

VOLUME 2

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# AMERICAN BEEETLES

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Polyphaga:  
Scarabaeoidea through Curculionoidea



ROSS H. Arnett, Jr. • Michael C. Thomas  
Paul E. Skelley • J. Howard Frank

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**Polyphaga:  
Scarabaeoidea through Curculionoidea**

Edited by  
the late Ross H. Arnett, Jr., Ph.D.  
Michael C. Thomas, Ph.D.  
Paul E. Skelley, Ph.D.  
and  
J. Howard Frank, D. Phil.



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**COVER FIGURES:** Center - Coccinellidae, *Harmonia axyridus* (Palles) [Photo by Fred J. Santana]. Outer rim, clockwise from top: Ripiphoridae, *Macrosiagon cruentum* (Germar) [by Fred J. Santana]; Meloidae, *Lytta magister* Horn [by Charles L. Bellamy]; Carabidae, *Rhadine exilis* (Barr and Lawrence) [by James C. Cokendolpher]; Melyridae, *Malachius mirandus* (LeConte) [by Max E. Badgley]; Lampyridae, *Microphotus angustus* LeConte [by Arthur V. Evans].

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To Ross H. Arnett, Jr.  
1919-1999

and

Mary Arnett  
1919-2002

# Preface

It has been nearly 40 years since Ross H. Arnett, Jr. published the first fascicle of *The Beetles of the United States: A Manual for Identification*. It quickly became an indispensable tool for professional and amateur coleopterists, general entomologists, and naturalists. Although there were four additional printings it has long been out of print and difficult to obtain. It was prepared to replace Bradley's *A Manual of the Genera of Beetles of America, North of Mexico*, which itself was some 30 years out of date in 1960. *American Beetles* is, in turn, designed to replace *The Beetles of the United States*. It is hoped that it will prove to be as useful as its predecessor.

Ironically, much of the preface to the original edition applies today as well as it did 40 years ago:

Many genera have since been described and reported within the area concerned, and many families have been revised. Extensive changes have been made in the family classification of the beetles of the United States during this period.

The aim of this series of fascicles is to provide a tool for the identification of adult beetles of the United States to family and genus with the aid of illustrations, keys, descriptions, and references to sources for keys and descriptions of the species of this area. All of the genera known to inhabit this area are included in the keys and lists of genera which follow.

The design and format of this work follow closely that of the original edition, but the way it was put together was quite different. Its predecessor was very much the work of one man, Ross H. Arnett, Jr. With a few exceptions (George Ball wrote the carabid treatment for both the 1960 edition and for this one), Dr. Arnett wrote the family treatments of *The Beetles of the United States*. Many specialists reviewed those chapters, but they were almost entirely Dr. Arnett's work.

When Dr. Arnett announced plans to prepare a work to replace *The Beetles of the United States*, coleopterists literally lined up to volunteer their time and expertise in preparing the family treatments. Ultimately, more than 60 coleopterists participated in the preparation of *American Beetles*. This has truly been a community project.

Due to the size of the ensuing work, *American Beetles* is being printed in two volumes. Volume 1 includes the introductory material, and family treatments for the Archostemata, Myxophaga, Adepaga, and Polyphaga: Staphyliniformia. The remainder of the Polyphaga and the keys to families appear here in Volume 2.

Sadly, although Dr. Arnett initiated this project and was instrumental in its planning, he did not live to see its fruition. He became seriously ill in late 1998 and died on July 16, 1999 at the age of 80. We hope he would be pleased with the outcome.

Michael C. Thomas, Ph.D.  
Gainesville, Florida  
April 3, 2002

## Acknowledgments for Volume II

Originally, Ross Arnett was to have authored many of the family treatments, especially for those families with no specialists available. His death in 1999 left many families without an author. Several volunteers stepped forward, but Dan Young of the University of Wisconsin took responsibility for more than his fair share and got several of his enthusiastic graduate students involved in the project also. The members of the Editorial Board, listed in the Introduction, provided guidance, advice, and constructive criticism, but J. Howard Frank of the University of Florida has been outstanding in his unwavering demands for scholarship and proper English, and joined Paul E. Skelley and Michael C. Thomas, both of the Florida Department of Agriculture and Consumer Services, as an editor of Volume II. John Sulzycki of CRC Press has been more than helpful throughout some trying times.

Many of the excellent habitus drawings beginning the family treatments were done by Eileen R. Van Tassell of the University of Michigan for *The Beetles of the United States*, and for Volume 2 of *American Beetles* she produced excellent new ones for families 100, 108, and 119.

Authors of the family treatments often have acknowledgments in their respective chapters throughout the body of the text.

Ross Arnett's widow, Mary, was always his support staff throughout his long and productive career. After Ross' death, she helped by providing free and gracious access to Ross' files, and by her steady encouragement and quiet conviction that we would indeed be able to finish this, Ross Arnett's last big project. Unfortunately, Mary Arnett did not live to see Volume II published. She became ill in the fall of 2001 and died on January 3, 2002.

And I would like to again acknowledge my wife, Sheila, for her patience and forbearance during the long and sometimes difficult path that led to this volume.

Michael C. Thomas, Ph.D.  
Gainesville, Florida  
April 3, 2002

## Contributors to Volume 2 of American Beetles

### Authors

**Rolf L. Aalbu, Ph.D.**

Department of Entomology  
California Academy of Sciences  
Golden Gate Park  
San Francisco, CA 94118-4599  
*106. Tenebrionidae.*

**Robert S. Anderson, Ph.D.**

Canadian Museum of Nature/Entomology  
P.O. Box 3443, Station D  
Ottawa, ON K1P 6P4 CANADA  
*125. Nemonychidae; 127. Belidae; 129. Brentidae; 130. Ithyceridae; 131. Curculionidae.*

**Fred G. Andrews, Ph.D.**

California Department of Food and Agriculture  
Plant Pest Diagnostics Laboratory  
3294 Meadowview Rd.  
Sacramento, CA 95832-1448  
*95. Latridiidae.*

**Ross H. Arnett, Jr., Ph.D.**

Senior Editor

**C. L. Bellamy, D.Sc.**

Entomology  
Natural History Museum  
900 Exposition Blvd  
Los Angeles CA 90007, U.S.A.  
*40. Schizopodiidae; 41. Buprestidae.*

**Marco A. Bologna, Ph.D.**

Dipartimento di Biologia  
Università degli studi "ROMA TRE"  
Viale G. Marconi, 446  
I-00146 ROMA  
*111. Meloidae.*

**Yves Bousquet, Ph.D.**

Eastern Cereal and Oilseed Research Centre  
Agriculture and Agri-Food Canada  
Ottawa, ON K1A 0C6, CANADA  
*79. Monotomidae.*

**Stanley Bowstead, Ph.D.**

Department of Entomology  
The Manchester Museum, The University  
Manchester M12 9PL England  
*94. Corylophidae.*

**Kirby W. Brown, Ph.D.**

P.O. Box 1838  
Paradise, CA 95967  
*106. Tenebrionidae.*

**J. Milton Campbell, Ph.D.**

420 Everetts Lane  
Hopkinsville, KY 42240  
*106. Tenebrionidae.*

**David C. Carlson, Ph.D.**

4828 Dauntless Way  
Fair Oaks, CA 95628  
*30. Ocbodaecidae; 33. Glaphyridae.*

**Donald S. Chandler, Ph.D.**

Department of Zoology  
University of New Hampshire  
Durham, NH 03824  
*117. Anthicidae; 118. Aderidae.*

**Shawn M. Clark, Ph.D.**

Monte L. Bean Museum  
Brigham Young University  
Provo, UT 84602  
*122. Megalopodiidae; 123. Orsodacnidae; 124. Chrysomelidae.*

**Arthur V. Evans, Ph.D.**

Department of Entomology  
National Museum of Natural History  
Smithsonian Institution  
c/o 1600 Nottoway Ave.  
Richmond, VA 23227  
*34. Scarabaeidae: Melolonthinae.*

**Zachary H. Falin**

Division of Entomology  
Natural History Museum and Biodiversity  
Research Center  
Snow Hall, 1460 Jayhawk Blvd.  
Lawrence, KS 66045  
*102. Ripiphoridae*

**R. Wills Flowers, Ph.D.**

Center for Biological Control  
Florida A & M University  
Tallahassee, FL 32307  
*124. Chrysomelidae.*

**J. Joseph Giersch**

Department of Entomology  
Montana State University  
Bozeman, MT 59717  
*65. Jacobsoniidae*

**Arthur J. Gilbert**

California Department of Food and  
Agriculture  
2889 N. Larkin St., Suite 106  
Fresno, CA 93727  
*124. Chrysomelidae.*

**Bruce D. Gill, Ph.D.**

4032 Stonecrest Road  
Woodlawn, ON K0A 3M0, CANADA  
*34. Scarabaeidae: Scarabaeinae.*

**Michael A. Goodrich, Ph.D.**

Department of Biological Sciences  
Eastern Illinois University  
Charleston, IL 61920  
*88. Byturidae; 89. Biphyllidae*

**Robert D. Gordon, Ph.D.**

Northern Plains Entomology  
P.O. Box 65  
Willow City, ND 58384  
*34. Scarabaeidae: Aphodiinae.*

**Dale H. Habeck, Ph.D.**

Entomology and Nematology Department  
University of Florida  
Gainesville, FL 32611  
*76. Brachypteridae; 77. Nitidulidae.*

**Robert W. Hamilton, Ph.D.**

Department of Biology  
Loyola University Chicago  
6525 North Sheridan Road  
Chicago, IL 60626  
*128. Attelabidae.*

**Henry A. Hespenheide, Ph.D.**

Department of Organismic Biology  
University of California  
Los Angeles, CA 90095-1606  
*131. Curculionidae: Conoderinae.*

**Frank T. Hovore, Ph.D.**

14734 Sundance Place  
Santa Clarita, CA 91387-1542  
*28. Pleocomidae.*

**Anne T. Howden, M.Sc.**

Canadian Museum of Nature  
P.O. Box 3443, Station D  
Ottawa, ON K1P 6P4 Canada  
*131. Curculionidae: Entiminae.*



**Michael A. Ivie, Ph.D.**

Department of Entomology  
Montana State University  
Bozeman, MT 59717

49. *Ptilodactylidae*; 50. *Chelonariidae*; 65. *Jacobsoniidae*; 67. *Nosodendridae*; 69. *Bostrichidae*; 90. *Bothriideridae*; 103. *Colydiidae*; 104. *Monommatidae*; 105. *Zopheridae*; Family Key.

**John A. Jackman, Ph.D.**

Department of Entomology  
412 Heep Center  
Texas A & M University  
College Station, TX 77843  
101. *Mordellidae*.

**Mary L. Jameson, Ph.D.**

W436 Nebraska Hall  
Systematics Research Collections  
University of Nebraska State Museum  
Lincoln, NE 68588-0514  
*Scarabaeoidea*; 24. *Diphyllostomatidae*; 26. *Glaresidae*; 27. *Trogidae*; 29. *Geotrupidae*; 31. *Hybosoridae*; 32. *Ceratocanthidae*; 34. *Scarabaeidae*.

**Paul J. Johnson, Ph.D.**

Insect Research Collection, Box 2207-A  
South Dakota State University  
Brookings, SD 57007  
42. *Byrrhidae*; 58. *Elateridae*; 55. *Cerophytidae*; 57. *Throscidae*.

**Kerry Katovich**

Department of Entomology  
University of Wisconsin-Madison  
Madison, WI 53706  
39. *Rhipiceridae*; 47. *Heteroceridae*.

**John M. Kingsolver, Ph.D.**

Florida State Collection of Arthropods  
P. O. Box 147100  
Gainesville, FL 32614  
68. *Dermestidae*; 121. *Bruchidae*.

**David G. Kissinger, Ph.D.**

24414 University Avenue #40  
Loma Linda, CA 92354  
129. *Brentidae*; *Apioninae*.

**Boris A. Korotyaev, Ph.D.**

Zoological Institute  
Russian Academy of Sciences  
Universitetskaya nab 1.  
St. Petersburg, 199034, Russia  
131. *Curculionidae*; *Ceutorhynchinae*.

**Nadine L. Kriska**

Department of Entomology  
University of Wisconsin-Madison  
Madison, WI 53706  
109. *Oedemeridae*.

**John F. Lawrence, Ph.D.**

12 Hartwig Road  
Mothar Mountain  
Gympie, QLD 4570 Australia  
98. *Cidae*.

**Richard A.B. Leschen, Ph.D.**

New Zealand Arthropods Collection  
Landcare Research, Private Bag 92170  
120 Mt. Albert Road, Mt. Albert  
Auckland, New Zealand  
66. *Derodontidae*; 72. *Trogossitidae*; 85. *Cryptophagidae*; 86. *Languriidae*; 92. *Endomychidae*; 94. *Corylophidae*.

**James E. Lloyd, Ph.D.**

Entomology and Nematology Department  
University of Florida  
Gainesville, FL 32611  
62. *Lampyridae*.

**Wenhua Lu**

Wes Watkins Agricultural Research and  
Extension Center  
Oklahoma State University  
P.O. Box 128  
Lane, OK 74555  
101. *Mordellidae*.

**Adriean J. Mayor, Ph.D.**

Department of Entomology and Plant  
Pathology  
205 Ellington Plant Sciences Bldg.  
University of Tennessee  
Knoxville, TN 37901  
74. *Melyridae*.

**Joseph V. McHugh, Ph.D.**

Department of Entomology  
University of Georgia  
Athens, GA 30602  
75. *Sphindidae*; 87. *Erotylidae*.

**Richard S. Miller, Ph.D.**

Department of Entomology  
Montana State University  
Bozeman, MT 59717  
59. *Lycidae*; 60. *Telegensidae*.

**Jyrki Muona, Ph.D.**

Division of Entomology  
Finnish Museum of Natural History  
P. O. Box 17, FIN-00014  
University of Helsinki, Finland  
56. *Eucnemidae*.

**Gayle H. Nelson, Ph.D.**

1308 N. W. Hawk Creek  
Blue Springs, MO 64015-1787  
40. *Schizopodidae*; 41. *Buprestidae*.

**Sean T. O'Keefe, Ph.D.**

Department of Biological and Environ-  
mental Sciences  
Morehead State University  
Morehead, KY 40351  
38. *Dascillidae*; 61. *Phengodidae*.

**Weston Opitz, Ph.D.**

Department of Biology  
Kansas Wesleyan University  
100 Claflin Avenue  
Salina, KS 67401  
73. *Cleridae*.

**T. Keith Philips, Ph.D.**

Department of Biology  
Western Kentucky University  
Bowling Green, KY 42101-3576  
65. *Jacobsoniidae*; 70. *Anobiidae*; 90. *Bothriideridae*.

**John D. Pinto, Ph.D.**

Department of Entomology  
University of California  
Riverside, California 92521  
111. *Meloidae*.

**Darren A. Pollock, Ph.D.**

Department of Biology  
Eastern New Mexico University  
Portales, NM 88130  
99. *Tetratomidae*; 100. *Melandryidae*; 112. *Mycteridae*; 113. *Boridae*; 114. *Pythidae*; 116. *Salpingidae*; 119. *Scrautiidae*.

**Michele B. Price**

Department of Entomology  
University of Wisconsin-Madison  
Madison, WI 53706  
78. *Smicripidae*.

**Robert J. Rabaglia, Ph.D.**

Maryland Department of Agriculture  
50 Harry S Truman Parkway  
Annapolis, MD 21401  
*131. Curculionidae: Scolytinae.*

**Alistair S. Ramsdale**

Department of Entomology  
University of Wisconsin-Madison  
Madison, WI 53706  
*63. Ometbidae; 64. Cantharidae.*

**Brett C. Ratcliffe, Ph.D.**

W436 Nebraska Hall  
Systematics Research Collections  
University of Nebraska State Museum  
Lincoln, NE 68588-0514  
*23. Lucanidae; 24. Diphylostomatidae; 34. Scarabaeidae.*

**Edward G. Riley**

Department of Entomology  
Texas A and M University  
College Station, TX 77843  
*122. Megalopodidae; 123. Orsodacnidae; 124. Chrysomelidae.*

**Jack C. Schuster, Ph.D.**

Universidad del Valle de Guatemala  
Aptdo. 82  
Guatemala, Guatemala  
*25. Passalidae.*

**William D. Shepard, Ph.D.**

Department of Biology  
California State University Sacramento  
6000 J Street  
Sacramento, CA 95819  
*43. Elmidae; 44. Dryopidae; 45. Lutrochidae;  
46. Limnichidae; 48. Psephenidae; 51. Eulichadidae.*

**Paul E. Skelley, Ph.D.**

Third Editor  
Florida State Collection of Arthropods  
Florida Department of Agriculture and  
Consumer Services  
P. O. Box 147100  
Gainesville, FL 32614-7100  
*34. Scarabaeidae: Aphodiinae; 85. Cryptophagidae; 86. Languriidae; 87. Erotylidae; 92. Endomychidae.*

**Andrew B. T. Smith**

W436 Nebraska Hall  
Systematics Research Collections  
University of Nebraska State Museum  
Lincoln, NE 68588-0514  
*34. Scarabaeidae.*

**Ronald E. Somerby, Ph.D.**

Plant Pest Diagnostics Branch  
California Department of Food and  
Agriculture  
3294 Meadowview Road  
Sacramento, CA 95832  
*106. Tenebrionidae.*

**Warren E. Steiner, Jr.**

Department of Systematic Biology -  
Entomology  
National Museum of Natural History  
Smithsonian Institution  
Washington, DC 20560  
*84. Phalacridae.*

**Margaret K. Thayer, Ph.D.**

Field Museum of Natural History  
1400 S. Lake Shore Drive  
Chicago, IL 60605  
*98. Ciidae.*

**Donald B. Thomas, Ph.D.**

USDA, ARS  
2301 S. International Blvd.  
Weslaco, TX 78596  
*106. Tenebrionidae.*

**Michael C. Thomas, Ph.D.**

Second Editor  
Florida State Collection of Arthropods  
Florida Department of Agriculture and  
Consumer Services  
P. O. Box 147100  
Gainesville, FL 32614-7100  
*80. Silvanidae; 81. Passandridae; 82. Cucujidae; 83. Laemophloeidae; 91. Cerylonidae; 120. Cerambycidae.*

**Charles A. Triplehorn, Ph.D.**

Museum of Biological Diversity  
Ohio State University  
1315 Kinnear Road  
Columbus, OH 43212  
*106. Tenebrionidae.*

**Robert H. Turnbow, Jr., Ph.D.**

ATZQ-DEL-PC  
1404 Dilly Branch Road  
Fort Rucker, AL 36362-5105  
*120. Cerambycidae.*

**Barry D. Valentine, Ph.D.**

2359 Eastcleft Drive  
Columbus, OH 43221  
*126. Anthribidae.*

**Natalia J. Vandenberg, Ph.D.**

Systematic Entomology Laboratory  
PSI, ARS, USDA  
c/o National Museum of Natural His-  
tory  
Washington, DC 20560-0168  
*93. Coccinellidae.*

**Daniel K. Young, Ph.D.**

Department of Entomology  
University of Wisconsin  
Madison, WI 53706  
*35. Encinetidae; 36. Clambidae; 37. Scirtidae;  
52. Callirhipidae; 53. Artemetopodidae; 54. Brachypsectridae; 71. Lymexylidae; 96. Mycetophagidae; 97. Archeocrypticidae; 99. Tetratomidae; 107. Prostomidae; 108. Synchronidae; 110. Stenotrachelidae; 115. Pyrochroidae.*

Editorial Board

**J. Howard Frank, D. Phil.**

Fourth Editor  
Entomology and Nematology Depart-  
ment  
University of Florida  
Gainesville, FL 32611

**David G. Furth, Ph.D.**

Department of Entomology  
Smithsonian Institution  
Washington, DC 20560-0165

**Michael A. Ivie, Ph.D.**

Department of Entomology  
Montana State University  
Bozeman, MT 59717

**Brett C. Ratcliffe, Ph.D.**

Systematic Research Collections  
University of Nebraska  
Lincoln, NE 68588-0514

**Daniel K. Young, Ph.D.**

Department of Entomology  
University of Wisconsin  
Madison, WI 53706

## 93. COCCINELLIDAE Latreille 1807

by Natalia J. Vandenberg

**Family common name:** The lady beetles**Family synonyms:** Epilachnidae Mulsant and Rey 1846; Securipalpes Mulsant 1846 (unavailable name, not based on genus).

Although officially called lady beetles, members of the family Coccinellidae are more commonly known as ladybugs (American) or ladybirds (Britain). The charismatic red and black dappled members of the tribe Coccinellini are easily recognized, even by young school children, but the family as a whole is somewhat difficult to characterize. Most species can be identified by the compact, rounded, body form with convex dorsum and flattened venter, clubbed antennae, and the presence of a postcoxal line on the first abdominal ventrite (lacking in *Paranaemia*, *Naemia*, and *Coleomegilla*). The tarsal formula of most species is 4-4-4 with the third tarsomere minute and tucked within the broad triangular second (cryptotetramerous or pseudotrimerous), only a few have the tarsomeres more equal (true tetramerous), some have tarsi reduced to 3-3-3 (true trimerous).

FIGURE 1.93. *Anatis mali* (Say)

**Description:** Shape (Figs. 2-4) rounded, varying from circular to elongate oval, and superhemispherical to somewhat depressed; size 0.8 to 11 mm (some exotic species up to 18 mm). Many are aposematically colored, red, orange or yellow with contrasting markings in black and or white, some less conspicuously colored, black, brown, ivory or gray, a few metallic blue, green, or violet; body glabrous to

finely pubescent.

Head deeply inserted into prothorax in most, but exposed, except basally, in more elongate species (e.g. *Coleomegilla* spp.) (Fig. 2); form subquadrate with epicranium, frons, genae and clypeus fused; surface punctate. Antennae (Figs. 20-28) moderately short, with eight to eleven antennomeres; terminating in a compact or loose club of one to six antennomeres and smooth to serrate lateral margins; antennae inserted (Figs. 7, 8, 9, 10, 20) at the inner front margin of the eyes, or below the eyes; antennal insertion exposed or covered dorsally by lateral extension of the fronto-clypeal region. Labrum short, transverse; mandibles (Figs. 36-39) moderately robust, strongly arcuate, the apices simple, bifid, or dentate, mola generally with two teeth (reduced or absent in some Epilachninae and Sticholotidinae), membranous prostheca present; maxillary palpus (Figs. 29-35) with four palpomeres, the apical palpomere typically large, securiform

**Acknowledgments:** I thank my colleagues, J. Mawdsley, Smithsonian Department of Entomology, Washington, D.C. and A. Solis, A. Norrbom and E. Roberts, USDA Systematic Entomology Laboratory, for providing scientific and editorial reviews of this manuscript. I also thank P. Skelley for helpful suggestions on manuscript and plate preparation.

(hatchet-shaped), cup-shaped, or barrel-shaped, in some species elongate conical or oval (many Sticholotidinae); gula quadrate, the sutures generally distinct; mentum (Figs. 17, 18) trapezoidal or triangular; ligula prominent, rectangular or oval; labial palpus with three palpomeres (two in Noviiini), the apical palpomere oval or conical, distally truncate. Eyes lateral, moderate, somewhat bulging, reniform (Fig. 9), entire (Fig. 5), or deeply divided by eye canthus (Figs. 10, 11), finely to coarsely faceted, glabrous or hirsute.

Pronotum (Figs. 8, 10, 11, 12) broader than the head; transversely oval to quadrate, weakly to strongly convex, with deep to shallow anterior emargination; lateral margins generally explanate, with fine raised border at sides and less commonly at base; surface punctate, pleural region broad; prosternum (Figs. 15, 16) long, generally T-shaped, elevated in many species; intercoxal process bicarinate, laterally margined, or unmodified; procoxal cavities generally closed behind, open in a few. Mesosternum short, trapezoidal to subquadrate, anteriorly emarginate or truncate; metasternum long and broad.

Legs (Figs. 40-44) short relative to body width (Figs. 3, 4) with most or all of femur hidden by elytra in dorsal view (except *Hippodamia*, *Coleomegilla*, and allies; Fig. 2); trochantins of the fore and middle legs exposed; procoxae transverse, separate; mesocoxae round, separate; metacoxae transverse, widely separate; trochanters small, triangular; femora swollen; tibiae cylindrical (Fig. 40) or flattened, in some externally toothed and or grooved (Figs. 42-44), finely spinose, with or without single (Fig. 41) or paired (Fig. 40) minute apical spurs on middle and hind leg; tarsal formula generally 4-4-4 but apparently 3-3-3 (cryptotetramerous or pseudotrimerous) (Figs. 40, 43, 44) with the first and second tarsomeres apically dilated and spongy-pubescent beneath, the third minute, appearing as a basal annulation of the elongate fourth tarsomere; alternatively, formula 3-3-3 (true trimerous) through loss of or fusion of tarsomere three with four (some Scymnini, Noviiini), exceptionally true tetramerous (4-4-4) with all tarsomeres more or less cylindrical and ventrally spinose

(*Litophilus* and allies; soil-dwelling species not occurring in North America); claws (Figs. 45-48) simple, cleft, or with basal to median quadrate or triangular tooth. Scutellum small, triangular.

Elytra entire; surface shagreened to highly polished, finely to moderately punctate, non-striate, laterally explanate or steeply descending; epipleural fold entire (most species) to obsolete in apical third, with or without foveae to receive retracted tibiae and tarsi. Hindwing normally present and functional; wing venation reduced, nervature of the cantharoid type, veins feebly marked or absent in distal half; anal lobe generally present, but reduced or absent in some minute species. Abdomen with five to seven ventrites (= visible sternites), sutures entire; first ventrite composed of the fused 1-3 morphological sternites, normally bearing a postcoxal line of variable form (Figs. 49-54), line absent (Fig. 55) in *Paranaemia*, *Naemia* and *Coleomegilla*.

Male genitalia with a curved tubular siphon (= penis); basal end of siphon typically enlarged to form a siphonal capsule with an outer arm through which the ejaculatory duct is threaded, and in most cases an inner arm or apodeme which articulates with a median tegminal strut known as the trabes. The predistal portion of the siphon is embraced by the tegmen which consists of the following identifiable parts: a central projection termed the basal lobe (or incorrectly known as the median lobe), pair of lateral projections known as parameres or accessory lobes, a basal portion called the basal piece and the median strut or trabes. Note: the parameres of this and related taxa are considered by some to be secondary developments not homologous to the parameres of non-cucujoid lineages. The entire coccinellid tegmen, therefore, is often referred to as the phallobase, while in other groups the term phallobase corresponds to the tegmen minus the parameres.

Female genital segments (ovipositor) composed of a well developed proctiger (tenth tergite), the paired ninth pleurites, and the paired coxites also called "hemisternites" (ninth sternites); the shape of the coxites are important taxonomically and may be oval, tapered distally or paddle-shaped, generally heavily chitinized and bearing a small apical stylus. Receptaculum seminis (spermatheca) present, or exceptionally absent, typically with three branches, but weakly developed or obsolete in some: the proximal branch or nodulus which communicates with the sperm duct, middle branch or ramus bearing the spermathecal accessory gland, and distal branch or cornu. Sperm duct straight or coiled, of variable length and rigidity, generally bearing a sclerotized "infundibulum" of variable form and position; sperm duct attached to bursa distally, basally or dorsally; bursa variously shaped, thin or thick-walled, membranous, in many enclosing a sclerotized plate-, rod-, or bulb-like extension of the infundibulum (for additional readings on morphology and anatomy of the adult coccinellid, see Sasaji 1968 and Kovár 1996a).

Eggs cream-colored, yellow or reddish orange, darkening prior to eclosion; typically oval to fusiform, positioned on end in clusters (e.g. Coccinellini, some Chilacorini), or ellipsoidal laid flat in loose groupings (most Scymnini), in some taxa rounded or flattened, deposited individually near leaf vein, in cracks and crevices, or adjacent to/under prey (e.g. Platynaspini, Chilacorinae).

Larva elongate fusiform or oblong to broadly ovate, slightly to strongly flattened; color gray, blue, brown, or pink, many with contrasting markings of white, yellow, orange, or red, particularly in the later instars; body surfaces rugose to microtrichose with or without glabrous patches, armed with setae and setose processes of variable architecture (strumae, verrucae, parascoli, scoli or senti), in some taxa well covered with white waxy exudates. Head exerted, circular or oblong, hypo- to prognathous; frontal sutures forming a V or inverted omega shape, lacking in some; epicranial stem obsolete except in Epilachninae. Antennae of one to three segments, not over three times as long as wide. Labrum distinct, mandibles moderate, stout, triangular, or sickle-shaped, apically acute, bidentate, or multidentate; mola generally present but reduced or absent in Epilachninae; maxillae with fused cardo and stipes; maxillary palpi with two or three palpomeres; labium with fused submentum and ligula, labial palpi with one to two palpomeres. Three pair of stemmata generally present. Thorax with distinct armature and normally with tergal plates on each segment; legs elongate, each with four segments plus tarsungulus; apex of tibiae with clavate or flattened setae. Spiracles on the mesothorax and abdominal segments one to eight, annular. Abdomen ten-segmented; most abdominal segments with scattered setae or chazae and transverse row of six setose processes visible in a dorsal view; the tenth segment provided with an anal organ or sucking disk (pygopod); pores of repugnatorial glands may occur on each lateral margin of the tergum in the coria between segments. Urogomphi absent. Rees et al. (1994) provide a key to genera and selected species of North America; LeSage (1991) provides family and tribal level diagnoses and a key to North American tribes; Pope (1979) describes the phenomenon of wax production by larvae in diverse tribes. Descriptions and keys to selected North American genera and species include Gordon and Vandenberg (1993: genus *Cycloneda*) and Gordon and Vandenberg (1995: genus *Coccinella*). Introduced species are described and illustrated in Gordon and Vandenberg (1991).

Pupa rounded or oval, attached to substrate at caudal end, exarate; generally exposed, but some enclosed within the last larval exuvium except for a narrow dorsolongitudinal strip (Chilacorini, Noviini, some Scymninae); most brightly colored or patterned. Phuoc and Stehr (1974) provide descriptions and a key to subfamilies and tribes of North America.

**Habits and habitats.** Adults and larvae of most species are predacious on aphids, psyllids, mealybugs, scales, or other small soft-bodied insects and mites. The larger, aposematically colored lady beetles can usually be found feeding amongst colonies of their prey or basking openly on vegetation. *Coleomegilla* species, which prefer a more humid microclimate, are frequently associated with aquatic vegetation, such as water lettuce. In agricultural plantings these beetles are often abundant inside the tightly whorled leaves of corn plants, feeding on wind blown pollen, aphids, mites, and the eggs or larvae of beetles and moths. Although most predacious lady beetles will consume pollen in the absence of prey, *Coleomegilla* is one of the few genera able to complete development on pollen alone. In North America, members of the subfamily Coccinellinae are typically aphidophagous.

In the United States, *Neobarmonia* species were assumed to be normal aphidophages until they were found feeding on the eggs and larvae of an exotic leaf beetle (Whitehead and Duffield 1982). In Central and South America the same and related species feed on native leaf beetles, suggesting that this is the more normal food preference for the genus. Many predacious coccinellids will feed occasionally on spider mites. The minute *Stethorus* species have specialized in this particular prey group. Many of the smaller predacious lady beetles are adept at squeezing into the tiny nooks and crannies provided by plant architecture, or crawling inside the folds of distorted leaves damaged by sucking insects and mites; they can even find their way inside of hollow thorns or insect galls if furnished with a tiny opening, often provided by an ant. Ants are inimical to most lady beetles, but some lady beetle taxa are either tolerated or ignored. The larvae of *Brachiacantha* species have been reported feeding on Homoptera housed within ant colonies, and the Australian *Scymnodes bellus* Blackburn has been recorded preying on the ants themselves under eucalyptus bark (Pope and Lawrence 1990). The blind larvae of *Ortalistes* are termitophiles and live in Central America. Although the entomophagous members of the lady beetle family can all be categorized as predators, the larvae of some minute scale feeding *Hyperaspis* species will complete their development by burrowing into the large egg sac attached to a single female scale and thus approach a parasitic mode of existence.

Lady beetles in the subfamily Epilachninae are exceptional in following a completely phytophagous diet, feeding primarily on the leaf parenchyma, particularly of plants in the families Solanaceae, Curcubitaceae and Leguminosae. This lady beetle subfamily is distributed worldwide, but is most diverse in the tropics. The adventive Mexican bean beetle, *Epilachna varivestis* Mulsant, is a notorious pest of bean and alfalfa crops in the Eastern United States. A North American native, the squash lady beetle, *Epilachna borealis* (Fabricius), damages squash and related crop plants.

The Halyziini (= Psylloborini) of the subfamily Coccinellinae feed on powdery mildews (Ascomycetes: Erysiphales). Their greatest diversity is also in the tropics. Systematists argue whether this group of mycetophagous Coccinellinae represents a single or multiple phyletic lines. As with pollenivory, consumption of mold spores occurs among the entomophagous lady beetle taxa as well. *Neocalvia*, a genus of Coccinellinae restricted to the Neotropics, feeds on the larvae of the Halyziini.

Lady beetles have their share of natural enemies, but they are well protected against most birds, mammals, ants, and other generalist predators. Adult lady beetles are capable of releasing a bitter fluid from specialized glands at the tibio-femoral articulations which serve as a repellent. This renders most species unpalatable, and some are even highly toxic if ingested. Larvae are similarly protected by repugnatorial glands on the abdomen.

In North America many lady beetle species become dormant during the hot dry summer or the cold winter when prey are scarce. Some species migrate to the mountains and form large aggregations, while others remain in situ or fly only a short distance to form smaller clusters at the bases of prominent objects such as fence posts or rocky outcrops. The introduced multicol-

ored Asian lady beetle, *Harmonia axyridis* (Pallas), annoys many home owners by moving indoors in large numbers toward the end of fall and remaining until spring.

Several predacious lady beetles have been used with great success as agents of biological control, particularly against scale insects (Drea and Gordon 1990). The vedalia beetle, *Rodolia cardinalis* (Mulsant) was successfully introduced from Australia into many parts of the world for control of a notorious citrus pest, the cottony cushion scale, *Icerya purchasi* Maskell. *Cryptognatha nodiceps* Marshall and *Rhyzobius pulchellus* Montrouzier were successfully employed against coconut scale in Fiji and New Hebrides respectively, and *Rhyzobius lophanthae* Blaisdell has proven to be an asset in controlling several scale pests in tropical areas of the world. The attempt to release generalist aphidophagous predators for biological control of introduced aphids has been less effective and sometimes produced undesirable side effects such as the displacement of native lady beetle species, predation on non-target species, or, in the case of the multicolored Asian lady beetle, *H. axyridis*, the creation of a new public nuisance. Further valuable readings on the habits and habitats of the Coccinellidae include Hodek and Honek (1996), Majerus (1994), Kuznetsov (1997), and Klausnitzer and Klausnitzer (1997).

**Status of the classification.** The family Coccinellidae belongs to the cerylonid series (8 families, 38 subfamilies), section Clavicornia, of superfamily Cucujoidea. Its closest affinities are believed to be with Corylophidae and Endomychidae (Crowson 1955, Sasaji 1971a) or with Alexiidae (=Sphaerosomatidae) and Endomychidae (Slipinski and Pakaluk 1991). Various viewpoints on the systematic position of the Coccinellidae are summarized by Sasaji (1971a), Slipinski and Pakaluk (1991), Pakaluk *et al.* 1994, and Kovár (1996b)). Many contemporary works recognize six subfamilies of Coccinellidae (Sticholotidinae (= Sticholotinae), Scymninae, Coccidulinae, Chilocorinae, Coccinellinae, and Epilachninae) (Booth *et al.* 1990, Pakaluk *et al.* 1994, Lawrence and Newton 1995, Kuznetsov 1997), a system first proposed by Sasaji (1968), and based on a detailed morphological study of adult and larval characteristics. Other authors have built upon this classification through the addition of one or more subfamilies. There is no current consensus for the higher classification of the Coccinellidae, despite an attempt by Chazeau *et al.* (1989) and Fürsch (1996) to develop one, soliciting the input of the greater community of coccinellid specialists. The tribal level classification in the system developed by Sasaji (1968) has proven to be even less stable. Although coccinellid subfamilies are more or less worldwide in distribution, many proposed tribes are restricted to particular biogeographic regions where they fall outside the consideration of regional revisionists. This has resulted in a proliferation of alternative classifications which can not be easily reconciled.

Even a cursory review of the New World Coccinellidae suggests that generic and higher level taxa have not been rigorously defined, nor do they maintain a consistent hierarchical value throughout the family. Often the more derived members of a taxon have been stripped away and isolated under a separate name, leaving the parent group with a para- or polyphyletic as-

semblage of residual taxa. Thus, some broadly defined genera with many species and species groups exist alongside other narrowly defined genera with one or only a few species (e.g., *Hyperaspis* vs. *Hyperaspidius*, *Hippodamia* vs. *Ceratomegilla*, *Coleomegilla* vs. *Paranaemia* or *Naemia*). To achieve a balanced classification, either these generic sets should be reunited, or the larger paraphyletic genera should be split into multiple genera.

The Halyziini (= Psylloborini, see Pakaluk *et al.* 1994) of North America are a small and easily recognized group consisting of the single genus *Psyllobora*, but the world fauna is much more diverse. Various authors have classified these mycophagous coccinellines in multiple tribes (Fürsch 1996, Kovár 1996b), or combined some or all of them with their predacious relatives in the tribe Coccinellini (Kuznetsov 1997, Iablokoff-Khnzorian 1982). The single tribe classification (Sasaji 1968) is followed here as a matter of convenience and without an independent attempt at evaluating alternatives.

Pope (1988) revised the Australian coccinellid fauna and identified the classification of subfamilies Coccidulinae and Scymninae (*sensu* Sasaji 1968) as one problem area in the higher classification of the family. He suggested that a single subfamily with 5 tribes would more accurately portray the phylogeny of the cocciduline–scymnine lineage, but unfortunately he did not employ or elaborate upon this suggestion. Other authors sought to solve the same problem through diverse methods involving either (1) reshuffling of scymnine and cocciduline tribes within the two existing subfamilies, (2) segregating specialized members of this lineage in additional subfamilies (3) elevating existing tribes to the subfamily level, and thus effectively sidestepping the issue of their relationship to one another, or a combination of the above (for further discussion, see Kovár 1996b, Gordon 1994a). None of these methods has proven entirely satisfactory, but the effect on the classification of the North American fauna has been minimized due to the fact that many of the problematic taxa do not occur in this region, or occur only as isolated introductions of exotic species.

The tribe Azyini Mulsant was resurrected by Gordon (1980) for two closely related genera (*Azya* Mulsant and *Pseudoazyia* Gordon) which were deemed sufficiently distinct from the rest of the neotropical fauna to justify their separation from Coccidulinae. Had exemplars from the Australian region been included in this study, it would have become evident that problematic allied taxa exist, in particular the probable sister genus *Bucolus* Mulsant (variously classified in Coccidulinae and Scymninae). The tribe Azyini is used here provisionally, but its subsequent elevation to subfamily status (Gordon 1994a), is not implemented as it does nothing to resolve existing problems. The classification of Scymninae and Coccidulinae is in need of serious study on a worldwide basis.

The classification presented here recognizes the split of Hyperaspidini (*sensu lato*) into Hyperaspidini and Brachiacanthini (Duverger 1989, as Hyperaspini and Brachiacanthadini), but does not employ Hyperaspidinae (= Hyperaspinae) as a subfamily level taxon (Duverger 1989). Although the separation of Hyperaspidinae from Scymninae has considerable merit, to achieve

a holophyletic classification, the Hyperaspidinae would need to include other taxa remaining in Scymninae, such as Selvadiiini and Diomini (in part). The Selvadiiini share important derived antennal characters with *Hyperaspis*, and neotropical members of Diomini appear to be polyphyletic with respect to Selvadiiini.

The tribe Scymnillini (Scymninae) shares many characteristics with members of Sticholotidini (Sticholotidinae), not only in external morphology (Sasaji 1971b), but in the genitalia of both sexes. Its placement is problematic. Kovár (1996b) identifies two major series within the Sticholotidinae, and it may be that this latter subfamily is polyphyletic. Gordon (1994b) uses the scymnilline genus *Zilus* Mulsant as an outgroup for his cladistic analysis of the West Indian Sticholotidini, remarking that they have many similarities. The correspondence between both internal and external character states of Scymnillini and Sticholotidini suggests that the similarities are not due merely to convergence.

An additional problem area is with the generic level classification of the subfamily Chilocorinae. Kovár (1995) briefly reviewed the New World classification in a work primarily focusing on palearctic members of the chilocorine genera *Brumus* Mulsant, *Exochomus* Redtenbacher, and *Brumoides* Chapin. He restricted use of these names to the Old World species, but provided no alternative placement for New World members.

The identification of Coccinellidae from America has been greatly facilitated by the publication of a comprehensive and well illustrated work (Gordon 1985) with keys and descriptions of 57 genera and 475 species. A few additional species have subsequently become established either by immigration or through biological control efforts, or represent earlier establishments which were overlooked until recent times (Vandenberg 1990, Gordon and Vandenberg 1991, Peck and Thomas 1998). Some native Coccinellini, once quite common, have become rare in the last decade, most likely due to competition with exotic species. Similarly, some species ranges reported here may no longer be accurate.

In the future, we can also expect changes in the number of recorded North American species due to a reassessment of the species versus subspecies or varietal status in some problematic groups, or the discovery of new species and species synonyms, particularly in the more minute, cryptically colored taxa. Changes in the higher classification of the Coccinellidae and a better understanding of their position within the group of related families can be anticipated, particularly as information is shared among specialists from around the world.

**Distribution.** Nearly 6,000 species occur worldwide in about 360 genera. Gordon (1985) documented 475 species in 57 genera from America north of Mexico. Additional records (Vandenberg 1990, Gordon and Vandenberg 1991, Peck and Thomas 1998) bring that figure up to 481 species and 60 genera.

#### KEY TO NEARCTIC GENERA

1. Eye deeply divided by transverse projection (canthus) from inner ventral margin (head positioned vertically); canthus broad, band-like, expanded to cover basal antennomeres from frontal view; clypeus not projecting, with semicircular emar-

- gination medially (Fig. 10); antenna of ten or fewer antennomeres with spindle-shaped flagellum (Fig. 21); mandible scythe-like with a single apical tooth (Fig. 37) (Chilocorinae: Chilocorini) ..... 2
- Eye usually weakly emarginate (Figs. 7, 8, 9) or with brief lobe-like or digitiform canthus (Fig. 13, 14); if canthus deeply dividing eye (some Sticholotidinae, Exoplectrini, Cryptognathini) then its form narrow and clypeus not as above (Fig. 11); other characters variable ..... 10
- 2(1). Postcoxal line of first abdominal ventrite merging with posterior margin of ventrite (Fig. 49) ..... *Chilocorus*
- Postcoxal line of first abdominal ventrite not merging with posterior margin of ventrite (Figs. 50, 52, 53, 54) ..... 3
- 3(2). Postcoxal line of first abdominal ventrite parallel and close to posterior margin of first ventrite (Fig. 50); antenna composed of 7 antennomeres ..... *Halmus*
- Postcoxal line of first abdominal ventrite recurved apically, complete or not; antenna of 8-10 antennomeres ..... 4
- 4(3). Postcoxal line of first abdominal ventrite complete (Figs. 53, 54) ..... 5
- Postcoxal line of first abdominal ventrite incomplete (Fig. 52) ..... 8
- 5(4). Tarsal claw simple, without basal tooth (Fig. 45); antenna composed of 8 antennomeres ..... *Brumoides (sensu lato)*
- Tarsal claw with basal tooth (Fig. 47); antenna composed of 10 antennomeres (exceptionally of 9 antennomeres but these species not occurring in North America) ..... 6
- 6(5). Pronotum finely margined at base ..... 7
- Pronotum not margined at base (North America natives) ..... *Exochomus (sensu lato; in part)*
- 7(6). Postcoxal line of first abdominal ventrite reaching or directed toward the inner end of lateral line (Fig. 54) ..... *Brumus (sensu Kovár 1995)*
- Postcoxal line of first abdominal ventrite reaching or directed toward midpoint of lateral line (Fig. 53) ..... *Exochomus (sensu stricto; Kovár 1995)*
- 8(4). Elytron metallic blue without spots ..... *Curinus*
- Elytron blackish with one or more red to yellow spots ..... 9
- 9(8). Elytral margin not reflexed, with marginal bead; length less than 3.6 mm ..... *Arawana*
- Elytral margin feebly reflexed, with or without marginal bead; length more than 5.0 mm ..... *Axion*
- 10(1). Mandible with apex multidenticulate, bearing three or more large irregular teeth (Fig. 38); all tibiae with one or two apical spurs present (Figs. 40, 41) (North American fauna); dorsal surfaces pubescent; antenna inserted dorsally between eyes and distant from inner ocular margin (Fig. 9), long, loosely articulated, with 11 antennomeres and inner margin of club weakly serrated; eye bean-shaped without an abrupt notch or emargination (Fig. 9); length 3.5mm or greater (Epilachninae: Epilachnini) ..... 11
- Mandible with bifid or single apex (Figs. 36, 37), a few with very weak subapical tooth (some Sticholotidinae), but then body size minute, length less than 3.0 mm; if with additional well developed apical teeth (Halzyiini (=Pssylloborini)) then teeth regular, comb-like (Fig. 39), all tibiae lacking apical spurs and dorsal surfaces glabrous; other characters variable ..... 12
- 11(10). Anterior tibia slender, not angulate at outer margin; anterior tibia with single spur at apex (as in fig. 41); body length more than 6.0 mm .... *Epilachna*
- Anterior tibia relatively robust, with outer margin angulate at apical 1/4; anterior tibia with pair of spurs at apex (as in fig. 40); body length less than 5.0 mm ..... *Subcoccinella*
- 12(10). Dorsal surfaces glabrous; distal maxillary palpomere broadly securiform (hatchet-shaped) with sides strongly divergent apically, base narrowly articulated with preceding palpomere (Fig. 29); antenna equal to 2/3 head width or longer (Fig. 20, right); femur not strongly flattened; tibia simple, without angulations (Fig. 40) (Coccinellinae) ..... 13
- Dorsal surfaces glabrous or pubescent; distal maxillary palpomere barrel-shaped, oblong, oval or conical (tapered toward apex) (Figs. 31-34); if securiform, then base rather broadly articulated with previous palpomere (Figs. 30, 35) and antenna less than 2/3 head width (Fig. 20, left), or dorsal surfaces pubescent; femur sometimes strongly flattened; tibia simple or modified (Fig. 42-44) ..... 14
- 13(12). Apex of mandible multidenticulate with small comb-like denticles (Fig. 39); eye bean-shaped without an abrupt emargination (Fig. 8); eye facets coarse, bead-like; spurs lacking on all tibiae; elytral ground color yellow or white with brown speckles or blotches; mycetophagous on powdery mildews (Halzyiini (=Pssylloborini)) ..... *Pssyllobora*
- Apex of mandible bifid (Fig. 36); eye circular or oval with an abrupt notch or digitiform emargination produced by eye canthus (Figs. 13, 14); eye facets fine, somewhat flattened; one or pair of spurs usually present on apex of middle and hind tibia (Figs. 40, 41), rarely absent (*Mulsantina*, *Neoharmonia*, *Harmonia*, *Aphidecta*); elytral color pattern variable; predacious on insects and mites (Coccinellini) ..... 45
- 14(12). Distal maxillary palpomere elongate: conical, or parallel-sided with an acute apex (Figs. 33, 32) (mouthparts may be hidden from view, see couplet 15, below); mentum usually narrowly articulated with submentum (Fig. 17); length of body less than 3.0 mm (Sticholotidinae) ..... 15
- Distal maxillary palpomere short and/or broad (although somewhat elongate in Scymnillini, Fig. 31): barrel-shaped, securiform, or with apex weakly convergent (Figs. 30, 31, 34, 35); mentum rather broadly articulated with submentum (Fig. 18); length of body variable ..... 20

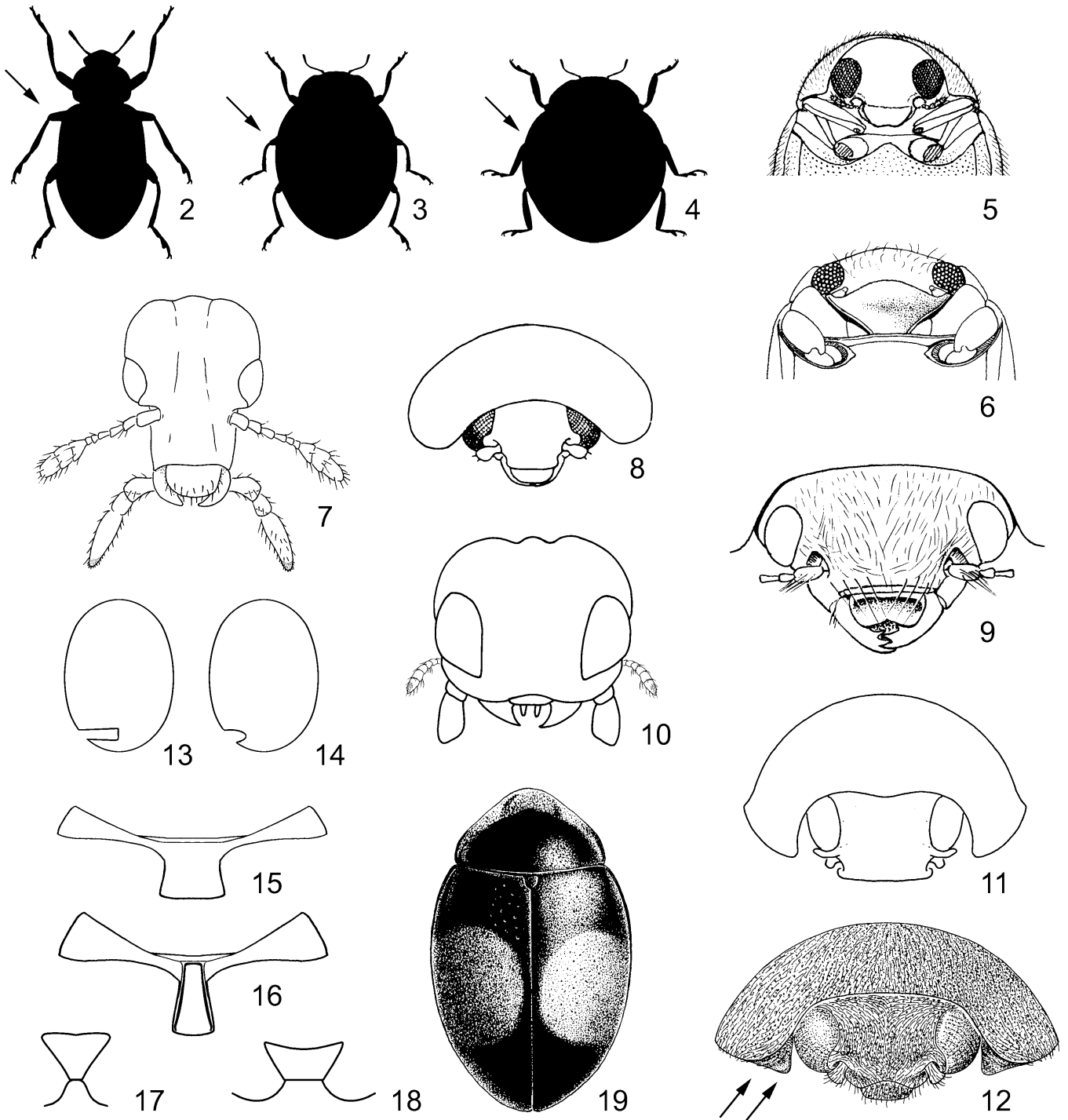
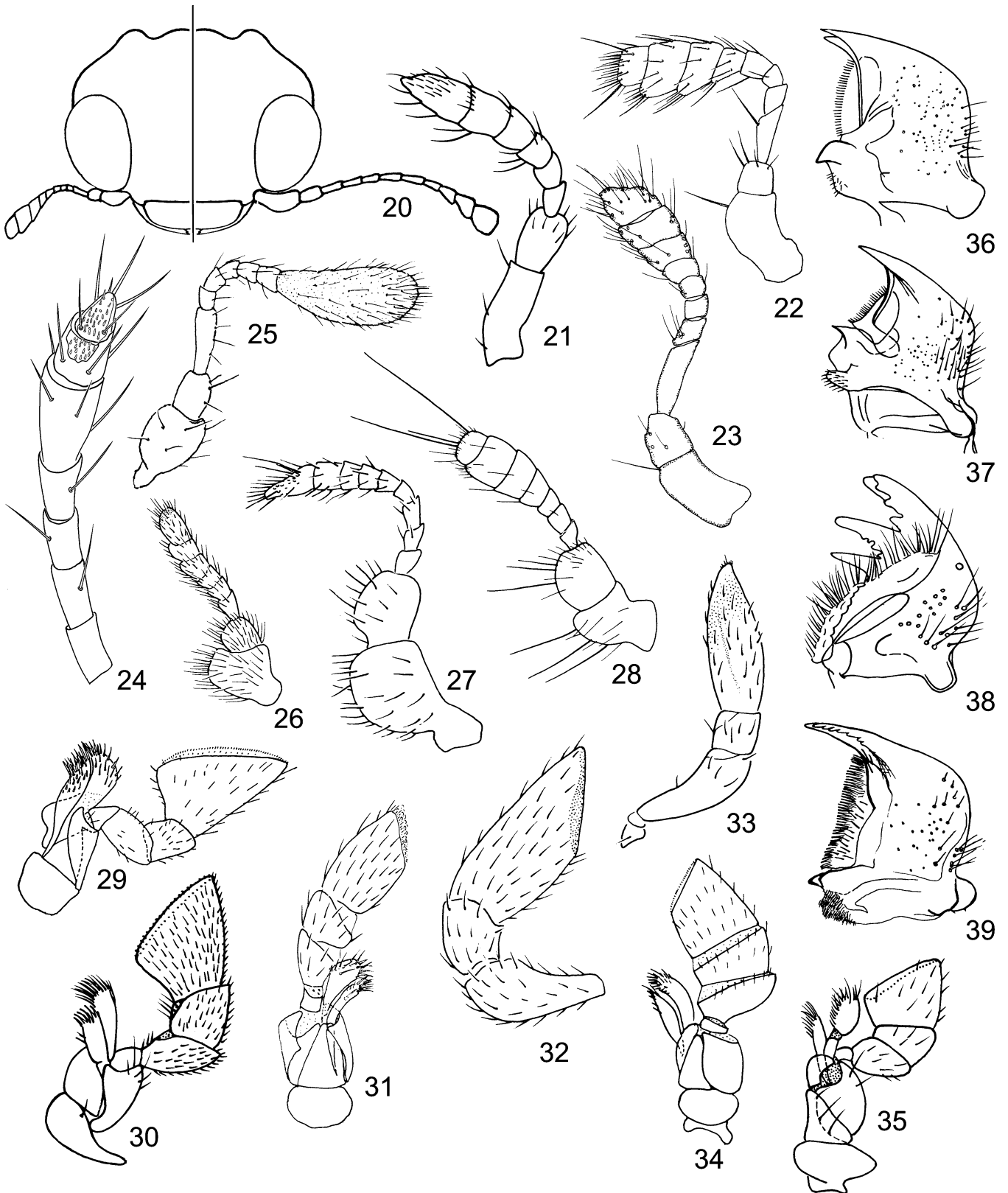


FIGURE 2.93-19.93. 2-4 silhouettes showing a range of coccinellid body types (arrow identifies apex of mesofemur); 5. *Nephaspis* sp., head, anterior part of thorax (ventral view of body); 6. *Delphaspis* sp., head, anterior part of thorax (ventral view of body); 7. *Gnathoweisea* sp., head, anterior part of thorax (ventral view of body); 8. *Psyllobora* sp. (Halyziini), head, pronotum; 9. *Epilachna* sp. (Epilachnini), head, anterior edge of pronotum; 10. *Chilocorus* sp. (Chilocorini), head; 11. *Cryptognatha* sp. (Cryptognathini), head, pronotum; 12. *Azya* sp. (Azyini), head, pronotum, arrows indicate inner and outer edge of thickened anterolateral margin; 13. left compound eye with elongate eye canthus (Scymnillini) (diagrammatic); 14. left compound eye with brief notch-like eye canthus (diagrammatic); 15. Scymnillini sp., prosternum (ventral view, diagrammatic); 16. *Scymnus* sp., prosternum (ventral view, diagrammatic); 17. mentum (above) showing narrow articulation with submentum (typical of Sticholotidinae, diagrammatic); 18. mentum (above) showing broad articulation with submentum (typical of most Coccinellidae, diagrammatic); 19. *Nipus* sp. (dorsal view, appendages retracted). (Some figures modified from the works of Sasaji and Gordon)



- 15(14). Prosternum greatly expanded to conceal mouthparts (Fig. 6); antennal club composed of a single oblong or elongate-oval antennomere (Fig. 25); femur broad, flat, fitting into depressions on ventral surface (Serangiini) ..... *Delphastus*  
 — Prosternum not expanded or with small lobe-like expansion that does not conceal mouthparts; antennal club composed of more than one antennomere, terminal antennomere not oblong or elongate-oval; femur not broad or flat; ventral surface without depressions for femora ..... 16
- 16(15). Dorsal surface clothed in conspicuous long semirecumbent pubescence; head large, exposed, vertical; eye large, narrow, elongate (Cephaloscymnini) ..... *Cephaloscymnus*  
 — Dorsal surface glabrous or with inconspicuous stubble-like pubescence; head small, concealed or exposed; eye small, round or oval (Microweiseini) ..... 17
- 17(16). Head entirely concealed beneath pronotum (Fig. 19) ..... *Nipus*  
 — Head exposed or only partially concealed ..... 18
- 18(17). Head unusually long and narrow (Fig. 7) ..... *Gnathowisea*  
 — Head more or less transverse ..... 19
- 19(18). Antenna composed of 10 antennomeres; length of antepenultimate antennomere subequal to penultimate antennomere ..... *Microwisea*  
 — Antenna composed of 9 antennomeres; antepenultimate antennomere much shorter than penultimate antennomere ..... *Coccidophilus*
- 20(14). Procoxa broad, obscuring lateral arm of prosternum; antenna of 8 antennomeres with weakly formed, spindle-shaped club (Fig. 26); eye densely pubescent; tarsi trimerous (Noviini). The two genera occurring in North America are distinguished primarily by larval characteristics; species specific colorpatterns are used to separate the adults, below) ..... 21  
 — Procoxa normal, not obscuring lateral arm of prosternum; antenna of 9-11 antennomeres, club of various forms (Figs. 22-24, 27, 28); eye glabrous or with sparse to moderate pubescence laterally; tarsi trimerous or cryptotetramerous ..... 22
- 21(20). Elytron reddish with a complicated pattern of dark marks (Fig. 56); apical one-third with a reddish mark entirely or partially enclosed by a darker border (color pattern of single introduced species: *Rodolia cardinalis* (Mulsant)); pronotum with outline of basal half not completely arcuate; posterior angles apparent ..... *Rodolia*  
 — Elytron predominantly dark with a median red spot and reddish anterolateral border, these reddish areas sometimes confluent; apical one-third dark without additional marks (color pattern of single native species *Anovia virginalis* (Wickham)); pronotum with outline of basal half completely arcuate; posterior angles obsolete ..... *Anovia*
- 22(20). Pronotum with anterolateral margin thickened, with sharply defined inner and outer edge (Fig. 12); hypomeron with foveae to accommodate the antennal club and part of anterior leg (Azyini) .. 23
- Pronotum with anterolateral margin not thickened; hypomeron not as above ..... 24
- 23(22). Prosternum with intercoxal process elevated, narrow ..... *Azya*  
 — Prosternum with intercoxal process flat, not elevated ..... *Pseudoazya*
- 24(22). Prosternum broadly rounded anteriorly (similar to Fig. 6), at least partially concealing mouthparts and antennae ..... 25  
 — Prosternum not as above ..... 27
- 25(24). Clypeus with anterior margin upturned; eye canthus long and narrow, nearly dividing eye (Cryptognathini) (Fig. 11) ..... *Cryptognatha*  
 — Clypeus with anterior margin not upturned; eye canthus short to obsolete (Figs. 5, 13, 14) ..... 26
- 26(25). Size 3.4 mm or greater; prosternal intercoxal process carinate; distal maxillary palpomere diverging toward apex (similar to Fig. 30) (Scymnini in part) ..... *Cryptolaemus*  
 — Size less than 2.0 mm; distal maxillary palpomere weakly tapered toward apex (Fig. 34); prosternal intercoxal process not carinate (Stethorini) ..... *Stethorus*
- 27(24). Eye canthus long and narrow, nearly dividing eye; basal antennomere greatly enlarged (Exoplectrini) ..... *Exoplectra*  
 — Eye canthus extending half way across eye or less (Figs. 13, 14); basal antennomere variable .... 28
- 28(27). Antennae long, more than 2/3 head width, inserted laterally; flagellum and club well differentiated, terminal antennomere usually large and quadrate (Fig. 20, right) (Coccidulini) ..... 29  
 — Antenna short, 2/3 head width or less (Fig. 20, left), inserted laterally or ventrally; flagellum and club merging gradually, not well differentiated, terminal antennomere reduced, often tapered (Figs. 22, 23, 24, 27, 28) ..... 30
- 29(28). Dorsal pubescence uniform, decumbent ..... *Coccidula*  
 — Dorsal pubescence of mostly decumbent hairs with some long, erect hairs scattered throughout .... *Rhyzobius*
- 30(28). Abdomen with 5 ventrites; prosternal intercoxal process very broad and flat, without carinae (Fig. 15); eye canthus extending about halfway across eye (Fig. 13) (Scymnillini) ..... 31  
 — Abdomen with 6 or 7 ventrites; prosternal intercoxal process normal, with (Fig. 16) or without carinae; eye canthus extending distinctly less than half-way across eye (Fig. 14) ..... 32
- 31(30). Elytron apparently glabrous or with only sparse hairs in evidence; often with metallic sheen ..... *Zilus*  
 — Elytron with dense, mostly erect pubescence; without metallic sheen ..... *Zagloba*
- 32(30). Dorsal surfaces glabrous ..... 33  
 — Dorsal surfaces pubescent ..... 37
- 33(32). Anterior tibia with external tooth or spine (Fig. 42); eye emarginate; male of many species with cusp



- on abdominal ventrite 3; female genitalia with simple spermathecal capsule, infundibulum present (Brachiacanthini) ..... *Brachiacantha*
- Anterior tibia without external tooth or spine; eye not emarginate; male without cusp on abdominal ventrite 3; female genitalia with retort-shaped appendage (= modified cornu?) on spermathecal capsule (Hyperaspidiini, in part), infundibulum absent or unsclerotized ..... 34
- 34(33). Epipleuron of elytron not excavated for reception of middle and hind femoral apices; tarsal claw simple (Fig. 45) ..... *Hyperaspidius*
- Epipleuron of elytron excavated for reception of middle and hind femoral apices; tarsal claw toothed (Fig. 47) or simple (Fig. 45) ..... 35
- 35(34). Epipleuron of elytron strongly slanting down and away from body; anterior tibia wide, rounded externally in basal one-third, subangulate externally at apical one-fourth (Fig. 44); elytron greenish black with red spot behind middle ..... *Thalassa*
- Epipleuron of elytron flat or only feebly inclined; anterior tibia slender throughout or with a lobe-like preapical expansion (Fig. 43); elytron not greenish black ..... 36
- 36(35). Femur short, stout; tibia with a lobe-like preapical expansion (Fig. 43); elytron reddish brown, without maculation ..... *Helesius*
- Femur slender; tibia slender, without a lobe-like preapical expansion; elytron usually black or brown with pale maculation, rarely immaculate ..... *Hyperaspis*
- 37(32). Head with mouthparts directed postero-ventrad in repose, concealing prosternum (Fig. 5); basal 2 antennomeres greatly enlarged relative to remaining antennomeres (Fig. 27) ..... *Nephaspis*
- Head with mouthparts not directed postero-ventrad, not concealing prosternum; basal 2 antennomeres of normal size (Figs. 22, 23), or at least not greatly enlarged relative to club (Fig. 28) ..... 38
- 38(37). Antenna very short, of 9 antennomeres, with two or more terminal setae much longer than last 3 antennomeres combined (Fig. 28); eye large, elongate ..... *Pseudoscymnus*
- Antenna longer, of 10-11 antennomeres; terminal setae never longer than last 3 antennomeres combined (Figs. 22-24); eye smaller, rounded ..... 39
- 39(38). Antennal club fusiform, symmetrical, with lower margin even; distal antennomere conical; last 2 antennomeres with concentration of shorter setae in membranous area on inner surface (Fig. 24); third antennomere subequal to remaining flagellomeres ..... 40
- Antennal club oval, asymmetrical, with lower margin somewhat uneven; distal antennomere quadrate or rounded with concentration of shorter setae on distal or oblique outer face; third antennomere often elongate relative to remaining flagellomeres (Figs. 22, 23) ..... 41
- 40(39). Head with clypeus more or less truncate in frontal view; postcoxal line of first abdominal ventrite not recurved at outer end (Fig. 50) (Selvadiini) ..... *Selvadius*
- Head with clypeus strongly arcuately emarginate in frontal view; postcoxal line of first abdominal ventrite recurved at outer end (Fig. 52) (Hyperaspidiini in part) ..... *Blaisdelliana*
- 41(39). Postcoxal line of abdomen reaching and joining posterior margin of ventrite; apex not recurved (Fig. 49); distal maxillary palpomere securiform, strongly expanded distally (as in fig. 30) (Diomini in part) ..... 42
- Postcoxal line of abdomen not reaching posterior margin of ventrite; continuing parallel to margin (Fig. 50) or with apex recurved (Figs. 52, 54); distal maxillary palpomere roughly parallel-sided or barallel-shaped (as in Fig. 31), at most only weakly expanded distally (Scymnini in part) ..... 43
- 42(41). Antenna with 11 antennomeres ..... *Diomus*
- Antenna with 10 antennomeres (Fig. 23) ..... *Decadiomus*
- 43(41). Prosternum with distinct carinae on intercoxal process; carinae often reaching anterior margin of prosternum (Fig. 16) ..... *Scymnus*
- Prosternum lacking distinct carinae, or with only abbreviated ridges near coxal cavities ..... 44
- 44(43). Postcoxal line complete, recurved to base of first abdominal ventrite (Fig. 54) ..... *Didion*
- Postcoxal line incomplete, not reaching base nor lateral margin of first abdominal ventrite; apex recurved (Fig. 52) or parallel to posterior margin (Fig. 50) ..... *Nephus*
- 45(13). Tarsal claws each with a small median triangular tooth (Fig. 46); postcoxal line of abdomen not recurved toward anterior margin of ventrite (Fig. 49); specimens 6.0 to 10.0 mm in length; elytron vittate, or solid brown to beige in color .... *Myziazia*
- Tarsal claws variable; if small triangular tooth present, then position of tooth more apical (Fig. 48) and postcoxal line of abdomen absent (Fig.

FIGURE 20.93-39.93. 20. diagram: variation in form/length of antenna: a shorter antenna with gradually formed club typical of scymnines (left), a longer antenna with more abruptly differentiated club typical of coccinellines and coccidulines (right); 21. Chilacorini, antenna; 22. *Scymnus* sp. (Scymnini), antenna; 23. *Decadiomus* sp. (Diomini) antenna; 24. *Brachiacantha* sp. (Brachiacanthini), antenna, apical part (rotated to expose inner surface) note specialized membranous sensory area of last two antennomeres, typical of Brachiacanthini, Hyperaspidiini, Selvadiini (art: E. Roberts); 25. *Delphastus* sp., antenna; 26. *Rodolia* sp. (Noviini), antenna; 27. *Nephaspis* sp., antenna; 28. *Pseudoscymnus* sp., antenna; 29. Coccinellini (generalized), maxillary palpus; 30. *Rodolia* sp. (Coccidulinae; Noviini), maxillary palpus; 31. *Zagloba* (Scymnini), maxillary palpus; 32. *Cephaloscymnus* (Sticholotidinae; Cephaloscymnini), maxillary palpus, apical part; 33. *Microweisea* (Sticholotidinae; Microweiseini), maxillary palpus, apical part; 34. *Stethorus* sp., (Stethorini; Scymninae), maxillary palpus; 35. *Hyperaspis* sp. (Hyperaspidiini; Scymninae), maxillary palpus; 36. Coccinellini, mandible; 37. Chilacorini, mandible; 38. Epilachnini, mandible; 39. Halyziini, mandible. (Some figures modified from the works of Sasaji and Gordon; Figures 36-39 after Kovár 1996a).

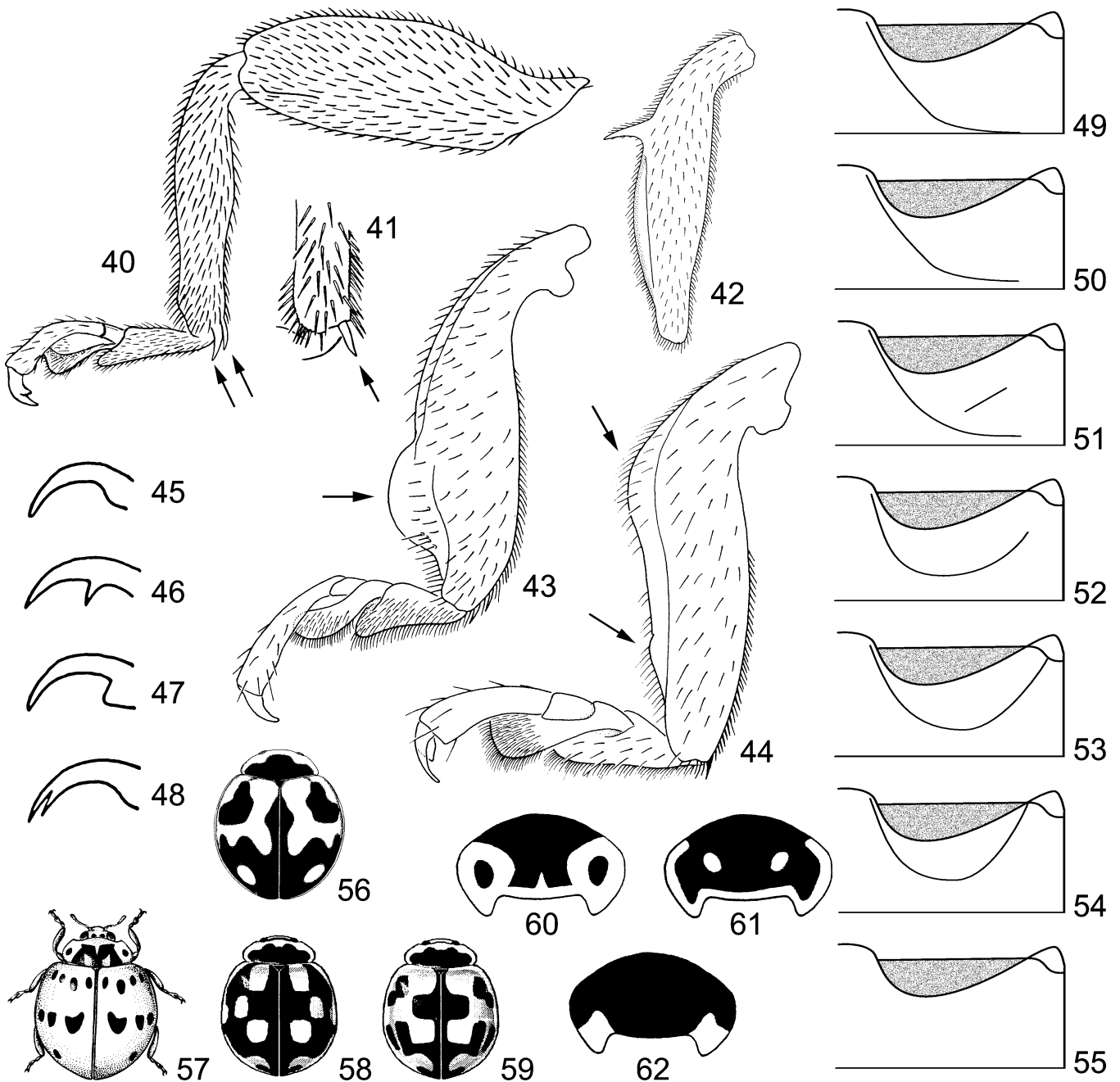


FIGURE 40.93-62.93. 40. *Myzia* sp. (Coccinellinae; Coccinellini), hind leg, arrows indicate position of paired tibial spurs; 41. *Anisosticta* sp. (Coccinellinae; Coccinellini), apex of hind tibia, arrow indicates position of single tibial spur; 42. *Brachiacantha* sp. (Brachiacanthini), front tibia; 43. *Helesius* sp. (Hyperaspidini), front leg, arrow shows position of preapical semi-circular expansion of tibia; 44. *Thalassa* sp. (Hyperaspidini), front leg, arrows show positions of rounded basal expansion (above) and subangulate preapical expansion (below); 45.-48. different configurations of the tarsal claw: 45. simple; 46. with triangular median tooth; 47. with subquadrate basal tooth; 48. with apical cleft; 49.-55. Left side of first abdominal ventrite showing different forms of postcoxal line(s): 49. postcoxal line merges with posterior margin of ventrite, not recurved at apex; 50. postcoxal line runs parallel to posterior margin of ventrite; 51. postcoxal line as above, but with oblique line present; 52. postcoxal line recurves at apex, incomplete; 53. postcoxal line reaches midpoint of lateral line; 54. postcoxal line reaches inner margin of lateral line; 55. postcoxal line obsolete; 56.-59. Dorsal color patterns: 56. *Rodolia cardinalis* (Mulsant); 57. *Olla v-nigrum* (Mulsant); 58. *Propylea quatuordecimpunctata* (L.), darker form; 59. as previous, lighter form; 60.-62. pronotal color patterns: 60. *Cycloneda* sp.; 61. *Cycloneda* sp. 62. *Coccinella* sp. (Some figures modified from the works of Gordon)

- 55) or recurved toward anterior margin of segment (Figs. 52-54) ..... 46
- 46(45). Surface between pronotal punctures not shagreened; anterior margin of mesosternum with deep, broad, triangular emargination ..... *Calvia*  
 — Surface between pronotal punctures shagreened; anterior margin of mesosternum truncate, with shallow emargination or with deep but narrow emargination ..... 47
- 47(46). Prosternum strongly convex and thickened along midline, with anterior face forming a wide, hairy, triangular platform at middle; antenna with distal margin of ninth and tenth antennomeres protuberant on inner side; body form rhomboidal to oval (Fig. 1); 7.0 to 10.0 mm in length ..... *Anatis*  
 — Prosternum and antenna not as above; body form and size variable ..... 48
- 48(47). Postcoxal line of first abdominal ventrite always present, joining or running parallel to posterior margin of ventrite (Figs. 49, 50); oblique dividing line often present (Fig. 51). Body form compact subcircular to slightly elongate oval (Figs. 4, 3); tips of femora hidden by or just visible beyond lateral margins of elytra (Figs. 4, 3) ..... 57  
 — Postcoxal line of abdomen absent (Fig. 55) or recurved toward anterior margin of segment (Figs. 52-54); body form elongate oval to highly elongate oval or elliptical (Figs. 3, 2); tips of femora just visible to well extended beyond lateral margins of elytra (Figs. 3, 2) ..... 49
- 49(48). Tarsal claw not toothed or cleft, simply widened basally (Fig. 45) ..... 50  
 — Tarsal claw toothed or cleft (Figs. 47, 48) ..... 53
- 50(49). Pronotal base with fine entire marginal bead; abdomen with postcoxal line obsolete (Fig. 55) .... 51  
 — Pronotal base without marginal bead; abdomen with postcoxal line distinct (Fig. 52) ..... 52
- 51(50). Elytron with large black spots; metasternum with postcoxal line ..... *Naemia*  
 — Elytron vittate; metasternum without postcoxal line ..... *Paranaemia*
- 52(50). Apex of middle and hind tibia each with 2 spurs (Fig. 40); elytron with straight, regular vittae; epipleuron declivitous ..... *Macronaemia*  
 — Apex of middle and hind tibia each with single spur (Fig. 41); elytron spotted, or with spots joined to form irregular and sinuous vittae; epipleuron horizontal ..... *Anisosticta*
- 53(49). Tarsal claw cleft near apical 1/3 (Fig. 48) ..... *Hippodamia*  
 — Tarsal claw with subquadrate basal tooth (Fig. 47) ..... 54
- 54(53). Metasternum and first abdominal ventrite (Figs. 52-54) with distinct postcoxal lines ..... 55  
 — Metasternum without postcoxal line; first abdominal ventrite without postcoxal lines (Fig. 55) or with a trace indication only ..... *Coleomegilla*
- 55(54). Apex of middle and hind tibia each with pair of spurs (Fig. 40) ..... 56
- Apex of middle and hind tibia each without spurs ..... *Aphidecta*
- 56(55). Pronotal base arcuate, without marginal bead; body form slightly elongate oval (Fig. 3) ..... *Adalia*  
 — Pronotal base sinuate, with marginal bead; body form highly elongate (Fig. 2) ..... *Ceratomegilla*
- 57(48). Apex of middle and hind tibia without spurs ..... 58  
 — Apex of middle and hind tibia with pair of spurs (Fig. 40) ..... 60
- 58(57). Postcoxal area of first abdominal ventrite without an oblique dividing line (Fig. 50) ..... *Mulsantina*  
 — Postcoxal area of first abdominal ventrite with an oblique dividing line (Fig. 51) ..... 59
- 59(58). Scutellum with apical angle much more acute and attenuated than basal angles ..... *Harmonia*  
 — Scutellum with apical and basal angles similar ..... *Neoharmonia*
- 60(57). Hind margin of mesepimeron with median triangular projection; pronotal hypomeron with a well defined fovea to accommodate the antennal club ..... *Coelophora*  
 — Hind margin of mesepimeron straight or curved, without projection; pronotal hypomeron without a well defined fovea ..... 61
- 61(60). Pronotum black with large, subtrapezoidal or triangular white spot on each anterolateral angle (Fig. 62); elytral ground color yellow to red with black bands or spots in many ..... *Coccinella*  
 — Pronotal and elytral color pattern not as above .... 62
- 62(61). Pronotum black with white lateral border and discal spot in each lateral third (Fig. 61); spot may be connected anteriorly and laterally to form a complete or broken ring-shaped mark (Fig. 60); elytra without black markings (Fig. 63) ..... *Cycloneda*  
 — Pronotum not as above; elytra with black markings ..... 63
- 63(62). Distal antennomere elongate, oval; scutellum with base slightly longer than side; maculation on elytron typically forming a yellow and black "checkerboard" pattern (Figs. 58, 59) .. *Propylea*  
 — Distal antennomere short, robust, obtriangular; scutellum with side slightly longer than base. Elytron black with red spot or pale, ashen with minute dark spots not forming a "checkerboard" pattern (Fig. 57) ..... *Olla*

## CLASSIFICATION OF THE NEARCTIC GENERA

## Coccinellidae Latreille 1807

For most of the genera listed below, keys to the North American species, morphological and habitus illustrations and other useful information can be found in Gordon (1985). This citation will not be repeated for each entry. More recent papers are referenced below along with older but more complete works when appropriate.

## Sticholotidinae Weise 1901

Pharini Casey 1899 (unavailable, preoccupied type genus)  
 Pharini Ganglbauer 1899 (unavailable, preoccupied type genus)  
 Sticholotini Weise 1901  
 Clanini Weise 1901 (unavailable, preoccupied type genus)  
 Coelopterini Della Beffa 1912  
 Sticholotidinae Gordon 1977 (emendation)

**Diagnosis.** North American members of this subfamily can be easily distinguished by the shape of the terminal maxillary palpomere which is distinctly elongate (Fig. 32, 33): conical, oval, or parallel-sided with an oblique apex (taxa from other parts of the world may have this palpomere shortened or distally expanded). Additional diagnostic characteristics include: mentum generally narrowly articulated with submentum (Fig. 17); middle coxal cavities broadly separated; size less than 3.0 mm; dorsal surfaces glabrous or hirsute.

Gordon (1977) discusses the taxonomy, phylogeny and zoogeography of the New World members. Kovár (1996b) provides a revised phylogeny which recognizes two phyletic series, each with a distinct form to the metendosternite and genitalia of both sexes. Gordon (1994b) contributes additional West Indian genera to the tribe Sticholotidini. Predominantly scale predators, but *Delphastus* (Serangiini) are predacious on whiteflies.

## Microweiseini Leng 1920

Pharini Casey 1899 (unavailable, preoccupied type genus)  
 Microweiseini Gordon 1985 (incorrect subsequent spelling)

*Microweisea* Cockerell 1903 (new name for *Epismilia* Cockerell 1900). New World, from southern Canada into South America; 5 species described from north of Mexico.

*Smilia* Weise 1891, not Germar 1833

*Epismilia* Cockerell 1900, not Fromental 1861 (new name for *Smilia* Weise)

*Pseudoweisea* Schwarz 1904 (name made available by accident)

*Coccidophilus* Brethes 1905. New World; 2 species described from north of Mexico; *C. atronitens* (Casey), California, Nevada, Arizona, Oregon, and Utah; *C. marginata* (LeConte), Maine, New York, Pennsylvania, New Jersey, and Michigan; 1 additional new species reported from Florida (Peck and Thomas 1998).

*Cryptoweisea* Gordon 1970

*Gnathoweisea* Gordon 1970. Known only from North America; 6 species, California, Nevada, Arizona, New Mexico, and Texas.

*Nipus* Casey 1899. Southwestern United States; 4 species, California, Utah, Wyoming, Arizona, and Colorado.

## Serangiini Pope 1962

Serangiini Blackwelder 1945 (unavailable name, published without description).

*Delphastus* Casey 1899. New World; 3 species from north of Mexico: Rhode Island, Connecticut, New York, west to California, south to Texas and Florida. Gordon (1994c) revises, keys and illustrates members of the genus from the Western Hemisphere.

*Oeneis* LeConte 1852, not Mulsant 1850

*Cryptognatha* Crotch 1874 (in part), not Mulsant 1850

*Lioscymnus* Champion 1913

## Cephaloscymnini Gordon 1985

*Cephaloscymnus* Crotch 1873. New World, most diverse in the tropics; 3 species from north of Mexico with scattered distributional data: Illinois, New Jersey, Maryland, Virginia, West Virginia, District of Columbia, Indiana, Tennessee, South Carolina, Texas, New Mexico, Arizona, California.

## Scymninae Mulsant 1846

Scymniens Mulsant 1846

Scymninae Della Beffa 1912

**Diagnosis.** Antennae relatively short (Fig. 22-24, 27, 28), usually two-thirds head width or less (Fig. 20, left); middle coxal cavities broadly separated; size generally less than 3.0 mm (except *Cryptolaemus*, *Thalassa*). Mentum broadly articulated with submentum (Fig. 18). This tribe is difficult to characterize and probably polyphyletic; antennae are of at least two different types, exemplified by *Scymnus* (Fig. 22) and allies, on the one hand, and *Hyperaspis* and allies (Fig. 24), on the other; maxillary palpus (Fig. 31, 34, 35) with terminal palpomere parallel-sided (e.g., Scymnillini) to barrel-shaped (e.g., Scymnini), short and weakly convergent apically (Stethorini), or more or less securiform and apically expanded (Hyperaspidini, Brachiacanthini, Selvadiini, Diomini). Predacious on various Homoptera and mites.

## Scymnillini Casey 1899

Zilini Gordon 1985 (unnecessary replacement name for Scymnillini)

Note: This tribe has many affinities with Sticholotidini (Sticholotidinae) and may be misclassified in Scymninae. The two included genera are predacious on whiteflies.

*Zilus* Mulsant 1850. Primarily neotropical with 4 species recorded from the United States; in the east, from Maryland to Florida and west to Wisconsin with disjunct localities in Louisiana; in the west from Idaho and Washington to California and Arizona.

*Scymnus* (*Zilus*) Mulsant 1850

*Scymnillus* Horn 1895

*Scymnillodes* Sicard 1922

*Zagloba* Casey 1899. New World tropical and temperate; 4 species from north of Mexico: Oregon, California, Arizona, Texas, and Florida.

#### Stethorini Dobzhansky 1924

*Stethorus* Weise 1885. Worldwide; 5 species widely distributed north of Mexico. Predators of spider mites. Gordon and Chapin (1983) treated the Western Hemisphere species.

#### Scymnini Mulsant 1846

Scymniaires Mulsant 1846

Scymnini Costa 1849

*Nephaspis* Casey 1899. 4 neotropical species, one of which, *N. oculatus* (Blatchley), established in scattered localities in the United States: Florida, Louisiana, Texas, Iowa, and Vermont.

*Nephasis*: Korschefsky 1931 (error)

*Cryptolaemus* Mulsant 1853. 1 species, *C. montrouzieri* Mulsant, introduced from Australia for biocontrol of *Planococcus citri* (Risso); established in Indiana, Missouri, Florida, and California.

*Didion* Casey 1899. Restricted to North America; 3 species, generally distributed.

*Scymnus* Kugelann 1794. Worldwide distribution. Gordon (1976b) revised the genus north of Mexico.

subgenus *Scymnus* Kugelann 1794. 11 species, widely distributed north of Mexico.

subgenus *Pullus* Mulsant 1846. 82 species, widely distributed north of Mexico.

*Pseudoscymnus* Chapin 1962 (replacement name needed; preoccupied by *Pseudoscymnus* Herre 1935). *Pseudoscymnus tsugae* McClure and Sasaji, imported from Japan to control woolly hemlock adelgid, *Adelges tsugae* Annand, has become established at release sites in Connecticut, Virginia, and New Jersey.

*Clitostethus* Kamiya 1961, not *Clitostethus* Weise 1885

*Nephus* Mulsant 1846. Worldwide (at least nominally); 5 subgenera are recognized in the New World fauna. Gordon (1976b, 1985) revised the genus from north of Mexico.

subgenus *Nephus* Mulsant 1846. 1 species, *N. (N.) ornatus* LeConte, with 2 subspecies, United States and Canada

subgenus *Sidis* Mulsant 1850 (as subgenus of *Scymnus*). 1 species, *N. (Sidis) binaevatus* (Mulsant), California.

subgenus *Turboscymnus* Gordon 1976b. 1 species, *N. (Turboscymnus) georgei* (Weise), California, Oregon, Idaho, Alberta, Ontario, and Quebec (Paquin and Duperré 2000).

subgenus *Scymnobius* Casey 1899. 9 species, widely distributed in the United States, extending into southern Canada.

subgenus *Depressoscymnus* Gordon 1976b. 1 species, *N. (Depressoscymnus) schwartzi* Gordon, Arizona.

Diomini Gordon 1999

*Diomus* Mulsant 1850. Worldwide; 18 species recorded from north of Mexico, generally distributed. The generic placement of some of these species may need to be reassessed. Primarily mealybug predators. Gordon (1999) revised the South American members of *Diomus* and related taxa.

*Decadiomus* Chapin 1933. Primarily Caribbean; 1 species, *D. babamicus* (Casey) reported in Florida (Peck and Thomas 1998).

Selvadiini Gordon 1985

*Selvadius* Casey 1899. A New World genus; 4 species occur north of Mexico: Texas, Arizona, California, and Colorado. Prey unknown; possibly scale insects.

Hyperaspini Mulsant 1846

Hyperaspiens Mulsant 1846

Iperaspini Costa 1849 (= Hyperaspini)

Hyperaspini Casey 1899

Hyperaspides Crotch 1873

Hyperaspidae Berg 1874

Hyperaspites Chapuis 1876

Hyperaspidina Jacobson 1916

Hyperaspini Wingo 1952 (emendation)

*Blaisdelliana* Gordon 1970. Monobasic genus; *B. sexualis* (Casey), California, Arkansas, and Utah.

*Helesius* Casey 1899. Only 3 known species; 2 species in North America: Montana, Colorado, and Texas; 1 species, Colombia.

*Thalassa* Mulsant 1850. Neotropical with 6 described species, 1 species, *T. montezumae* Mulsant, penetrating north of Mexico: Arizona, Texas, and Louisiana.

*Hyperaspis* Redtenbacher 1844. Worldwide; 94 species north of Mexico, generally distributed. Predators of various Homoptera.

*Oxynebus* LeConte 1850

*Hyperaspidius* Crotch 1873. New World; 26 species, generally distributed in the United States and southern Canada; undescribed species occur in Mexico and Central America. Predators of scale insects and mealybugs.

Brachiacanthini Mulsant 1850

Brachyacanthaires Mulsant 1850

Brachiacanthadini Duverger 1989:143

Brachyacanthadini Duverger 1989 (misspelling)

Brachiacanthini Pakaluk *et al.* 1994 (emendation)

*Brachiacantha* Dejean 1837. New World; 25 species north of Mexico, generally distributed. Predators of coccids in ant nests and possibly other Homoptera.

*Brachyacantha* Chevrolat 1842 (unjustified emendation).

#### Cryptognathini Mulsant 1850

Cryptognathaires Mulsant 1850

Pentiliaires Mulsant 1850

Oeneini Casey 1899 (genus preoccupied)

Cryptognathini Gordon 1971

Oeniini Gordon 1985 (error)

*Cryptognatha* Mulsant 1850. Neotropical; 1 species, *C. nodiceps* Marshall, introduced from Trinidad for biocontrol of *Aspidiotus destructor* Signoret, established in Florida.

#### Chilocorinae Mulsant 1846

Chilocoriens Mulsant 1846

Exochomaires Mulsant 1850

Chilocorinae Sasaji 1968

Clanini Pakaluk *et al.* 1994 (presumably based on *Clanis* Mulsant 1850, misspelling of *Cladis* Mulsant 1850; not Clanini Weise 1901, see entry under Sticholotidinae)

**Diagnosis.** North American members of this subfamily all belong to the tribe Chilocorini (tribes Telsimiini, Platynaspini and Aspidimerini occur in the Eastern Hemisphere), and can be readily identified by the following combination of character states: eye canthus deeply dividing eye (Fig. 10), broad, band-like, expanded to cover basal antennomeres from dorsal or frontal view; clypeus not projecting, with semicircular emargination medially; antenna (Fig. 21) of ten or fewer antennomeres, with spindle-shaped flagellum; mandible (Fig. 37) scythe-like with single apical tooth; tibia angulate externally in many species; dorsum apparently glabrous (North America natives), but may exhibit lateral pubescence at least on pronotum; only the introduced species *Exochomus metallicus* Korschefsky has the pronotum and elytron evenly covered with moderately long silky hair. Predominantly scale predators, but some species known to feed on mealybugs, aphids, adelgids and psyllids.

#### Chilocorini Mulsant 1846

Chilocoriens Mulsant 1846

Exochomaires Mulsant 1850

Chilocorini Costa 1849

Clanini Pakaluk *et al.* 1994 (presumably based on *Clanis* Mulsant 1850, misspelling of *Cladis* Mulsant 1850; not Clanini Weise 1901, see entry under Sticholotidinae)

Chapin (1965) revised the genera of the World. Kovár (1995) treated members of the genera, *Brumus*, *Brumoides* and *Exochomus*, but focused primarily on the palearctic fauna.

*Brumoides* Chapin 1965 (*sensu lato*, not *Brumoides sensu* Kovár 1995 who restricted use of this name to certain Old World species). 3 species, 1 with 3 subspecies, widely distributed in the United States but absent from the southeastern states, extending into Canada.

*Brumus* (of authors; not Mulsant 1850)

*Brumus* Mulsant 1850 (in part). 1 introduced palearctic species, *B. quadripustulatus* (L.), transferred from *Exochomus* by Kovár (1995).

*Axion* Mulsant 1850. 2 species; *A. plagiatum* (Olivier), Pacific Coast and southwestern states from Oregon to Louisiana; *A. tripustulatum* (De Geer), Pennsylvania south to Florida, west to Colorado and Texas.

*Curinus* Mulsant 1850. Neotropical; 1 adventive species, *Curinus coeruleus* (Mulsant), reported in Florida (Peck and Thomas 1998).

*Arawana* Leng 1908. New World; 1 species in North America, *A. arizonica* (Casey), Arizona.

*Exochomus* Redtenbacher 1843 (*sensu lato*). Worldwide; 9 species north of Mexico, generally distributed. The 7 native nearctic species which have a non-bordered pronotal base are excluded from *Exochomus sensu* Kovár (1995), but as no alternative placement is provided, they remain in *Exochomus* for the time being. Only the two introduced species, *E. flavipes* and *E. metallicus* with bordered pronotal base belong to *Exochomus sensu* Kovár (1995) (see also *Brumus*).

*Halmus* Mulsant 1850. 1 species, *H. chalybeus* (Boisduval), introduced from Australia, established in California.

*Orcus* Mulsant 1850

*Chilocorus* Leach 1815, in Brewster. Worldwide; 8 species in North America, generally distributed.

#### Coccidulinae Mulsant 1846

Cocciduliens Mulsant 1846

Trichosomides Mulsant 1846 (unavailable name, not based on genus)

Coccidulinae Sasaji 1968

**Diagnosis.** Members of this subfamily are difficult to characterize, but can usually be recognized by the following combination of character states: Dorsal surfaces conspicuously pubescent; body length 2.0 to 7.5 mm; antenna usually long (more than two-thirds head width) (Fig. 20, right), loosely articulated, with irregularly shaped club (externally serrate or papillate), but shorter, more compact in Noviini (Fig. 26) and Exoplectrini; meso- and metasternum narrowly articulated; maxillary palpus securiform (Fig. 30) to parallelsided; legs slender, simple, to flattened and highly modified. Predominantly scale predators.



## Coccidulini Mulsant 1846

Coccidulini Costa 1849  
 Rhizobiares Mulsant 1846  
 Cocciduliens Mulsant 1846  
 Coccidulides Crotch 1873  
 Rhizobiides Crotch 1874  
 Rhizobiini Weise 1885  
 Rhizobiinae Della Beffa 1912  
 Coccidulina Jacobson 1916

Gordon (1994a) revised the South American genera and species.

*Coccidula* Kugelann 1798. Europe and North America; 1 species, *C. lepida* LeConte, in northern United States and southern Canada.  
*Strongylus* Panzer 1813  
*Cacidula* Curtis 1827  
*Cacicula* Stephens 1828

*Rhyzobius* Stephens 1829. 2 species, southern United States.  
*Rhyzobius* Stephens 1832 (error)  
*Rhyzobius* Agassiz 1846 (unjustified emendation)  
*Lindorus* Casey 1899  
*Rhyzobiellus* Oke 1951 (unnecessary replacement name)

## Noviini Mulsant 1850

Noviaries Mulsant 1850  
 Rodoliares Mulsant 1850  
 Noviini Ganglbauer 1899

*Rodolia* Mulsant 1850. 1 species, *R. cardinalis* (Mulsant), South Carolina, Florida, Louisiana, Texas, New Mexico, Arizona, and California; introduced from Australia for biocontrol of *Icerya purchasi* Maskell.  
*Rodolia* (*Macronovius*) Weise 1885

*Anovia* Casey 1920. New World; 1 species, *A. virginalis* (Wickham), occurring north of Mexico: Texas, New Mexico, Arizona, and Utah.

## Exoplectrini Crotch 1874

Chnoodiens Mulsant 1850  
 Chnoodiaires Mulsant 1850  
 Siolaires Mulsant 1850  
 Exoplectrae Crotch 1874  
 Exoplectrides Gorham 1895  
 Exoplectrinae Weise 1904  
 Exoplectrini Casey 1908

*Exoplectra* Chevrolat 1837. Primarily neotropical; 1 species, *E. schaefferi* Gordon occurring north of Mexico: Arkansas.

## Azyini Mulsant 1850

Azyaires Mulsant 1850  
 Azyae Crotch 1874  
 Azyini Schilder and Schilder 1928  
 Azyinae Gordon 1994

Gordon (1980) revised the neotropical members of this tribe.

*Azya* Mulsant, 1850. Neotropical; 1 adventive species, *A. orbiger* Mulsant 1850 (= *A. luteipes* Mulsant 1850, misidentification in Woodruff and Sailer 1977) established in Florida.

*Pseudoazyia* Gordon 1980. Neotropical; 1 species, *P. trinitatis* (Marshall), released in the Miami, Florida area in 1938 and recovered in 1939, but no evidence to suggest survival in Florida after 1939.

## Coccinellinae Latreille 1807

Coccinellides Leach 1815, in Brewster  
 Aphidiphages LaPorte 1840  
 Gymnosomides Mulsant 1846  
 Coccinelliti Costa 1849  
 Coccinellidae Crotch 1873  
 Coccinellides Aphidiphages Chapuis 1876  
 Coccinellidae Aphidiphages Weise 1885  
 Coccinellinae Ganglbauer 1899

**Diagnosis.** This subfamily contains some of the larger, more conspicuously colored members of the North American lady beetle fauna, and can be easily recognized by the following combination of character states: dorsal surfaces glabrous; body length 1.75 to 10.5 mm; terminal maxillary palpomere securiform (Fig. 29); antenna two-thirds head width or longer (Fig. 20, right), with 11 antennomeres (except in some neotropical species). Primarily predacious on aphids and other Homoptera, but occasionally specializing in other prey groups; all members of the Halyziini feed on powdery mildews.

## Coccinellini Latreille 1807

Coccinellinae Latreille 1807  
 Adoniates Mulsant 1846  
 Coccinellaires Mulsant 1846  
 Coccinellates Mulsant 1846  
 Coccinelliens Mulsant 1846  
 Hippodamiaires Mulsant 1846  
 Micraspaires Mulsant 1846  
 Mysiates Mulsant 1846  
 Hippodamiini Costa 1849  
 Micraspidarii Costa 1849  
 Cariaires Mulsant 1850  
 Alesiaires Mulsant 1850

Coelophoraires Mulsant 1850  
 Cydoniaires Mulsant 1850  
 Coccinellina Thomson 1866  
 Coccinellides Thomson 1866  
 Coccinellidae Berg 1874  
 Hippodamiidae Berg 1874  
 Tythaspides Crotch 1874  
 Cariites Chapuis 1876  
 Coccinellites Chapuis 1876  
 Hippodamiutes Chapuis 1876  
 Coccinellini Weise 1885  
 Synonychini Weise 1885  
 Halyziides Gorham 1892 (in part)  
 Synonychinae Della Beffa 1912  
 Anisostictini Jacobson 1916  
 Coccinellina Jacobson 1916  
 Synonychina Jacobson 1916  
 Hippodamiina Dobzhansky 1926

*Paranaemia* Casey 1899. Monobasic genus; 1 species, *P. vittigera* (Mannerheim), western United States, western Canada.

*Naemia* Mulsant 1850. North America through Central America and the Caribbean; currently treated as 1 species with 2 subspecies; in the United States *N. s. seriata* Melsheimer ranges from Rhode Island, south to Texas (coastal localities); *N. s. litigiosa* Mulsant is recorded from southern California and southern New Mexico. This genus is in need of revision.

*Coleomegilla* Timberlake 1920. Restricted to the New World, most diverse in the tropics. Gordon (1985) followed Timberlake (1943) in recognizing 3 subspecies of *C. maculata* (DeGeer) from north of Mexico: *C. m. lengi*, eastern United States; *C. m. strenua*, south-western United States; and *C. m. fuscilabris* (Mulsant), South Carolina to Florida and west to Louisiana (coastal localities). Problems with the current species level classification are discussed in Krafusur and Obrycki (2000). This genus is in need of revision.

*Megilla* Mulsant 1850 (in part), not Fabricius 1805, not Erichson 1804

*Ceratomegilla* Crotch 1873. Monobasic; *C. ulkei* Crotch, Alaska, and arctic and subarctic Canada. Although separable from indigenous North American members of *Hippodamia*, *Ceratomegilla* is not so easily distinguished if the entire holarctic fauna is considered; generic limits in need of reassessment.

*Ceratomegilla* Malkin 1943 (in error)

*Megilla* Mulsant 1850 (in part), not Fabricius 1805, not Erichson 1804

*Spiladelphia* Tian-Shanskij and Dobzhansky 1923

*Hippodamia* (*Ceratomegilla*) Iablokoff-Khuzorian 1982

*Hippodamia* Dejean 1837. Primarily holarctic; 18 species occur north of Mexico (1 recently introduced), generally distributed. Chapin (1946) illustrates some of the variability of color patterns within the New World species.

*Hemisphaerica* Hope 1840

*Adonia* Mulsant 1846

*Anisosticta* Dejean 1837. Holarctic; 2 species in North America: *A. bitriangularis* (Say), Labrador to New Jersey, west to Alaska, California, and British Columbia; *A. borealis* Timberlake, Manitoba to Alaska.

*Anisostica* Malkin 1943 (error)

*Macronaemia* Casey 1899. Oriental and Nearctic; 1 species, *M. episcopalis* (Kirby) in North America: Ontario to New York, west to Yukon Territory and northern California.

*Micronaemia* Weise 1905

*Aphidecta* Weise 1899 (emendation). A monotypic, palearctic genus; *A. obliterata* (Linnaeus) was released in the United States and Canada for biocontrol of *Adelges piceae* (Ratzeburg); established in North Carolina.

*Aphidecta* Weise 1893 (error)

*Adalia* Mulsant 1846 (addenda). Worldwide; 1 holarctic species, *A. bipunctata* (L.), widely distributed in the United States and Canada, as well as temperate parts of South America (Argentina, Chile).

*Idalia* Mulsant 1846, not Hübner 1819

*Arrowella* Brethes 1925

*Coccinella* Linnaeus 1758. Primarily holarctic; 12 species occur in the United States, generally distributed. Brown (1962) and Brown (1967) provide keys, illustrations and additional discussion of this genus in the United States and Mexico respectively.

*Spilota* Billberg 1820

*Neococcinella* Savoyskaya 1969

*Dobzhanskia* Iablokoff-Khuzorian 1970

*Cycloneda* Crotch 1871. Primarily neotropical; 3 species, generally distributed north of Mexico. Gordon and Vandenberg (1993) provide a larval key to the North American species.

*Daulis* Mulsant 1850 (not Erichson 1842)

*Coccinellina* Timberlake 1943

*Harmonia* Mulsant 1850. An exotic genus with 3 introduced species, now widely distributed in the United States. Gordon and Vandenberg (1991) provide a key and illustrations of the introduced species. (Volume 2, Color Figure 31)

*Anatis* Mulsant 1846. Holarctic and neotropical (species from the latter region previously placed in other genera); 4 species occur north of Mexico; most common in coniferous forests, woodland habitats, urban plantings of mature trees.

*Myzgia* LeConte 1852 (in part)

*Pelina* Mulsant 1850

*Palla* Mulsant 1850, not Hübner 1819, not Billberg 1820

*Neopalla* Chapin 1955 (new name for *Pelina* Mulsant and *Palla* Mulsant)

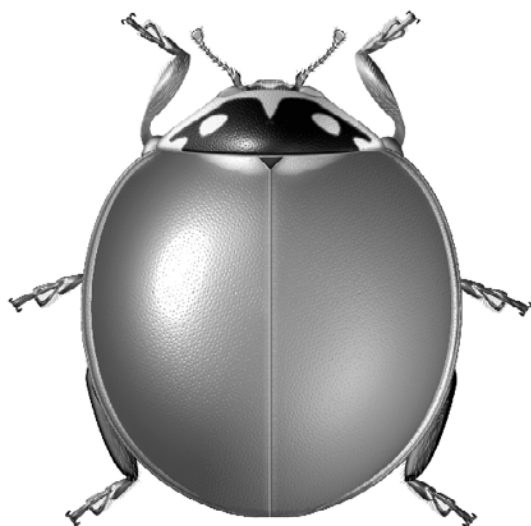


FIGURE 63.93. *Cycloneda sanguinea* Linnaeus.

*Myzina* Mulsant 1846. Holarctic and neotropical; 3 species north of Mexico, generally distributed; arboreal.

*Mysia* Mulsant 1846

*Neomysia* Casey 1899

*Calvia* Mulsant 1850. Primarily Old World; 1 holarctic species, *C. quatuordecimguttata* (L.), with numerous color forms, northern United States and Canada.

*Anisocalvia* Crotch 1871

*Eocaria* Timberlake 1943

*Propylaea* Mulsant 1846. Old World; 1 species, *P. quatuordecimpunctata* (L.) introduced into North America for control of various aphid species; established in eastern Canada southward along the eastern United States from Maine into New York, New Jersey, and Pennsylvania. Vandenberg and Gordon (1991) review and illustrate the known species.

*Propylaea* Mulsant 1846 (error)

*Coelophora* Mulsant 1850. Primarily Old World tropics, including Africa, Asia and Australia; 1 species, *C. inaequalis* (Fabricius 1775), introduced from Puerto Rico; eastern United States and Hawaii.

*Olla* Casey 1899. New World with 4 described species; 1 species, *O. v-nigrum* (Mulsant), generally distributed in the United States, complete range from southern Canada as far South as Argentina. Vandenberg's revision (1992) provides a key and illustrations of the known species.

*Neobarmonia* Crotch 1871. Only 1 species, *N. venusta* (Melsheimer), with 2 subspecies currently recognized, but these may well prove to be distinct; in North America, *N. v. venusta* widely distributed in the eastern half of the United States; *N. v. ampla* (Mulsant) recorded from Arizona, Texas and New Mexico. These and re-

lated taxa are well represented in the Neotropics as predators of chrysomelid eggs and larvae.

*Agrabia* Casey 1899

*Neobarmonia* Casey 1899, not Crotch 1871

*Harmoniaspis* Casey 1908

*Mulsantina* Weise 1906. Restricted to the New World; 4 species widely distributed in North America; primarily arboreal in habits. Chapin (1985) provides a key and illustrations of the known species (mostly North American). The diverse related fauna of South America has not been studied.

*Cleis* Mulsant 1850, not Guerin 1831

*Pseudocleis* Casey 1908

Halyziini Mulsant 1846

Halyziaires Mulsant 1846

Halyziates Mulsant 1846

Aliziarii Costa 1849 (= Halyziini)

Halyziides Gorham 1892 (in part)

Psylloborini Casey 1899

Halyziini Capra 1927

*Psyllobora* Dejean 1836. Worldwide, most diverse in the tropics; 6 species occur north of Mexico, generally distributed. Feed on powdery mildew.

*Psyllobora* (*Psyllobora*) Mulsant 1850

*Thea* Mulsant 1846

Epilachninae Ganglbauer 1899

Epilachniens Mulsant 1846

**Diagnosis.** North American members of this subfamily all belong to the tribe Epilachnini, and can be easily identified by the following combination of character states: Mandible (Fig. 38) with apex multidenticulate, bearing three or more large irregular teeth; all tibiae with one or two apical spurs present (North American fauna); dorsal surfaces pubescent; antenna inserted dorsally between eyes and distant from inner ocular margin (Fig. 9), long, loosely articulated, with 11 antennomeres and inner margin of club weakly serrated; eye bean-shaped without an abrupt notch or emargination; length 3.5 mm or greater. Gordon (1976a) revised the species of the Western Hemisphere.

Epilachnini Costa 1849

*Epilachna* Dejean 1837. Primarily neotropical; 3 species occur in the United States, but absent from western and northern central states. Two plant families serve as hosts for the North American species. *Epilachna borealis* (F.) and *E. tredecimnotata* (Latreille) feed on members of the Cucurbitaceae, *E. varivestis* Mulsant feeds on members of the Leguminosae.

*Solanophila* Weise 1898

*Afissa* Dieke 1947

*Subcoccinella* Huber 1842. Old World; 1 species, *S. vigintiquatuorpuntata* (L.), accidentally introduced from Europe where it is a pest of alfalfa; established in Illinois, Maryland, New Jersey, New York, Ohio, Pennsylvania, and West Virginia. Fortunately the established biotype feeds primarily on bouncing bet (*Saponaria officinalis* L.).

## BIBLIOGRAPHY

- BOOTH, R. G., M. L. COX and R. B. MADGE. 1990. IIE guides to insects of importance to man. 3. Coleoptera. University Press. Cambridge, 384 pp.
- BROWN, W. J. 1962. A revision of the forms of *Coccinella* L. occurring in America north of Mexico. Canadian Entomologist, 94: 785-808.
- BROWN, W. J. 1967. The Mexican forms of *Coccinella* (Coleoptera: Coccinellidae). Canadian Entomologist, 99: 107-108.
- CHAPIN, E. A. 1946. Review of the New World species of *Hippodamia* Dejean (Coleoptera: Coccinellidae). Smithsonian Miscellaneous Collections, 106(11): 1-39, pl. 1-22.
- CHAPIN, E. A. 1965. The genera of the Chilacorini (Coleoptera: Coccinellidae). Bulletin of the Museum of Comparative Zoology, 133: 227-271.
- CHAPIN, J. B. 1985. Revision of the genus *Mulsantina* Weise (Coleoptera: Coccinellidae). Annals of the Entomological Society of America, 78: 348-368.
- CHAZEAU, J. H., H. FÜRSCH and H. SASAJI. 1989. Taxonomy of Coccinellids. *Coccinella*, 1: 6-8.
- CROWSON, R. A. 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd. London, 187 pp.
- DREA, J. J. and R. D. GORDON. 1990. Coccinellidae. Pp. 19-40. In: D. ROSEN, ed. The armored scale insects, their biology, natural enemies and control, vol. B. Elsevier Science. Amsterdam.
- DUVERGER, C. 1989. Contribution à l'étude des Hyperaspinæ. 1ère note (Coleoptera, Coccinellidae). Bulletin de la Société Linnéenne de Bordeaux, 17: 143-157.
- FÜRSCH, H. 1996. Taxonomy of Coccinellids. *Coccinella*, 6: 28-30.
- GORDON, R. D. 1976a. A revision of the Epilachninae of the Western Hemisphere (Coleoptera: Coccinellidae). Agricultural Research Service, United States Department of Agriculture, Technical Bulletin, No. 1493: 1-409.
- GORDON, R. D. 1976b. The Scymnini (Coleoptera: Coccinellidae) of the United States and Canada: Key to genera and revision of *Scymnus*, *Nephus* and *Diomus*. Bulletin of the Buffalo Society of Natural Sciences, 28: 1-362.
- GORDON, R. D. 1977. Classification and phylogeny of the New World Sticholotidinae (Coccinellidae). Coleopterists Bulletin, 31: 185-228.
- GORDON, R. D. 1980. The tribe Azyini (Coleoptera: Coccinellidae): historical review and taxonomic revision. Transactions of the American Entomological Society (Philadelphia), 106: 1149-203.
- GORDON, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. Journal of the New York Entomological Society, 93: 1-912.
- GORDON, R. D. 1994a. South American Coccinellidae (Coleoptera) Part III: definition of Exoplectrinae Crotch, Azyinae Mulsant, and Coccidulinae Crotch; a taxonomic revision of Coccidulini. Revista Brasileira de Entomologia, 38: 681-775.
- GORDON, R. D. 1994b. West Indian Coccinellidae VI (Coleoptera): new genera and species of Sticholotidini and a cladistic analysis of included genera. Journal of the New York Entomological Society, 102: 232-241.
- GORDON, R. D. 1994c. South American Coccinellidae (Coleoptera) Part III: taxonomic revision of the Western Hemisphere genus *Delphastus*. Frustula Entomologica, (1994) 17(30): 71-133.
- GORDON, R. D. 1999. South American Coccinellidae Part IV: A systematic revision of the South American Diomini, new tribe. Annales Zoologici (Warsaw), 49 (Supplement 1): 1-219.
- GORDON, R. D. and E. A. CHAPIN. 1983. A revision of the New World species of *Stethorus* Weise (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington, 84: 250-255.
- GORDON, R. D. and N. J. VANDENBERG. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. Proceedings of the Entomological Society of Washington, 93: 845-864.
- GORDON, R. D. and N. J. VANDENBERG. 1993. Larval systematics of North American *Cycloneda* Crotch (Coleoptera: Coccinellidae). Entomologica Scandinavica, 24: 301-312.
- GORDON, R. D. and N. J. VANDENBERG. 1995. Larval systematics of North American *Coccinella* L. Entomologica Scandinavica, 26: 67-86.
- HODEK, I. and A. HONEK. 1996. Ecology of Coccinellidae. Kluwer Academic Publishers. Netherlands, 464 pp.
- IABLOKOFF-KHNZORIAN, S. M. 1982. Les Coccinelles, Coléoptères-Coccinellidae. Tribu Coccinellini des Régions Paléarctique et Orientale. Société Nouvelle des Éditions Boubée, Paris, 568 pp.
- KLAUSNITZER, B. and H. KLAUSNITZER. 1997. Marienkäfer (Coccinellidae). Die Neue Brehm-Bücherei, 451 pp.
- KOVÁR, I. 1995. Revision of the genera *Brumus* Muls. and *Exochomus* Redtb. (Coleoptera, Coccinellidae) of the Palaearctic Region. Part I. Acta Entomologica Musei Nationalis Pragae, 44(1995): 5-124.
- KOVÁR, I. 1996a. Morphology and anatomy. Pp. 1-18. In: I. Hodek and A. Honek, eds. Ecology of Coccinellidae. Kluwer Academic Publishers. Netherlands, 464 pp.
- KOVÁR, I. 1996b. Phylogeny. Pp. 19-31. In: I. Hodek and A. Honek, eds. Ecology of Coccinellidae. Kluwer Academic Publishers. Netherlands, 464 pp.
- KRAFSUR, E. S. and J. J. OBRYCKI. 2000. *Coleomegilla maculata* Degeer (Coleoptera: Coccinellidae) is a species complex. Annals of the Entomological Society of America, 93: 1156-1163.

- KUZNETSOV, V. N. 1997. Lady beetles of the Russian Far East. Memoir No. 1, Center for Systematic Entomology, Sandhill Crane Press. Gainesville, 248 pp.
- LAWRENCE, J. F. and A. F. NEWTON, Jr. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779-1006. *In*: J. Pakaluk and S.A. Slipinski, eds. Biology, phylogeny and classification of Coleoptera; papers celebrating the 80<sup>th</sup> birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw.
- LESAGE, L. 1991. Coccinellidae (Cucujoidea), the lady beetles, ladybirds. Pp. 485-494. *In*: F. W. Stehr, ed. Immature Insects. Vol. 2. Kendall/Hunt. Dubuque, Iowa.
- MAJERUS, M. E. N. 1994. Ladybirds. Harper Collins. London, 367 pp.
- PAKALUK, J., S. A. SLIPINSKI and J. F. LAWRENCE. 1994. Current classification and family-group names in Cucujoidea (Coleoptera). *Genus*, 5: 223-268.
- PAQUIN, P. and N. DUPÉRRÉ 2000. Biologie, répartition géographique et variation du patron élytral d'une coccinelle rarement trouvée en Amérique du Nord: *Nephus georgei* Weise (Coleoptera: Coccinellidae: Scymnini). *Faberies*, 25: 7-14.
- PECK, S. B. and M. C. THOMAS. 1998. A distributional checklist of the beetles (Coleoptera) of Florida. *Arthropods of Florida and Neighboring Land Areas*, 16: i-viii, 1-180.
- PHUOC, D. T. and STEHR, F. W. 1974. Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contributions of the American Entomological Institute*, 10: 1-125.
- POPE, R. D. 1979. Wax production by coccinellid larvae (Coleoptera). *Systematic Entomology*, 4: 171-196
- POPE, R. D. 1988. A revision of the Australian Coccinellidae (Coleoptera). Part I. Subfamily Coccinellinae. *Invertebrate Taxonomy*, 2: 633-735.
- POPE, R. D. and J. F. LAWRENCE. 1990. A review of *Scymnodes* Blackburn, with the description of a new Australian species and its larva (Coleoptera: Coccinellidae). *Systematic Entomology*, 15: 241-252.
- REES, B. E., D. M. ANDERSON, D. BOUK, and R. D. GORDON. 1994. Larval key to genera and selected species of North American Coccinellidae (Coleoptera). *Proceedings of the Entomological Society of Washington*, 96: 387-412.
- SASAJI, H. 1968. Phylogeny of the family Coccinellidae (Coleoptera). *Etizenia, Occasional Publications of the Biological Laboratory, Fukui University*, 35: 1-37.
- SASAJI, H. 1971a. Fauna Japonica. Coccinellidae (Insecta: Coleoptera). Academic Press of Japan, Keigaku Publishing. Tokyo, ix + 340pp, 16pls.
- SASAJI, H. 1971b. Phylogenetic positions of some remarkable genera of the Coccinellidae (Coleoptera), with an attempt of the numerical method. *Memoirs of the Faculty of Education, Fukui University, Series II (Natural Science)*, 21: 55-73.
- SLIPINSKI, S. A. and J. PAKALUK. 1991. Problems in the classification of the Cerylonid series of Cucujoidea (Coleoptera). Pp. 79-88. *In*: M. Zunino, X. Belles and M. Blas, eds. *Advances in Coleopterology*. European Association of Coleopterology. Barcelona.
- TIMBERLAKE, P. H. 1943. The Coccinellidae or ladybeetles of the Koebele collection. Part 1. *Bulletin of the Experiment Station of the Hawaiian Sugar Planters' Association, Entomological Series*, 22: 1-67.
- VANDENBERG, N. J. 1990. First North American records for *Harmonia quadripunctata* (Pont.) (Coleoptera: Coccinellidae); a lady beetle native to the palaearctic. *Proceedings of the Entomological Society of Washington*, 92: 407-410.
- VANDENBERG, N. J. 1992. Revision of the New World lady beetles of the genus *Olla* and description of a new allied genus (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America*, 85: 370-392.
- VANDENBERG, N. J. and R. D. GORDON. 1991. Farewell to *Pania* Mulsant (Coleoptera; Coccinellidae); a new synonym of *Propylea* Mulsant. *Coccinella*, 3: 30-35.
- WHITEHEAD, D. R. and R. M. DUFFIELD. 1982. A specialized predator-prey association (Coleoptera: Coccinellidae, Chrysomelidae): failure of a chemical defense and possible practical application. *Coleopterists Bulletin*, 36(1): 96-97.
- WOODRUFF, R. E. and R. I. SAILER. 1977. Establishment of the genus *Azya* in the United States. Florida Department of Agriculture and Consumer Services, Division of Plant Industry, *Entomology Circular*, 230: 1-2.