128
Picaultia Distant, 51
Picrops La Rivers, 134
Pileosigara Hungerford, 117
Pseudoabedus De Carlo, 83
Pseudocallicorixa Soos, 117
Pseudoverrucaria Jaczewski, 117
Ranatra Fabricius, 72
Rastielovelia Poisson, 52
Retrocorixa Walton, 117
Rheumatobates Bergroth, 61
Salda Fabricius, 19, 21, 31, 33
Salidoia Osborn, 19, 21
Salonia Popov, 16
Saldula Van Duze, 16, 19, 21, 22, 23
Salduncula Brown, 21
Scidoperus Amyot & Serville, 31
Scylaus Stal, 128
Selcorixa Walton, 117
Serphus Stal, 83
Sigara Fabricius, 109, 112, 117
Speoevelia Esaki, 39
Staromulineria Poisson, 52
Stenocyctus Mayr, 83
Stephania Leseur, 68
Stephania White, 68
Stridulivelia Hungerford, 51
Subhebrus Poisson, 35
Subsigarla Stichel, 117
Syncollus La Rivers, 134
Teloeluea Reuter, 19, 21, 32
Timasielloides Poisson, 35
Trepobates Uhler, 68
Trepobatopsis champion, 67
Trichocorixa Kirkaldy, 98, 104, 118
Trichocorixa Hungerford, 52
Trochosop Carpenter, 9, 15, 51, 55
Tropocorixa Hutchinson, 117
Usingena La Rivers, 131, 132
Velia Laterreille, 9, 51
Velomorpha Carlini, 51
Velohebraria Stys, 49
Vernicorixa Walton, 117
Xenosigara Hungerford, 117
Xipho!voeloidea Hoferlandt, 51
Zaitha Amyot & Serville, 81

SPECIES AND SUBSPECIES NAMES

abdominalis (Say), Graptocorixa, 93, 96, 97, 98
acapulcana Drake & Chapman, Hebrus, 37
acuminata (Uhler), Ramphocorixa, 88
aestivalis (Fabricius), Aphelocheirus, 132
alaepennis (Reuter), Saldula, 28
alpina (Scopoli), Saldula, 30
amargosus La Rivers, Ambyrus, 138, 138
amargosus La Rivers, Pelocoris, 134
americana Fabricius, Notonecta, 142
americana Montandon, Ranatra, 73
americana (Uhler), Microvelia, 50
americana Uhler, Microvelia, 54
americana (Leidy), Lethocerus, 79
amnicus Drake & Chapman, Hebrus, 35
amoauhla Uhler, Mesovelia, 41
andersoni Hungerford, Cenocorixa, 113
andersoni Hungerford, Notonecta, 144
andre Drake, Saldula, 25
angulata Hungerford, Notonecta, 144
angustipes (Mayr), Lethocerus, 2, 79, 83
annulipes (Herrich-Schaeffer), Letho-
ceru, 76
antigone (Kirkaldy), Buenoa, 145
arenici!au (Scholz), Saldula, 24, 26
arizonensis Gould, Rhagovelia, 56
audeni Hungerford, Callicorixa, 109
aurantiacum (Leidy), Belostoma, 82
australis La Rivers, Ambyrus, 136
australis Say, Hydrometra, 45
austrina Torre-Bueno, Microvelia, 50
bakeri Montandon, Belostoma, 81, 82, 83
balli Drake, Saldula, 26, 31
banki Barber, Ochterus, 124
barberi Schell, Ochterus, 125
barberi Torre-Bueno, Gelastocorix, 128
basingeri Drake, Saldula, 26
bassingeri Drake, Saldula, 26
beamer McKinstry, Microvelia, 53
becki Drake & Harris, Trepobates, 68
bellatrix (Torre-Bueno), Teleleuca, 33
bifasciata (Thomson), Teleleuca, 33
bifida (Hungerford), Cenocorixa, 113
bifoveatum (Haldeman), Belostoma, 81
bisignata Uhler, Mesovelia, 42
blackburni (White), Trichocorixa, 101
blaisdelli (Hungerford), Cenocorixa, 113, 115, 117
bohartorum Usinger, Ambyrus, 136
borealis Torre-Bueno, Microvelia, 53
boucherviellei Provancher, Salda, 32
boucherviellei (Provancher), Saldula, 17
brachonyx (Mayr), Aedus, 85
breviceps Stal, Aedus, 85
brevicollis Montandon, Ranatra, 73, 74
brevis Champion, Merragata, 38
brimley (Kirkaldy), Hesperocorix, 110
brunea Drake, Merragata, 34
buonoi Drake & Harris, Hebrus, 36
buonoi Drake, Microvelia, 53
buonoi Kirkaldy, Gerras, 63
buonoi (McDunnough), Salda, 32
burmeisteri Lethierry & Severin, Hebrus, 34
burmeisterii (Fiebet), Trichocorixa, 101
cady Gould, Rhagocorix, 56
c-album (Fiebet), Saldula, 26
californica (Hungerford), Graftocorixa, 96, 97, 98
californica Sailer, Trichocorixa, 102, 103
californicus Montandon, Ambyrus, 135
californiensis McKinstry, Microvelia, 54
californiensis Melin, Gelastocorix, 128
caloregon Calabrese, Gerras, 63
calva (Say), Trichocorixa, 101, 102, 103
canadensis Walley, Callicorixa, 109
canaliculatus (Say), Limnopus, 65
capitata Guerin-Meneville, Microvelia, 53
caprai Tamanini, Velia, 50
caraiba Jacezewski, Mesovelia, 42
carolinensis Torre-Bueno, Pelocoris, 131
cerifera McKinstry, Microvelia, 53
caron Kirkaldy, Notonecta, 144
chinensis Mayr, Ranatra, 71
choreutes Hussey, Rhagovelia, 56
cimicoides (Linnaeus), Ilyocoris, 13, 132
cobbeni Polhemus, Iosscytus, 22
INDEX

cochisiana Hungerford, Notonecta, 144
coloradensis Polhemus, Salda, 18
columbiensis Lansbury, Cenocorixa, 113
comata Parshley, Saldula, 27
comata Parshley, Saldula, 27
connexus Uhler, Hebrus, 35, 36
disfluens (Reuter), Saldula, 29
distifusus Lauck, Belostoma, 81, 82
distincta (Westhoff), Saldula, 30
dolomedensis Hungerford, Mesovelia, 41
dowesi Lansbury, Cenocorixa, 113
dumetula Montandon, Ranatra, 73
dulis Distant, Microvelia, 50
dimidia (Curtis), Saldula, 29
dispersa (Uhler), Corisella, 104
dispersa (Uhler), Saldula, 26
dissortis (Drake & Harris), Limnoporus, 65
distincta Champion, Rhagovelia, 56
distincta (Westhoff), Saldula, 30
douglasensis Hungerford, Mesovelia, 41
dowesi Lansbury, Cenocorixa, 113
dumetula Montandon, Ranatra, 73
dulis (Champion), Corisella, 104, 107
demasticum Latreille, Belostoma, 81
d excellentis Drake & Harris, Rhagovelia, 56
expana (Uhler), Saldula, 27, 29
fakir (Gistel), Lethocerus, 77, 79
femorata (Guerin-Meneville), Krizozas-
corax, 88
femoratus (Palisot de Beauvois), Pel-
coris, 131, 132, 133
fennica Reuter, Micracanthia, 23
fernaldis Drake, Saldula, 24, 27, 29
fieberi Mayr, Lymnogeton, 76
flavicosta Reuter, Isocyclus, 22
fluineum Say, Belostoma, 6, 82
formosanus (Matsumura), Ochterus, 124
foveata Drake, Merragata, 38
franciscanus (Drake), Isocyclus, 22
franciscanus (Stal), Limnonogus, 66
funereis La Rivers, Ambrus, 2, 134, 138
furcata Mulsant & Rey, Mesovelia, 40
furvis Polhemus & Chapman, Hebrus, 36
fusca Palisot de Beauvois, Ranatra, 73
fusca (Mulsant & Rey), Mesovelia, 40
fuscinum (Dufour), Belostoma, 81, 82
 gamma (Fieber), Saldula, 26
gerhardi Hussey, Microvelia, 54
gilletti Lethierry & Severin, Gerris, 64
glauc Linnaeus, Notonecta, 140
griseus (Say), Lethocerus, 79
grossolineata Hungerford, Sigara, 118, 119, 122, 123
guerini (Lethierry & Severin), Limno-
gonus, 66
harmonia Goulder, Rhagovelia, 56
hebridus White, Merragata, 37, 38
heidelmanni La Rivers, Ambrus, 136
heberi Hidalgo, Abenus, 84
hesione (Kirkaldy), Neogerris, 61
hesperius Uhler, Metrobates, 67
hinei Drake, Microvelia, 53
hirsuta (Reuter), Saldula, 30
hoffmani Hungerford, Notonecta, 142, 143
hoffmanni Hungerford, Notonecta, 142
hornii Uhler, Macrovelia, 47
howardii Torre-Bueno, Notonecta, 142
hubbardi Porter, Hebrus, 36, 37
humilis (Say), Micracanthia, 22, 23
impressa (Haldeman), Lethocerus, 79
incasoi Poisson, Limnonogus, 66
incerta (Kirby), Microvelia, 53
incognitus Drake & Hottes, Gerris, 64
inconstans (Distant), Saldula, 29
incurvatus Drake & Hottes, Gerris, 61,
64
indentatus (Haldeman), Abenus, 85
indica Linnaeus, Notonecta, 142, 144
infuscatus Usinger, Metrobates, 68
inscripta (Uhler), Corisella, 104, 109
insulata Kirby, Notonecta, 143
interstilialis (Say), Saldula, 29
irregularis (Westhoff), Saldula, 30
kirbyi Hungerford, Notonecta, 142, 143
kuiterti Hungerford, Corisella, 113, 115, 116, 117
lacustris (Linnaeus), Gerris, 61
laevigata (Uhler), Hesperocorixa, 111, 112
laticollis (Reuter), Saldula, 29
laviniae (Hodgden), Saldula, 25
illianis Torre-Bueno, Hydrometra, 45
limbosa Horvath, Saldula, 29
limnocastoris Hungerford, Buenoa, 140
lindbergi Poisson, Merragata, 38
linearis (Linnaeus), Ranatra, 72
ligiogius (Dufour), Lethocerus, 79
litoralis (Linnaeus), Salda, 31
lucitiosa (Stal), Saldula, 28
lucitosa (Westhoff), Saldula, 29
lugubris (Say), Salda, 19, 32
lutatarium (Stal), Belostoma, 81
lutzi La Rivers, Limnocorix, 133
macgregori Kirkaldy, Microvelia, 50, 51
macronyx (Mayr), Abenus, 85
macrotibia Hunterford, Buenoa, 140
maculata (Latrelle), Saldula, 30
maculatus Fabricius, Naucoris, 132
major Champion, Hebrus, 35, 37
malikini Hungerford, Cenocorixa, 113
manni Todd, Nerthra, 126
margaritacea Torre-Bueno, Buenoa, 146
margaritacea Torre-Bueno, Buenoa, 147
marginalis (Fallen), Micracanthia, 22
marginata (Morvan), Saldula, 29
marginatus (Guerin-Meneville), Limnon-
gonus, 66
marginatus (Latrelle), Ochterus, 124
marginatus Say, Gerris, 61, 66
marginella (Herrich-Schafer), Micra-
canthia, 22
marginella (Puton), Saldula, 28
mariae Champion, Trichocorixa, 101
mariantarum Usinger, Halovelia, 50
martini Kirkaldy, Hydrometra, 45
martini Todd, Nerthra, 129, 130
maximus De Carlo, Lethocerus, 77
mayri De Carlo, Abenus, 85
mazza De Carlo, Lethocerus, 77
mckinstryi Hungerford, Sigara, 118, 119,
121, 122, 123
medius (Guerin-Meneville), Lethocerus, 79
mercenario (Say), Corisella, 88, 103
meridionalis Jaczewski, Mesovelia, 42
mexicana de la Llave, Ahuautlea, 88
mexicana Signoret, Rhagovelia, 56
mexicana (Van Duzee), Enalosalda, 18
mexicanus Eschscholtz, Halobates, 66
minor La Rivers, Ambrus, 136
moapensis La Rivers, Usingerina, 132
modesta Gould, Rhagovelia, 56
mormon Montandon, Ambrus, 136,
137
mulsanti White, Mesovelia, 41
myrae Torre-Bueno, Hydrometra, 45
nasti Drake & Hottes, Isocyclus, 22
nearcticus (Kelton), Limnoporus, 65
nepaeformis (Fabricius), Nerthra, 126
nevadensis (Walley), Sigara, 118
nigrescens Cobben, Saldula, 26
nigricans (Burmeister), Rhagovelia, 55
nigricans Cobben, Saldula, 28
nigripes Wagner, Saldula, 26
nigrita Parshley, Saldula, 28
notabilis (Drake & Hottes), Limnoporus, 65
notalis Drake, Saldula, 27
nyctalis Drake & Hottes, Gerris, 61
obesa Uhler, Rhagovelia, 56
obscura Provancher, Saldula, 32
obscurella (Wagner), Saldula, 30
obscurus (Dufour), Lethocerus, 79
obscurus Polhemus & Chapman, Hebrus, 37
occidentalis La Rivers, Ambrysus, 136, 137
ocellata (Costa), Saldula, 29
ochrothoe Kirkaldy, Notonecta, 141
oculatus (Fabricius), Gelastocoris, 127, 128
omanis (Hungerford), Sigara, 104, 112, 118, 120, 123
omani Truxal, Buenoa, 146
opacipenizis Champion, Saldula, 29
opaca (Zetterstedt), Saldula, 28
opiparia Drake & Hottes, Saldula, 28
orba Stal, Gerris, 63
orbiculata (Uhler), Saldula, 30, 31
orobus Drake & Harris, Microvelia, 53
ornata (Stal), Pentacora, 20
orthocilia (Fieber), Saldula, 17
ourayi Drake & Hottes, Saldula, 29
ovatus Stal, Abedus, 83, 84
pallida Cobben, Saldula, 30
pallidula Cobben, Saldula, 26
pallipes (Fabricius), Saldula, 24, 26, 27, 29
paludicola Champion, Microvelia, 54, 55
palustris (Douglas), Saldula, 24, 27
parkeri Menke, Abedus, 85
pege Drake & Chapman, Oravelia, 47
pellucens (Fabricius), Teloleuca, 32, 33
pellucida (Geoffroy), Saldula, 29
pellucida (Gezee), Saldula, 29
pexa Drake, Saldula, 30, 31
picus (Herrich-Schaeffer), Trepobates, 68
piercei Porter, Hebrus, 36
platyemis (Fieber), Buenoa, 146
plumbeus (Uhler), Trochopus, 55
politus (Uhler), Jazzetus, 82
praestusa (Fieber), Callicorixa, 109
produca Fieber, Anisops, 139
productus Spinola, Gerris, 64
productus (Uhler), Gerris, 64
provancheri Kelton & Lattin, Salda, 32
proxima Gould, Rhagovelia, 56
pulchella Westwood, Microvelia, 51, 53
punctata Fieber, Notonecta, 144
puncticollis Stal, Ambrysus, 138
pusillus Van Duze, Micranthia, 23
pusillus (Fallen), Hebrus, 35
putoni (J. Sahlberg), Saldula, 28
pygmaea (Fieber), Trichocorixa, 98, 103
quadrimaculata (Champion), Micranthia, 23
remigis Say, Gerris, 63, 65
reptora (Uhler), Saldula, 29
reticulata (Guerin-Meneville), Trichocorixa, 101, 102, 103
reuteri Stichel, Saldula, 26
riparia Fallen, Salda, 33
riparia (Zetterstedt), Teloleuca, 33
rivale Torre-Bueno, Rhagovelia, 50, 56, 57
robusta Uhler, Microvelia, 53
robustus (Uhler), Gerris, 63
rotundatus Champion, Gelastocoris, 128
rubromaculata (Heideman), Pentacora, 21
rubrocephala Thomson, Hebrus, 35
rufoscutellata (Latreille), Limnoporus, 65
rugosa (Desjardins), Nerthra, 15
saltatorius (Linnaeus), Saldula, 30
saltoni Sailer, Trichocorixa, 101, 103
saragotae Cobben, Pentacora, 20, 21
saragota Menke, Belostoma, 2, 82, 83
scimitra Bare, Buenoa, 146
scutellaris Fieber, Notonecta, 142, 96
serrata (Hungerford), Saldula, 30
serrulata (Uhler), Graptocorixa, 93, 96, 97, 98
setipes Champion, Microvelia, 53
severini Harris, Saldula, 30
shooterii Uhler, Notonecta, 141, 142
shoshone La Rivers, Pelocoris, 134
sinalus Champion, Gelastocoris, 128
signata Uhler, Microvelia, 53
signoreti Stal, Ambrysus, 134
signoretii (Guerin-Meneville), Pentacora, 102
simulator (Reuter), Saldula, 26
slossoni Van Duze, Merragata, 38
soberinus Uhler, Hebrus, 36, 37
soberinus White, Halobates, 67
sonorenis Menke, Abedus, 84
spahelata (Uhler), Pentacora, 20, 21
spinoso Hungerford, Notonecta, 144
spinosus, (Rossi), Patapius, 1
stagnorum (Linnaeus), Hydrometra, 45
striata (Linnaeus), Sigara, 117
striola (Fieber), Neoplea, 1
styltica (Say), Nerthra, 128
subassimilis Blatchley, Gelastocoris, 128
tarsalis (Fieber), Corisella, 107
testaceopallidum Latreille, Belostoma, 80
testaceum (Leidy), Belostoma, 81
texcocana Iaczewski, Corisella, 107
thomasi Lauck, Belostoma, 81
torquata Champion, Microvelia, 54
tropicalis (Champion), Saldula, 29
trux (Torre-Bueno), Metrobates, 67
tuckahoanus Drake & Chapman, Hebrus, 35
tumida (Uhler), Corisella, 107
uhlieri (Hungerford), Graptocorixa, 96, 97, 98
uhlieri (Montandon), Lethocerus, 79
uhlieri Sailer, Trichocorixa, 101, 102, 103
uhlieri Truxal, Buenoa, 146, 147
uhleoroidea Hungerford, Graptocorixa, 96, 97
undulata Say, Notonecta, 142, 144
unifasciata Guerin-Meneville, Notonecta, 3, 144
usingeri Polhemus, Saldula, 31
usingeri Todd, Nerthra, 130
usingeri Wygodzinsky, Cryptostemma, 1
utahensis Drake & Hottes, Micranthia, 22, 23
utahensis (Hungerford), Clenocorixa, 113, 116
valentina Gould, Rhagovelia, 56
vallis Lauck, Sigara, 119, 121, 122, 123
dandyei Hungerford, Sigara, 119, 120, 121, 122
variegatus (Guerin-Meneville), Gelastocoris, 128
varionis Drake & Hottes, Saldula, 26, 31
verticalis (Fieber), Trichocorixa, 98, 101, 102, 103
villosa (Hodgden), Saldula, 31
vittata (Westhoff), Saldula, 30
vittigera Horvath, Mesovelia, 40
vulgaris (Hungerford), Hesperocorixa, 111, 112
vulnerata (Uhler), Callicorixa, 110
wallengreni (Stal), Trichocorixa, 101
washingtonensis Hungerford, Sigara, 118, 119, 121, 122, 123
watsoni (Drake), Paravelia, 50
westhoffi (Verhoeff), Saldula, 30
wileyae (Hungerford), Cenocorixa, 112, 113, 115, 117
wileyi (Hungerford), Cenocorixa, 117
yucatanica Hodgden, Pentacora, 20