# Adult heteropteran thoracic endoskeleton (Insecta: Hemiptera): A family-level study 

Adult Heteropteran Thoracic Endoskeleton<br>A Family-Level Study<br>Gale E. Ridge, Ph.D.<br>University of Connecticut, 2008

The integument is the outer layer of the insect, comprising the epidermis and the cuticle.
Relative shape and degree of development of the integument show extensive variation, associated with body proportion and form. The endoskeleton is a series of cuticular invaginations of the cuticle into the body cavity that provides structural support for trunk and appendicular muscle attachment.

This study examines endoskeletal structures in the hemipteran suborder Heteroptera ("true bugs"), to determine their homologies and to learn if there is sufficient variation within the suborder to draw tentative conclusions as to similarities among heteropteran families. The endoskeleton has been described in many arthropod lineages, and the various structures have been termed apodemes, apophyses, fasciae, furcae, phragmata, bridges etc. Much has been written about soft tissue anatomy in Heteroptera, but little notice has been paid to the endoskeleton, especially to the thoracic endoskeleton. Previous authors briefly examined the thoracic endoskeleton of some species, but because of their focus on soft tissue (muscles) there was no detailed analysis of the internal cuticle. Although the heteropteran thorax has long been regarded as taxonomically important and scientists have observed and illustrated the endoskeletal structures the fact that these structures may have morphological and/or phylogenetic relevance seems to have escaped attention.

Nomenclature used in previous literature has been somewhat inconsistent. This study on the thoracic endoskeleton and its structures addresses this deficit. Because of the lack of
consistency among earlier works, terminology had to be standardized and so a new and consistent morphological nomenclature is provided here.

Understanding at what level character variation occurs is important and the suborder Heteroptera, a well studied group, was chosen for this purpose. It is a reasonably well-known group with a well supported phylogeny. The group contains seven infraorders, Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha or possibly eight including Aradimorpha, 75 families, and approximately 37,000 described species. Species from the orders Hymenoptera and Diptera as well as from the hemipteran suborder Auchenorrhyncha were also examined, to determine if identical or similar structures occur in other insect groups.

Gale E. Ridge - University of Connecticut, 2008
The abstract is not paginated.

# Adult Heteropteran Thoracic Endoskeleton 

(Insecta: Hemiptera)
A Family-Level Study
Book 1 (Part I)
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A Dissertation<br>Submitted in Partial Fulfillment of the<br>Requirements for the Degree of<br>Doctor of Philosophy at the<br>The University of Connecticut

2008

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## APPROVAL PAGE

Doctor of Philosophy Dissertation

## Adult Heteropteran Thoracic Endoskeleton (Insecta: Hemiptera)

A Family-Level Study

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## ACKNOWLEDGMENTS

This is a project of broad scope. With a single stroke it encompasses the study of numerous families in the suborder Heteroptera with many thousands of species existing in all corners of the earth. Work such as this could not have be undertaken, but for contributions of many who generously gave their invaluable assistance and expertise without reserve. Foremost among these, is Dr. Carl Schaefer, an indomitable spirit of wit and intellectual sagacity, who in spite of fighting cancer during the creation of this thesis, never faltered in offering a giant's eye view of the field. My special thanks also extends to my committee, Dr. Charles Henry, Dr. Steven Burian and Dr. Louis Magnarelli for their contributions and support in shepherding this document through to its conclusion. Thanks to the insect collections archivists Dr. Jane O'Donnell, University of Connecticut and Dr. Ray Pupedis, Yale Peabody Museum for their assistance with specimens.

The scanning electron micrographs could not have been made, but for the assistance of Mr. Jim Romanow, in the Department of Physiology and Neurobiology at the University of Connecticut, who sat at my elbow for many hours, as I pushed the equipment to perfect the skills for making nearly 600 images, and additionally Dr. Marie Cantino who gave me the opportunity to use the electron microscope for long very periods with an implicit trust in my skills.

Others who deserve thanks are, Dr. Claire Rutledge, Dr. Kirby Stafford, Mr. Mike
Thomas, Dr. Charles Vossbrinck, Mr. Steven Daniels and my patient family.

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## Introduction

The integument is the outer layer of the insect, comprising of epidermis and cuticle (Chapman2006), with the combined functions of skin and body armor (Neville 1990). The endoskeleton is "a cuticular invagination into the body cavity from the body wall (integument) that provides structural support and serves for points of muscle attachment." (Gordh 2001, p 317; Bitsch 2002, Duporte 1959, Goel 1967, Khamma 1963, Larsén 1945, Parsons 1960, 1963, Snodgrass 1942, Weber 1930) (Figs. 1a, 33b). The endoskeleton has various structures termed apodemes, apophyses, fasciae, furcae, phragmata, and bridges (Figs. 1, 35, 37c, etc.). All are used for trunk and appendicular muscle attachment, weight management, flexibility, and body cavity strength. Relative shape and degree of development depend on body form and taxon.

The purpose of the study is to examine these structures in the Hemiptera: Heteroptera ("true bugs"), to assess their homologies and determine if there is sufficient variation within the suborder to draw tentative hypotheses of relationship among heteropteran families.

Endoskeletal structures have been described in many arthropod lineages. Generalized morphological examinations are found in Snodgrass (1935, 1952), Bitsch \& Bitsch (2002), and Manton (1964). Although studies of the head capsule and genitalia of insects are numerous (e.g., Rempel 1975, Scudder 1971, Akbar 1957,and Snodgrass 1935, 1957), there are no all-inclusive studies specific to the thoracic endoskeleton. In particular, there is no comprehensive account of the endoskeleton in Heteroptera. Larsén (1942), Malouf (1932), and Parsons (1960, 1963) briefly examined the thoracic endoskeleton of some species, but because their focus was on soft
tissue (muscles) there was no detailed analysis of the internal cuticle. In fact much has been written about soft tissue anatomy in Heteroptera, with little notice paid to the endoskeletal structures (Weber 1930; Goel 1967; Lauck 1959; Larsen 1945; Malouf 1932; Matsuda 1960; Snodgrass 1929, 1942, 1947; Bitsch \& Bitsch 2002; Parsons 1960, 1963, Gibson 1985). Although the heteropteran thorax has long been regarded as taxonomically important (Taylor 1918; Larsen 1945; Brindley 1934, 1938; Crampton 1914; Weber 1930), and scientists have observed the endoskeletal structures and illustrated them, (Parsons 1960; Weber 1930), the notion that these structures may have morphological and/or phylogenetic relevance seems to have escaped their attention.

Nomenclature used in previous literature (Snodgrass 1935, Duporte 1959, Lauck 1959, Gibson 1985) was somewhat inconsistent. Here, I address this deficit, and a new and consistent morphological nomenclature for the thoracic endoskeleton is provided.

Understanding at what level character variation occurs is important and Heteroptera, a well studied group, was chosen for this purpose. Heteroptera, a suborder of the order Hemiptera, is a reasonably well-known group with a well supported phylogeny. The group contains seven infra-orders, Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha (Schuh 1979; Schuh and Slater 1995) or eight including Aradimorpha (Schaefer 1981, 1993; Sweet 1996, 2006); 75 families, (Schuh and Slater 1995); and approximately 37,000 described species. Species from the orders Hymenoptera and Diptera as well as the Hemipteran suborder Auchenorrhyncha were also examined to determine if identical or similar structures occur in other insect groups.

## Materials and Methods

## Specimen records

178 species from 39 families in 6 of 7 infraorders were studied (Appendix 1).
Dipsocoromorpha were not examined because specimens were unavailable. The sample size was small for a suborder of 37,000 described and possibly 25,000 undescribed species (Schaefer, unpublished). However, these specimens provided a wide range of morphological features that included 32 identifiable endoskeletal characters with useful information on family-level phenotypic trends. Collections and/or holdings numbers follow each record. Species names were taken from specimen labels, but many subsequently changed after being checked in the modern literature (e.g., Miridae [Schuh 1995, Kerzhner 2001]). Abbreviations for institutions and private collections were as follows: CAES, Connecticut Agricultural Experiment Station; CWS, Carl W. Schaefer collection, University of Connecticut; GR, Gale E. Ridge collection; LM, Louis A. Magnarelli collection, Connecticut Agricultural Experiment Station; PMNH, Peabody Museum of Natural History, Yale University; UCONN, University of Connecticut.

## Heteroptera

## Enicocephalidae

UNITED STATES: Hymenocoris formicinia Uhler, apterous female, California: Marin Co., Mill Valley, 360 Lee St, 6. VIII.1966, det. G. E. Ridge (UCONN). H. formicinia, apterous male, California: Marin Co., Mill Valley, 360 Lee St, 6. VIII.1966, det. G. E. Ridge (UCONN). TANZANIA: Enicocephalidae species undetermined; macropterous female, light trap,

Mlingano: 9. X. 1965, det. G. E. Ridge (CWS). Enicocephalidae species undetermined; macropterous male, light trap, Mlingano: 9. X. 1965, det. G. E. Ridge (CWS).

## Gerridae

UNITED STATES: Aquarius remigis Say, female, Minnesota: 1 male, 2 females, Anoka Co., Cedar Creek, County Rd., 31. XI. 1978, det. D.V. Bennett (UCONN). A. remigis, Connecticut: Tolland Co., Storrs, 3. V. 1959, det. K. Stedhens (UCONN). A. remigis, female with 50 unlaid eggs, male Wyoming: Teton Co., Leigh Lake, $3 / 4$ mile north of effluent, 18. VII. 1979, det. D.V. Bennett (UCONN). A. remigis, California: Scott R., T44-AS, RQW, SEC 32, SE ¼ Mobam, III. 1973, det. Calabrese (UCONN). Gerris insperatus Drake \& Hottes, Connecticut: Tolland Co., Storrs, 12. IV. 1954, det. Calabrese 1973 (UCONN). Limnoporus canaliculatus (Say)

Connecticut: Windham Co., Scotland pond by Merrick Brook, 1. X.1975, det. V. Picchi. (UCONN). L. notabilis (Drake \& Hottes), Washington State, Okanogan Co., pond at R23E T33, 2. IX. 1977, det. G. Stonedahl (\#107462 PMNH). Gerris nyctalis Drake \& Hottes, 2 specimens, Washington State, Whatcom Co. Canyon lake, 19. VIII. 1977, det. G. Stonedahl (\#105046 PMNH). Rheumatobates palosi Blatchley, Minnesota, Bengall, 18. VII. 1922, det. D. V. Bennett 1980 (UCONN). ECUADOR: Halobates robustus Barber, 2 specimens, Galápagos Islands: Isabela Island, IS: Bahia Cartago, 10. II.1978, det. Lanna Cheng 1983 (\#106671 PMNH).

Veliidae
UNITED STATES: Rhagovelia obesa Uhler, Connecticut: Hartford Co., Canton, Farmington River, off Route 44, 7. X. 1973, det. M. I. Wallans (CAES). Microvelia americana (Uhler)

Connecticut: Tolland Co., Mansfield, Chafville Pond, 24. IX. 1965, det. C. L. Smith (UCONN).

Rhagovelia distincta Chapman, Connecticut: Tolland Co., Mansfield, Fenton River, 19.
IX.1975, det. W. Starkel (UCONN). R. distincta, 2 specimens, Oregon: Benton Co., Corvallis, Willamette River, 1 mile south, 28. IX. 1961, det. G. Stonedahl 1980 (\#107899 PMNH). M. californiensis McKinstry, Oregon: Linn Co. Holly, 9 miles east, 800 ft., 29. IV. 1961, det. C. L. Smith (\#107900 PMNH).

## Macroveliidae

UNITED STATES: Macrovelia hornii Uhler, Oregon: Coos Co., Bandon, 1 mile south of Sunset Motel, 1. IX. 1961, det. J. D. Lattin (\#107997 PMNH). M. hornii, Oregon: Coos Co., Bandon, 1 mile south of Sunset Motel, 1. IX. 1961, det. J. D. Lattin (\#107991 PMNH).

## Hydrometridae

ENGLAND: Hydrometra stagnorum (Linnaeus) Cambridgeshire Co: Cambridge, 7. VII. 1918, det. G. E. Hutchinson (\#107476 PMNH). UNITED STATES: H. martini Kirkaldy, Connecticut: Tolland Co., Storrs, 7. V. 1955, det. N. T. Davis (CAES).

## Mesoveliidae

UNITED STATES: Mesovelia mulsanti White, apterous, Connecticut: Tolland Co., Eagleville, 7. X. 1965, det. G. E. Ridge (UCONN). M. mulsanti, macropterous, Connecticut: Tolland Co., Mansfield, 26. X. 1965, det. G. E. Ridge (UCONN, macropterous). M. mulsanti, apterous, Connecticut: Tolland Co., Mansfield Center, 18. VII. 1968, label damaged det. G. E. Ridge (CAES). M. mulsanti, macropterous, Connecticut: Tolland Co., Mansfield Center, 18. VII. 1968, det. G. E. Ridge (CAES). M. mulsanti, Oregon: Benton Co., Corvallis, McFadden Pond, 20. IX. 1952, det. J. D. Lattin 1963 (\#108043 PMNH). ITALY: M. furcata Mulsant \& Rey, male,

Campania: Agnano, 4. X.1925, det. G. E. Hutchinson (\#107468 PMNH). M. furcata, female,

Campania: Agnano, 4. X.1925, det. G. E. Hutchinson (\#48120 PMNH).
Hebridae
UNITED STATES: Hebrus buenoi Drake \& Harris, Oregon: Malheur Co., Adrian, Snake River, 2,200 ft., 14. VII. 1964, det. G. Stonedahl 1980 (\#107965 PMNH). H. burmeisteri Lethierry \& Severin, Connecticut: New Haven Co., North Haven, 2. VII. 1924, det. W. E. Britton (CAES). H. burmeisteri, Connecticut: New Haven Co., North Haven, 2. VII. 1924, det. W. E. Britton (CAES).

## Pleidae

UNITED STATES: Neoplea striola (Fieber), Connecticut: Fairfield Co., Ridgefield, Norwalk River, QL7, 22. IX. 1983, (CAES). Paraplea puella (Barber), Ohio: Franklin Co., 19. IV. 1968, (\# 34304 PMNH). Pleidae species undetermined, Connecticut: Tolland Co., Route 6, small pond opposite Hop Rd., near oxbow, 30. V. 1990, (\#34392 PMNH).

## Notonectidae

UNITED STATES: Notonecta undulata Say, Connecticut: Tolland Co., Mansfield, Dennis Pond, near dam, 9. X. 1965, det. E. Dennis (UCONN). N. undulata, Connecticut: Tolland Co., Mansfield, Dennis Pond, near dam, 9. X. 1965, det. E. Dennis (UCONN). N. irrorata Uhler, Connecticut: Tolland Co., Windsor, 2. X. 1962, det. J. B. Kring (CAES). SOUTH AFRICA: Viridis meridionalis Hutchinson, (species complex), Napier to Caledon Rd., grassy pool, 1.IV. 1929, det. G. E. Hutchinson (\#107471 PMNH).

## Naucoridae

UNITED STATES: Pelocoris femoratus (Palisot), Connecticut: Litchfield Co., Salisbury, 19. VI. 1935, det. M. P. Zappe (CAES).

## Gelastocoridae

UNITED STATES: Gelastocoris sp., Connecticut: Tolland Co., Coventry Twp., Wrights Mill Rd., 3. VII. 1975, det. H. B. Hodge (UCONN). Gelastocoris oculatus (Fabricius), Oregon:

Wasco Co., Maupin City Park, Bakeoven Creek, 17. VI. 1964, det. G. Stonedahl 1980 (\# 34349
PMNH). G. oculatus, New Jersey: Cape May Co., Belmar, 10. IX. 1940, det. G. E. Ridge (\#34462 PMNH). BRAZIL: Nerthra hapaeformis (Fabricius), Nova Teutonia, $27^{\circ} 11^{\prime}$ B. $52^{\circ} 23^{\prime}$ L, VIII.1958, det. J. T. Polhemus (\#34440 PMNH).

## Corixidae

UNITED STATES: Hesperocorixa sp. macropterous, California: Siskiyou Co., Scott River, 6. I. 1973, det. S. S. Dunlap (UCONN). H. interrupta (Say), Connecticut: Tolland Co., Tolland Township, Ladd Rd., near Kendall Hill, 16. X. 1971, det. A. Jansson (UCONN). H. atopodonata (Hungerford), Connecticut: Tolland Co., Mansfield Township, Separatist Pond, 5.X.1971, det. A. Janssen (UCONN). Trichocorixa louisianae Jaczewski, Florida: Highland Co., Archbold Biological Station, 7. VI. 1969, det. A. Jansson (UCONN). SCOTLAND: Callicorixa alaskensis Hungerford, Inner Hebrides: Gigha, Loch 3, VI. 1922, det. G. E. Hutchinson (\#107457 PMNH). C. wollastoni (Douglas \& Scott), Inner Hebrides: Jura hills west of Craighouse, 23. VI. 1922, det. G. E. Hutchinson (\#107466 PMNH). ENGLAND: Retrocorixa semistriata (Fieber), Cumberland Co.: Edenhale, Whiris Pond, 11.X. 1921, (\#107474 PMNH).

## Nepidae

UNITED STATES: Ranatra fusca Palisot, female, Minnesota: Koochiching Co., Birchdale, Rainy River, 3 miles west of Birchdale, T159N R37 W525, 19. X. 1979, det. D. V. Bennett 1980 (CWS). Nepa apiculata Uhler, Minnesota: Isanti Co., Lader Ct., at county road 36, bridge, 13.
X. 1978, det. D. V. Bennett (CWS).

## Belostomatidae

UNITED STATES: Belostoma flumineum Say, Connecticut: Middlesex Co., Cromwell, 9 IV. 1919, det. K. F. Chamberlain (CAES). Lethocerus griseus (Say), Connecticut: New London Co., New London, 7, V. 1923, det. G. E. Ridge (CAES). L. americanus (Leidy), Connecticut:

Litchfield Co., Winchester, 27. IV. 1937, det. G. E. Ridge (CAES).

## Saldidae

UNITED STATES: Pentacora hirta (Say), female, Connecticut: Tolland Co., Stonington, Barn Island salt marsh, 26. VII. 1978, 1981 (UCONN). P. hirta, male, Connecticut: Tolland Co., Stonington, Barn Island salt marsh, 26. VII. 1978, 1981 (UCONN). P. sphacelata (Uhler), Connecticut: New London Co., Pattagansett marshes, high tide area, 2 VII. 1975, det. D. Calabrese (CAES). Saldula saltatoria (Linnaeus), Connecticut: Fairfield Co., Greenwich, Audubon Sanctuary, 2 IX. 1970, det. R. T. Schuh (UCONN).

## Cimicidae

UNITED STATES: Cimex lectularius Linnaeus, Connecticut: New Haven Co., New Haven, 18.
XII. 2001, det. G. E. Ridge 2 specimens. C. lectularius, Connecticut: Fairfield Co., Danbury, Hotel Green, 20. VI. 1919, det. J. A. Slater 1972 (\#106119 PMNH). C. lectularius, Connecticut:

Fairfield Co., Bridgeport, 10. IV.2001, det. G. E. Ridge. Oeciacus vicarious Horvath, California:
Orange Co., cliff swallow nest, birds absent, 17. XII. 1983, det. G. E. Ridge (UCONN).

## Anthocoridae

UNITED STATES: Orius insidiosus (Say), female, macropterous, Massachusetts: Berkshire Co., Pittsfield, 3. VII. 1969, det. G. E. Ridge (UCONN). Anthocoridae sp. Nevada: Washoe Co.,

Reno, Caughlin Park, found on Salix, 17. VIII. 1982 (\#105685 PMNH). ISRAEL: Anthocoridae sp. Jordan Valley: Tibeirias, 22. I. 1984 (\#105683 PMNH).

## Nabidae

CANADA: Nabis americoferus Carayon, female, New Brunswick: Fredericton, 13. IX.1961, det. D. E. Leonard (UCONN). UNITED STATES: N. rufusculus Reuter, 2 specimens,

Connecticut: Tolland Co., Colebrook, 12. IX. 1937, det. N. Turner (CAES). Nabicula subcoleoptrata Kirby, Connecticut: New Haven Co., Woodbridge, 29. VII. 1936, det. G. H. Nettleton (CAES).

## Miridae

UNITED STATES: Adelphocoris lineolatus (Goeze), Connecticut: Hartford Co., Poquonock, Farmington River, 22. VII. 1970, det. F. P. Maroney (CAES). Capsus ater (Shilling),

Connecticut: New Haven Co., West Haven, 27. VI. 1905, det. Van Duzee (CAES).
Coccobaphes frontifer Walker, Connecticut: New Haven Co., South Meriden, 26. VI. 1939, det. H. J. Johnson (CAES). C. frontifer, Connecticut: Hartford Co., Windsor, 24. VI. 1937, det. M. P. Zappe (CAES). Leptopterna dolabrata Linnaeus, Connecticut: New Haven Co., New Haven, 16. VI. 1902, det. E. J. Moore (CAES). Lygocoris quercalbae (Knight), 2 specimens, Connecticut: New Haven Co., New Haven, on paper under peaches after spraying, 12. VI. 1936, det. P. Garman (CAES). L. pabulinus Linnaeus, Connecticut: New Haven Co., New Haven, 3. X. 1920, det. H. H. Knight (CAES). L. pabulinus, Connecticut: New Haven Co., New Haven, 25. VI. 1920, det. H. H. Knight (CAES). Poecilocapsus lineatus (Fabricius), Connecticut: New Haven Co., New Haven, 13.VI.1918, det. M. P. Zappe (CAES). P. lineatus, Connecticut: New Haven Co., Stonington, 5.VII.1906, det. J. A. Hyslop (CAES). Tropidosteptes amoenus Reuter,

Connecticut: New Haven Co., East New Haven, on Ash, 25. VI. 1938, det. M. P. Zappe (CAES). T. cardinalis Uhler, Connecticut: New London Co., Lyme, 16. VI. 1918, det. H. H. Knight (CAES). T. cardinalis, Connecticut: New Haven Co., North Branford, 8. VI. 1912, det. H. H. Knight (CAES). T. palmeri (Reuter), male, Connecticut: Tolland Co., Colebrook, 21. VII. 1905, det. H. L. Vaillant (CAES). T. palmeri, female, Connecticut: Tolland Co., Colebrook, 21. VII. 1905, det. H. L. Vaillant (CAES). T. palmeri, male, on Ash, Connecticut: Litchfield Co., Washington, 24. VI. 1914, det. H. L. Vaillant (CAES). T. palmeri, female, on Ash, Connecticut: Litchfield Co., Washington, 24. VI. 1914, det. H. L. Vaillant (CAES). Microphylellus flavipes Provancher, Connecticut: New Haven Co., Mt., Carmel, 10. VI. 1908, det. W. E. Britton (CAES). Lygidea mendex Reuter, Connecticut: New Haven Co., New Haven, 1. VII. 1914, det. H. H. Knight (CAES). L. mendex, Connecticut: New Haven Co., Wallingford, 5. VII. 1911, det. H. H. Knight (CAES). L. rosacea Reuter, male, Minnesota: Ramsey Co., 18. VII. 1922, det. H. H. Knight 1923 (CAES). Prepops fraternus (Knight), Pennsylvania: Harrisburg, 28. VI. 1912, det. Chamberlain (CAES). P. nigricollis (Reuter), Connecticut: New Haven Co., Branford, 21. VII. 1920, det. G. E. Ridge (CAES). P. nigricollis, Connecticut: Litchfield Co., Sharon, 10. VII. 1936, det. M. P Zappe (CAES). P. insitivus (Say), Connecticut: Mount Carmel, 2. VI. 1936, det. N. Turner (CAES). Slaterocoris atritibialis (Knight), female, Connecticut: New Haven Co., West Haven, 27. VI.1905, det. G. E. Ridge (CAES). Inacora malina (Uhler), Middlesex Co., Portland, 21. VI. 1925, det. B. H. Walden (CAES). Collaria oculata (Reuter), Connecticut: Fairfield Co., Stratford, 24. VII. 1942, det. J. P. Johnson (CAES). C. oculata, Connecticut: Litchfield Co., Woodbury, 17. VI. 1939, det. G. E. Ridge (CAES). Lygus lineolaris (Palisot \& Beauvois), Connecticut: New Haven Co., Orange, 2. VII. 1970, det. G. E. Ridge (CAES).

Microphylellus flavipes Provancher, Connecticut: New Haven Co., 10. VI. 1908, det. W. E. Britton (CAES). M. flavipes, Connecticut: Hartford Co., 14. VI. 1938, det. M. P. Zappe (CAES). Orthotylus cruciatus Van Duzee, Connecticut: New Haven Co., South Meriden, 30. VI. 1937, det. L. Johnson (CAES). O. cruciatus, Connecticut: Tolland Co., East Granby, 2. VII. 1936, det. N. Turner (CAES). Pseudoxenetus regalis Uhler, Connecticut: New Haven Co., Milford, 3. VI. 1941, det. M. P. Zappe (CAES). P. regalis, Connecticut: New Haven Co., New Haven, 16. VI. 1928, det. J. L. Rogers (CAES). Plagiognathus albatus (Van Duzee), Connecticut: New Haven Co., New Haven, collected from Sycamore, 16. VII. 1940, det. G. E. Ridge (CAES). P. albatus, Connecticut: New Haven Co., Guilford, collected from Butternut, 13. VII. 1920, det. H. H. Knight (CAES). P. politus Uhler, Connecticut: New Haven Co., New Haven, 23. VII. 1904, det. Van D. (CAES). P. politus, Connecticut: New Haven Co., New Haven, 7. VII. 1920, det. G. E. Ridge (CAES). P. obscurus Uhler, Connecticut: New Haven Co., Meriden, 7. VII. 1910, det. W. E. Britton (CAES). P. obscurus, Connecticut: New Haven Co., New Haven, 6. VII. 1904, det. Von D. (CAES). Orectoderus obliquus Uhler, Connecticut: Tolland Co., Gilead, 18. VI. 1936, det. N. Turner (CAES). Atractotomus mali (Meyer-Dür), male, on apple tree, Connecticut: New Haven Co., Mount Carmel, 11. VI. 1964, det. D. E. Leonard (CAES). A. mali, female, on apple tree, Connecticut: New Haven Co., Mount Carmel, 11. VI. 1964, det. D. E. Leonard (CAES). Lopus decolor (Fallén), Connecticut: New Haven Co., New Haven, 9. VII. 1921, det. H. H. Knight (CAES). L. decolor, Connecticut: Litchfield Co., Cornwall, 18. VII. 1921, det. H. H. Knight (CAES). Pilophorus laetus Heidemann, Connecticut: New Haven Co., New Haven, 29. VII. 1921, det. H. H. Knight 1922 (CAES). P. laetus, Connecticut: Litchfield Co., Cornwall, 17. VII. 1921, det. H. H. Knight 1922 (CAES). Lopidea caesar (Reuter), Connecticut: New Haven

Co., Oxford, 7. VII. 1939, det. H. J. Johnson (CAES). L. robiniae (Uhler), Connecticut: New Haven Co., 11. VII. 1920, det. B. H. Walden (CAES). L. robiniae, caught in Japanese beetle trap, Connecticut: New Haven Co., 1. VIII. 1932, det. G. E. Ridge (CAES). L. media (Say), insect internally injured, Connecticut: Tolland Co., Mansfield Center, 26. VI. 1957, det. J. A. Slater (CAES). L. media, on salix, Connecticut: Tolland Co., Mansfield Center, 22. VI. 1957, det. J. A. Slater (CAES). Melanotrichus flavosparsus Carvalho \& Afonso, male, on Cherry and Peach trees, Connecticut: Hartford Co., Southington, 28. VIII. 1936, det. G. E. Ridge (CAES). M. flavosparsus, female, on cherry and peach trees, Connecticut: Hartford Co., Southington, 28. VIII. 1936, det. G. E. Ridge (CAES). Ceratocapsus modestus (Uhler), Connecticut: Hartford Co., Collinsville, East river, 30. VII. 1910, det. G. E. Ridge (CAES). Trigonotylus ruficornis (Geoffroy), Connecticut: Hartford Co., Rocky Hill, 3. VIII. 1938, det. J. B. Kaston (CAES). T. ruficornis, Connecticut: Hartford Co., Rocky Hill, 25. VI. 1936, det. J. B. Kaston (CAES). Tupiocoris rubi (Knight), Massachusetts: Berkshire Co., Monterey, 3. VII. 1939, det. H. L. Johnson (CAES). T. rubi, Connecticut: New Haven Co., Guilford, 13. VII. 1920, det. H. H. Knight 1921 (CAES). Monalocoris americanus Wagner \& Slater, Connecticut: New Haven Co., New Haven, 6. VII.. 1924, det. W. E. Britton (CAES). M. americanus, Connecticut: New London Co., Lyme, 20. VIII. 1910, det. G. E. Ridge (CAES).

## Tingidae

UNITED STATES: Corythucha marmorata (Uhler), Connecticut: New Haven Co., Durham, 2. X. 1965, det. L. Torres-Miller \& J. A Slater (UCONN). C. caryae carya Bailey, Massachusetts: Essex Co., Byfield, 22. VIII. 1947, (\#35033 PMNH). C. pergandei Heidemann, Massachusetts: Essex Co., Forest Hills, N.S.B. Arboretum, 9. VIII. 1945, det. N. S. Bailey (\#35272 PMNH).

Gargaphia angulata Heidemann, Massachusetts: Middlesex Co., Framingham, 15. VI. 1948, det. N. S. Bailey (\#35200 PMNH). Melanorhopala clavata (Stål), Connecticut: New Haven Co., Orange, 2. VII. 1970, det. J. A. Slater (UCONN).

## Reduviidae

UNITED STATES: Arilus cristatus (Linnaeus), female, New Haven Co., Madison, 1. IX. 1946, det. M. P. Zappe (CAES). Reduvius personatus (Linnaeus), North Carolina: date ?, det. G. E. Ridge (UCONN). Pselliopus cinctus (Fabricius), Connecticut: Tolland Co., Mansfield Township, Storrs, 7. X. 1956, det. N. T. Davis (UCONN). Sinea diadema (Fabricius), male, Connecticut: Tolland Co., Mansfield Township, Storrs, 12. XI. 1972, det. G. E. Ridge (UCONN). S. diadema, female, Connecticut: Tolland Co., Mansfield Township, Storrs, 12. XI. 1972, det. G. E. Ridge (UCONN). Zelus exsanguis Stål, Connecticut: Tolland Co., Vernon Township, Rockville, 8. VIII. 1971, det.G. E. Ridge (UCONN). Melanolestes picipes (HarrichSchaeffer), Connecticut: New Haven Co., Hamden, 2. IV. 1968, det. G. E. Ridge (CAES). Acholla multispinosa (DeGeer), Connecticut: New Haven Co., Madison, 10. VIII. 1919, det. K. F. Chamberlain (CAES). S. diadema, Connecticut: New Haven Co., Hamden, 23 IX. 1931, det. G. H. Plumb (CAES). Stenopodainae sp. Amyot \& Serville, Florida: Highland Co., Archbold Biological Station, 11. VIII. 1964, det. J. A. Slater (UCONN). GUATEMALA: Triatoma dimidiata Latreille, male, date ?, coll, J. F. Anderson, det. G. E. Ridge (CAES). Rhodnius prolixus Stål, female, date?, coll, J. F. Anderson, det. G. E. Ridge (CAES). R. prolixus, male, date?, coll., J. F. Anderson, det. G. E. Ridge (CAES).

Phymatidae
BRAZIL: Phymatidae sp. a. Nova Teutonia, $27^{\circ} 11^{\prime}$ B. $52^{\circ} 23^{\prime}$ L, $300-500 \mathrm{~m}, \mathrm{X} .1963$, (\#37672

PMNH). UNITED STATES: Phymatidae sp. b. Texas: Taylor Co., New Abilene, Camp Berkley, 31. VII. 1943, det. C. L. Remington (\#37783 PMNH). Phymatidae sp. c. Massachusetts: Franklin Co., Heath, 10. VIII. 1982, (\#37720 PMNH).

## Aradidae

UNITED STATES: Mezira sp. Amyot \& Serville, brachypterous, Texas: Dallas, III, 2002, det. J. O'Donnell (UCONN). Aradus robustus robustus Uhler, Connecticut: New Haven Co., Stonington, V. 1914, det.G. E. Ridge (CAES). Aradus quadrilineatus Say, Connecticut: Middlesex Co., Hampton, 29. V. 1942, det. M. P. Zappe (CAES). A. quadrilineatus, Texas: Lamar Co., near Paris, Camp Maxey, 23. I. 1944, det. J. A. Slater 1972 (\#105589 PMNH). A. similis Say, Connecticut: New Haven Co., New Haven, 27.IV.1962, det. J. A. Slater 1972 (\#105555 PMNH). A. crenatus Say, Indiana: Monroe Co., Bloomington, 3. V. 1954, det. R. F. Hussey (\#105593 PMNH). COSTA RICA: Aradus sp., La Selva: 1. II. 2000, det. C. Rettenmeyer (UCONN).

## Cydnidae

BRAZIL: Cydnidae. Nova Teutonia, $27^{\circ} 11^{\prime}$ B. $52^{\circ} 23^{\prime}$ L, 300-500m, XI. 1963 (\#39307 PMNH). UNITED STATES: Cydnidae. small specimen, North Carolina: Granville Co., Bullock, 13. VII. 1983, (\#39379 PMNH). Amnestus sp., light trap, Florida: Highland Co., Archbold Biological Station, 7. VI. 1969, coll. J. Harrington, T. Schuh, J. Slater.

## Pentatomidac

UNITED STATES: Acrosternum hilare (Say), Connecticut: Tolland Co., Mansfield Township, Storrs, 22. V. 1944, det. L. R. Penner (UCONN). Mormidea lugens (Fabricius), Connecticut: Tolland Co., Mansfield Township, Storrs, 30.V. 1964, det. J. A. Slater (UCONN). TURKEY:

Codophila sp. female, Bornova-Izmir, 26. VII. 1955, det. C. W. Schaefer (CWS). Brochymena arborea (Say), Connecticut: Hartford Co., Wallingford, 13. VII. 1910, det. G. E. Ridge (CAES). BRAZIL: Edessa sp. Nova Teutonia, $27^{\circ} 11^{\prime}$ B. $52^{\circ} 23^{\prime}$ L, 300-500m, IX. 1967, (\#195239 PMNH).

## Scutelleridae

UNITED STATES: Eurygaster alternata (Say), Connecticut: Tolland Co., Union, 2 miles N. E., E. N. E., 17. V. 1970, det. J. A. Slater (UCONN). Homaemus aeneifrons (Say), Connecticut: Windham Co., Scotland, 30. VII. 1904, det. Van Duzee (CAES).

Acanthosomatidae

UNITED STATES: Elasmucha lateralis (Say), Alaska: North Star Co., Fairbanks, II. 1956, det.
C. O. Esselbaugh (UCONN). Elasmostethus cruciatus (Say), New Hampshire: Carroll Co., Crawford Notch, 21. VIII. 1930, (\#105460 PMNH).

## Tessaratomidae

INDIA: Tessaratoma javanica (Thunberg), Kerala State: Quilon District, V. 1985, det. C. W. Schaefer (CWS).

Thyrecoridae
UNITED STATES: Thyreocoridae sp., small, Florida: Sarasota Co., Myakka River State Park, 5. IV. 1985, (\#44225 PMNH). Thyreocoridae sp., large, Colorado: Gunnison Co., Gothic, Virginia Mine, 10,500ft, 12,VIII, 1967, (\#44233 PMNH). Galgupha atra Amyot \& Serville,

Connecticut: Tolland Co., Union, 25. VI. 1937, det. M. P. Zappe (CAES). Galgupha aterrima Malloch, Connectcut: Litchfield Co., Salisbury, 30, VI. 1955, det. G. E. Ridge (CAES).

## Parastrachiidae

JAPAN: Parastrachia japonensis (Scott), E. I. Kagoshima: Genkawa, 16. VIII. 1961, det. T. Kawanahe (CWS).

## Coreidae

UNITED STATES: Anasa tristis (DeGeer), 11 males \& 14 females, Connecticut: New Haven Co., Cheshire, 6 North Pond Rd., 2. XI. 2000, det. G. E. Ridge. A. tristis: 5 males \& 5 females, Connecticut: New Haven Co., Cheshire, 152 Talmadge Rd., 20. IX. 2001, det. G. E. Ridge. Leptoglossus corculus (Say), male, light trap, North Carolina: Wake Co., Raleigh, 26. VII. 1969, det. G. E. Ridge (UCONN). L. corculus, female, taken from Pinus virginiana, North Carolina: Montgomery Co., Uwharrie National Forest, Junction SR1179 \& Governor Rd., 597, 4. VIII. 1992, det. G. E. Ridge (UCONN). L. phyllopus (Linnaeus), Florida: Duval Co., Jacksonville, 10. VII. 1913, det. G. E. Ridge (CAES). L occidentalis Heidemann, male and female, Connecticut: Fairfield Co., Fairfield, 10. X. 1997, det. G. E. Ridge. Loccidentalis, male, North Carolina: 15. XI. 1997, det. G. E. Ridge. L occidentalis, female, North Carolina, 15. XI. 1997, det. G. E. Ridge. Acanthocephala terminalis (Dallas), Ohio: Erie Co., Sandusky, 21. VI. 1924, det. G. E. Ridge (UCONN). A. terminalis, taken from Willow, Maryland: Anne Arundel Co., Crownsville, 9. VII. 1907, det. G. E. Ridge (UCONN). Thasus neocalifornicus Brailovsky \& Barrera, Arizona: Santa Cruz Co., 12 miles south of Sonoita, Hidden Springs Canyon, 22. VIII. 1968, det. R. Packauskas (\#43156 PMNH). T. neocalifornicus, Baja California, Boca de la Sierra, 30. IX. 1967, det. C. W. Schaefer (CWS). Petillia calcar Dallas, Arizona: date ?, det. C. W. Schaefer (CWS). JAPAN: Hygia opaca Uhler, taken from Circium nipponicum, Tokyo: Hachioji, Mount Mitake, 14. VII. 1976, det. H. Mori (CWS).

## Alydidae

UNITED STATES: Alydus eurinus (Say), Connecticut: Tolland Co., Mansfield Center, 12. IX. 1967, det. G. E. Ridge (UCONN). A. pilosulus Herrich-Schaeffer, Connecticut: Tolland Co., Mansfield Center, 19. IX. 1967, det. G. E. Ridge (UCONN). A. pilosulus Connecticut: Tolland Co., Mansfield Center, 9. IX. 1967, det. J. A. Slater (UCONN). Megalotomus quinquespinosus (Say), Connecticut: Hartford Co., South Meriden, 29. IX. 1936, det. H. L. Johnson (CAES). KOREA: Alydus eurinus, Kyungpoale Province: Taegu, 18. VII. 1960, det. C. E. Lee (UCONN).

## Rhopalidae

UNITED STATES: Liorhyssus hyalinus (Fabricius), Arizona, Yuma Co., 3 miles east of East Roll, 20. X. 1952, det. N. P. Chopra 1966 (CWS). L. hyalinus (Fabricius), Kyungpoale

Province: Taegan, 18, VII. 1960, det. J. A Slater (UCONN).

## Pyrrhocoridae

UNITED STATES: Dysdercus sp. a. Arizona: Cochise Co., Huachuca Mountains, Ramsey Canyon, 16. VI. 1968, (\#39195 PMNH). Dysdercus sp. b. California: Marin Co., Mill Valley, Fire road, near West Blythedale, 14. V. 1967, (\#39419 PMNH). INDIA: Odontopus nigricornis Stål, South India: Agumbe, Shinogn District, Mymare St., 9. V. 2000, det. C. W. Schaefer (CWS).

## Largidae

GHANA: Physopelta analis (Signoret), female, black light trap, Accra: 28. XI. 1969, identifier unknown (UCONN). UNITED STATES: Largus sp. male, Texas: Bexar Co., San Antonio, Olmos Park, 10. XII. 1989, det. D. L. W. (UCONN). Largus sp., male North Carolina: date ?

Largus sp., det. G. E. Ridge (UCONN).

## Berytidae

UNITED STATES: Jalysus sp. male, Connecticut: Tolland Co., Voluntown, 1. VII. 1970, det. J. A. Slater (UCONN). Jalysus sp., light trap, Florida: Highlands Co., Archbold Biological Station, 7. VI. 1969, Jalysus sp., det. G. E. Ridge (UCONN). Jalysus spinosus (Say), Connecticut: New Haven Co., New Haven, 5. VI. 1932, det. W. E. Britton (CAES). J. spinosus, Connecticut: New Haven Co., New Haven, 23. III. 1962, det. J. A. Slater (\#106210 PMNH). Connecticut: J. wickhami Van Duzee, off tobacco, Connecticut: New Haven Co., New Haven, 29. VII.1957, det. J. B. Kring (CAES). Berytinus sp. Michigan: Cheboygan Co., 29. VI. 1949, (\#106209 PMNH).

## Lygaeidae

UNITED STATES: Lygaeus kalmii Stål, Connecticut: Tolland Co., Mansfield Township, Storrs, 27. VII. 1964, (UCONN). L. kalmii, male, North Carolina: date ?, det. G. E. Ridge (UCONN). Oncopeltus fasciatus (Dallas), male, North Carolina: date ?, (UCONN). O. fasciatus, Connecticut: Tolland Co., Mansfield Township, Storrs, Forest Rd., 28. VII. 1972, (UCONN).

## Rhyparochromidae

UNITED STATES: Myodocha serripes Oliver, Connecticut: New London C., Lyme, 30. IV. 1911, det. G. E. Ridge (CAES). M. serripes, Connecticut: New Haven Co., Lyme, 21. IV. 1911, det. G. E. Ridge (CAES).

## Blissidae

BRAZIL: Ischnodemus bosqui (Slater \& Wilcox), Rio Grande do Sul: Eldorado do Sul, 4. IX. 1991, det. E. Ferronatto (CWS). I. bosqui, Rio Grande do Sul: Eldorado do Sul, 4. IX. 1991, det. E. Ferronatto (CWS). I. bosqui, Rio Grande do Sul: Eldorado do Sul, 8. VIII. 1991, det. E.

Ferronatto (CWS).

## Auchenorrhyncha

## Cercopidae

UNITED STATES: Philaenus spumaria Linnaeus, Connecticut: Tolland Co., Mansfield, 7. X. 1959, det. G. E. Ridge (UCONN).

## Cicadidae

UNITED STATES: Tibicen canicularis (Harris), male, Connecticut: Tolland Co., Mansfield Township, Storrs, 3. VIII. 1973, det. G. E. Ridge (UCONN). T. canicularis, Connecticut: New Haven Co., Milford, 19. X. 1963, det. G. E. Ridge (CAES).

## Cicadellidae

UNITED STATES: Graphocephala coccinea (Forster), Connecticut: Tolland Co., Vernon
Township, Hale St., Exit, 14. VII. 1973, det. G. E Ridge (CAES). Helochara communis Fitch, Connecticut: Tolland Co., Mansfield, 7. X. 1959, det. Lewis (UCONN).

## Membracidae

UNITED STATES: Ceresa bubalus Fabricius, Connecticut: New Haven Co., Waterbury, Mr. Tracy's Pond, 31. VII. 1973, det. G. E. Ridge (CAES). Campylenchia latipes (Say),

Connecticut: Windham Co., Ashford, Yale Forest, 17. VII. 1981, det. R. Clayton (CAES).
Stictocephala lutea Kopp \& Yonke, Connecticut: New Haven Co., 22. V. 1903, det. G. E. Ridge (CAES).

## Hymenoptera

## Anthophoridae

UNITED STATES: Xylocopa virginica (Linnaeus), Connecticut: New Haven Co., Bethany, 139

Lebanon Rd., 20. V. 2002, det. G. E. Ridge (GR).

## Vespidae

UNITED STATES: Vespula maculifrons Brysson, Connecticut: New Haven Co., Bethany, 139
Lebanon RD., 20. V. 2002, det. G. E. Ridge (GR). V. maculifrons, queen, Connecticut: New Haven Co., Bethany, 139 Lebanon Rd., 6. VI. 2002, det. G. E. Ridge (GR). V. maculifrons, Connecticut: New Haven Co., Bethany, 139 Lebanon Rd., 10. VI. 2002, det. G. E. Ridge (GR). Polistes sp. Latrielle, Connecticut: Middlesex Co., Chester, 2. IV. 1948, det. G. E. Ridge, (CAES).

## Diptera

## Calliphoridae

UNITED STATES: Phormia regina (Meigan), Connecticut: New Haven Co., Bethany, 139
Lebanon Rd., 20. V. 2002, det. G. E. Ridge (GR).
Tabanidae
UNITED STATES: Tabanus sulcifrons Macquart, New York State: Tompkins Co., Ithaca, 12.
VIII. 1973, det. L. A. Magnarelli (LM).

## Choice and preparation of specimens

The suborder Heteroptera was selected because its members have been well studied and their thoraces regarded as taxonomically important (Goel 1966; Larsen 1942, 1945; Taylor 1918; Brindley 1934, 1938; Crampton 1914; Weber 1930). There have been some published descriptions of the endoskeleton (Parsons 1960, 1963; Malouf 1932; Matsuda 1960; Lauck 1959; Leston 1954 a, b; Snodgrass 1935, 1952; Bitsch \& Bitsch 2002). Adults were selected, rather than nymphs, because nymphs lack a fully developed integument. Choice of species was based on availability of well identified material; additionally, four families from Auchenorrhyncha and two each from Hymenoptera and Diptera were included for comparison. Auchenorrhyncha are closely related to Heteroptera while Hymenoptera and Diptera more distant. All were chosen to see if the heteropteran characters were also present in other insect groups.

Before the body of the research was started 3 questions were addressed, to check for morphological traits in Heteroptera that might undermine the research. Do males and females differ in their thoracic endoskeletons, is the thoracic endoskeleton bilaterally symmetrical, and can a single species represent a family? These were largely answered with a series of 80 specimens from two Connecticut (USA) populations of Anasa tristis (DeGeer) (Coreidae). Forty males and 40 females were longitudinally bisected, cleaned, and examined under a dissecting scope. Sixteen males and 19 females were further examined using a scanning electron microscope. Species from Gerridae, Miridae and Corixidae were also examined for variability. Selection of specimens was based on availability and taxonomic interest. Thirty nine of the 75 heteropteran families were represented in the study.

Live specimens were freeze-killed and preserved in 70\% ethyl alcohol (EtOH) to avoid
damage to the cuticle by killing jar chemicals. Dry museum specimens were re-hydrated at room temperature in $10 \%$ soap and water solution for four hours and stored in $70 \% \mathrm{EtOH}$. Specimens went through a three step process of cleaning, drying, and sputter coating before examining under the scanning electron microscope.

Legs, antennae, and wings were removed from larger specimens ( $>1.25 \mathrm{~cm}$ ). Appendages were not removed from smaller specimens because they were used for securing the specimen in position. When the cuticle of the pronotal shield and scutellum was thick, a medial pre-cut with dissecting scissors was made. Holding the abdomen with forceps, a feather razor was placed on the longitudinal midline of thorax and gently rocked with slight downward pressure, cleanly bisecting the body. (A sawing motion tore specimens, especially small ones, making them useless.) Once the razor had sliced the insect, pressure was continued onto the cutting surface while the insect was pushed along the razor with forcepts. This separated remaining connective tissue between the halves. Abdomens of large specimens were removed by cutting through abdominal segment 2 , which allowed insertion into the critical-point dryer baskets and left enough abdomen for holding. In most specimens, abdomens were retained. Specimens difficult to dissect such as corixids and thyreocorids with dorsally round bodies were placed in a trough of beeswax for partial dissection and then transferred to a flat cutting surface. Soft tissue and tracheae were removed by putting dissected halves into boiling $15 \%$ potassium hydroxide $(\mathrm{KOH})$ solution for specific time periods, depending on body length (Table 1).

Table. 1: Boiling times for different body lengths of terrestrial Heteroptera specimens.

| Body length (mm) | $15 \% \mathrm{KOH}$ boiling time (sec) |
| :--- | :--- |
| $1.0-3.0$ | 15.0 |
| $3.0-5.0$ | 25.0 |
| $5.0-8.0$ | $30.0-40.0$ |
| $8.0-10.0$ | $60.0-90.0$ |
| $10.0-20.0$ | $120.0-150.0$ |

Conservative boiling times were observed, because KOH quickly dissolved delicate internal apodemes. Aquatic insects needed $10 \%$ more time than terrestrial insects due to thicker tracheae. After boiling, specimens were immediately rinsed in warm tap water to remove KOH . Any heat gradient between hot and cold fluids interfered with rapid diffusion of water through thoracic cavities. Speed is important to protect delicate apodemes. Rinsing was repeated a least twice until water became clear. Specimens were then monitored in a warm water bath for 20 minutes to check for further indications of tissue dissolving (browning of water). If this was seen, rinses were repeated. In museum specimens, muscle and tracheae often remained partially intact after initial KOH boiling, especially the dorsal indirect flight muscles, musculi mesonoti primus and m. mesonoti secundus. Re-boiling for a shorter time ( $20 \%$ of specified time limit) helped loosen tissue. Specimens were rinsed again in warm water through several cycles until water was clear. Specimens were always monitored in water.

After rinsing, specimens were submerged in a petri dish of water for more cleaning. Tissues and tracheae were removed using fine-tipped forceps, and difficult to reach structures
were gently flushed using a bulb pipette. When necessary, shaving away cut edges of the thorax with dissecting scissors opened the cavity for better observation and easier access. After dissection, specimens were stored in $70 \% \mathrm{EtOH}$ for one week to stabilize cuticle. If this was not done, the cuticle became brittle.

Samples were placed into $100 \%$ EtOH for 12 hours in preparation for critical point drying. Absolute $100 \% \mathrm{EtOH}$ tans cuticle slightly, making it tough.

Before drying, several specimens were placed into each of 5 baskets inserted into a critical-point dryer boat. The location, size, and shape of each specimen was recorded to help retrieval after the drying process. Here, protective powder-free rubber gloves were worn to prevent contamination with skin oils. The boat was placed into a petri dish for final flush cleaning using EtOH in a wash bottle. After filling the boat with EtOH, the baskets were covered with a security mesh and put into the critical-point dryer.

To remove alcohol from specimens, liquid $\mathrm{CO}_{2}$ was used. Because of a specimen's physical mass, a procedure of 6-minute flushings repeated 3 times with13-minute rest intervals was followed. These times are longer than the standard procedure (3 repeats of 3-minute flushings with 10 -minute rest interval). Shrinkage and twisting of delicate structures were mostly avoided by using longer times. Following removal of alcohol, samples were kept in the dryer for a 1-hour wait period. Finally, the critical-point dryer chamber was warmed with hot water to vaporize $\mathrm{CO}_{2}$, and a vent valve opened, returning chamber to atmospheric pressure. Again, since specimen mass was high, pressure in the chamber was lowered very slowly (10 minutes instead of the usual 3 to 5 minutes). If pressure was released too rapidly, recondensation of gas by adiabatic cooling could occur, damaging specimens.

Maintaining natural form of delicate structures, such as apodemes and phragmata, was important; careless drying caused shrinkage or twisting of structures. This was avoided through the slow drying approach, and the cuticle retained its shape. Comparisons were made with fresh and museum specimens to check for deformation and, when drying was done correctly, there was no deformation. Once removed from the critical-point dryer, specimens were immediately mounted onto scanning electron microscope stub heads using two-sided sticky STR carbon tape. Specimens were placed on their sides with thoracic openings facing up and further cleaned using pressurized air and microscalpels under a dissecting microscope. Extreme care was taken with pressurized air, because it could cause delicate apodemes to vibrate and snap. Breathing on specimens was avoided because moisture in exhaled breath could damage specimens. Around areas where specimens touched the carbon tape, silver paint was applied with a small wooden specimen stick to improve electrical conductivity in the scanning electron microscope. Not all specimens needed this. Those specimens treated with silver paint were stored overnight in a vacuum flask at high vacuum to draw out any moisture in the silver.

Samples were put into a sputter coater. The position and name of each specimen was recorded. Argon was used to purge moisture from specimens before application of gold palladium. The standard number of argon purge cycles was 3 to 4 . There were usually 8 insect specimens in the chamber at one time, constituting a higher than usual volume. The number of argon purges was raised to 9 to 10 cycles because of higher amount of water vapor. To get good coverage of gold palladium, the HT control was set to 1.8 kv with a current of 6 mA for 3 minute (standard time, 1 minute). After removal from the sputter coater, samples were put in SEM specimen boxes, labeled, and stored under vacuum. Later the specimens were examined and
electron micrographed using a Zeiss DSM-982 Gemini scanning electron microscope.
An unexpected problem occurred in pinned museum specimens. The pins were pushed through the right side of the thorax, often damaging internal structures. I frequently saw apodeme alpha or the posterior mesothoracic phragma damaged by this practice. In these cases, only left halves were used and right halves were used for reference.

The Zeiss DSM-982 Gemini scanning electron microscope had a 5 -stub holder disc. Before installation into the SEM, a final check was made with a light microscope for flaps and fragments that might impede viewing.

Specimens of similar size were mounted on the goniometer stage inside the SEM observation chamber. Specimens of similar sizes were selected for each examination. This reduced the chances of sample crashes into the pole piece because spatial judgment was impaired when viewing through IR camera monitors. Large and small specimens were not mixed. Specimens were oriented outward in a starlike formation, which improved observation when the stage was tilted.

Adjustments were made to the SEM to enhance imaging. The gamma control was raised from 2 to 3 , increasing contrast, and the kV control was raised from 2 to 4 kV , improving wide field imaging.

The endothoracic cavity posed a unique challenge for electron microscopy focusing. The deeply concave shape resulted in overcharging of high points (streaking), undercharging of deeper regions (blackening and washing out of image), and peripheral astigmatism. To overcome these problems, a middle-distance structure was chosen located halfway between the back wall of the thorax and the cut edge. An apodeme head or stem was not suitable, because
those move under the intensity of the electron beam. Initial focusing was most successful using the base of apodeme beta, or another similarly-placed structure. For initial focus, the slow small scan mode (postage-stamp-shaped focusing square) was used. Magnification was then raised to 5000x. It was important to complete initial focusing quickly, because the electron beam, if left on, burns a permanent image into the cuticle. Cuticle tolerates approximately 30 seconds of exposure before damage. When examining specific structures, for example the head of apodeme beta, I focused quickly to 1000 x in slow small scan mode, and immediately exited to protect structure. Focusing at the base of the head, where it progresses into the stem, was a medial position for good head images (Appendix 4: Fig. 17).

High point charging was prevented by careful tilting and alignment of specimens on the stage. There can be no standard approach, because each specimen is different and requires different adjustments. The blackening and washing out of the image was alleviated by using the above initial focusing procedure. With skill, the darkening and washing out of images became useful in providing a background to highlight foreground structures. Astigmatism remained a problem. Again by using middle distance focusing the astigmatism was manipulated to the periphery of many micrographs, resulting in a weak fish-eye effect (Fig. 16a).

To get a good image, the Slow Scan Mode B 512/1024 with scan speeds 1 through 4 was used. As scan speed numbers go up, the beam speed slows down, so speed 4 is the slowest, producing the sharpest image. The aim of developing a good image is to go stepwise up the scan speeds from 1 to 4 without damaging the samples. Mode B scan speed 1 with a $512 \times 512$ image was done first, cycling 3 times ( 3 rasters) for the first image (this looks grainy); next was scan speed 2 at $1024 \times 1024$ with 3 rastors; scan speed 3 also at $1024 \times 1024$ and programmed to do one
raster was skipped, because it unnecessarily extended exposure time for the specimens; scan speed 4 at $1024 \times 1024$ with one raster produced the best and sharpest image. The image was recorded on a zip disc. 598 scanning electron micrographs were made.

## Pen and ink drawings

Electron micrographs were photocopied and reduced to desired drawing size. Using tracing paper, each micrograph, representing an exemplar species for each family, was traced and transferred onto 100 lb white drawing paper. Details were added from observations of original specimens mounted on the electron microscope stubs. Rapidograph ${ }^{\mathrm{TM}}$ drafting ink pens were used in the final renderings with constant reference to the specimens for absolute accuracy. Forty-seven drawings were completed.

## The phenogram and bootstrap trees

Using the pen and ink illustrations, electron micrographs, and direct observations of the specimens, data were compiled for a Neighbor-joining phenogram. The CRiSP 9.1.2b Foxtrot System was selected because it was designed to manage large character-state data matrices. States were numbered 0-9 in a nonpolarized transformation series. Some characters, such as the posterior mesothoracic phragmata were broken into subsets because of high numbers of states ( p $\mathrm{ms} \mathrm{ph}=48$ states $)($ Appendix 2). Originally there were 178 taxa in the study but 160 were used for the phenogram analysis. Thirteen specimens were found too damaged after critical point drying to be of use, and five Hymenoptera and Diptera species were not included. Each character/character subset with its states was observed in progression in the 160 specimens and a data set was recorded. Assumptions were not made, because each character had a unique series of states which were clearly observed. None of the character states were polarized, and do not
represent any phylogenetic sequence.
Eighty-nine characters/character features with 403 states were entered into the CRiSP 9.1.2b Foxtrot System (Appendix 3). This data set was then entered into a PAUP 4.0 b 10 (PPC/altivec) program on a Macintosh computer. Four analyses, were considered; maximum parsimony (MP), maximum likelihood (ML), neighbor-joining (NJ), and Bayesian analyses. There were too many taxa for the MP or ML analyses, with initial runs taking to long to finish. In later analyses of smaller taxa subsets, they may be used, but not in this study. Basian analysis was not available. The NJ test of similarity was chosen because it could process the large data set and produce a visual representation of percent pairwise distances among taxa in a single tree. To assess confidence in the result of the NJ tree, a bootstrap analysis was run, which replicated and recalculated the NJ tree 1000 times. This resulted in phenogram and bootstrap trees seen in figures 50,51 . These results were preliminary and exploratory. Data are shown in Appendices 3 and 4.

## Results

Before research began three questions were addressed: whether there was sexual dimorphism and/or bilateral symmetry, and if a single species represent a family. A preliminary study of 80 male and female Anasa tristis (Coreidae) specimens in addition to conspecific specimens in Gerridae (Fig. 3), Corixidae (Fig 14), and Miridae (Fig. 22), showed no evidence of sexual dimorphism; endoskeletons were bilateral, and there was negligible intraspecific variation. I therefore suggest that a single specimen may be used to represent a family, although of course this must be done with great caution. Observations of most other families in the study were consistent with this finding (Appendix 4). However, there were exceptions, including Reduviidae (Figs. 24, 24a-h), Nepidae (Figs. 15, 15a), Aradidae (Figs. 26, 26a-c), and species with wing polymorphism such as Mesovelia mulsanti (Mesoveliidae) (Figs. 7, 7a,b) (Appendix 4).

## The characters

In aquatic and terrestrial predatory heteropteran families, the prothorax is usually larger than in phytophagous families. The mesothorax in all heteropterans examined is large and bares the majority of endoskeletal structures. The metathorax is comparatively small and serves as a connection with the abdomen.

Endoskeletal structures were identified by observation of their various forms across the suborder. These homologous structures, although variable, were easily identified because of location, size, and form. For example, the posterior mesothoracic phragma in many families was
usually a broad triangular sheet of cuticle e.g., Coreidae, Saldidae, and Tessaratomidae [Figs. 18, 31, 33]). In gelastocorids and aradids (Figs. 13, 26) it was tubular and could be interpreted as an apophysis, but it is, in fact, a tubular form of the phragma.

Although the structures termed apodemes alpha and beta appear to be apophyses which are solid, cross sections of these structures in Anasa tristis and Leptoglossus occidentalis (Fig.1) showed they were hollow which makes them apodemes. Insect morphology is full of subtle differences, so many morphologists understand that apodemes and apophyses, both elongate invaginations of the integument, are merely extremes of a continuum of variation.

Ridges 1, 2, and 3 were linear folds of cuticle fused with the anterior mesothoracic phragma (Fig. 34b). "Apodeme" could be applied to these structures (Snodgrass 1935), but because they are linear and progress along the thoracic wall without projecting into the thoracic cavity, the term "ridge" seemed more appropriate. The finlike structures found on the anterior mesothoracic phragma and thoracic floor were termed "keels" because they resembled boat keels (Figs. 22, 22e-f).

The character-rich mesothorax possesses anterior and posterior dorsal phragmata with numerous other structures. Regions of the mesothorax which more endoskeletal structures than elsewhere include the anterior and posterior edges of the segment. The pro- and metathoraces usually did not have this characteristic. The mesothorax had most of the 22 primary, 3 intermediate, and 7 secondary structures and features. Twenty one of these were either fused with or had some connection to the anterior or posterior edges of the segment. Apodeme alpha, usually fused with ridge 3 , was the only medial primary character. There were other medial features, such as ventral thoracic floor keels and medial keels on the anterior mesothoracic
phragma which were less morphologically informative. Most endoskeletal structures were bilateral, but some were single, such as the medial keels found on the anterior mesothoracic phragma and mesothoracic floor.

Not all families and figures are listed here when a character is described; only the best and clearest examples are referenced. Often numerous other families possessed the same character, but it would be too cumbersome to list them all. A complete list of families showing the characters and their states are included in Appendix 4. A list of some unique family-level characters may be found in Table 3. For quick reference, Table 2 lists the characters.

I grouped the characters into three categories: primary, intermediate, and secondary (Table 2). Primary characters were most common and showed highest variability; intermediate characters lacked much morphological variability but were always present; and secondary characters were the least widespread but provided many important, unique family-level features.

## The primary characters:

## 1. Anterior mesothoracic phragma (a ms ph)

This is a sheet of usually thin cuticle, covering the anterior dorsal half of the mesothorax, leaving the ventral half open for the cervical organs and muscles (Fig. 1). It separates the proand mesothoraces and supports the indirect flight muscles musculi mesonoti primus and $m$. mesonoti secundus. Originating on the anterior side of the phragma, are the prothoracic $m$. pronoti quartus used to raise the prothorax and the m. pronoti tertius used to raise the head. Size of phragma usually corresponded to degree of flight activity. In insects that frequently fly, e.g.,

Coreidae and Largidae, the anterior mesothoracic phragma was large, domed, with dorsoventral keels (Figs. 33, 38); in insects with infrequent flight, e.g., Gelastocoridae, Belostomatidae, and Gerridae it was smaller (Figs. 3, 13, 17); and in insects that did not fly, e.g., Cimicidae and apterous Mesoveliidae, it was either small or vestigial (Figs. 7, 19).

Progressing along the posterior surface of the phragma are keels, dorsoventral fins of cuticle. They vary in number from none (Fig. 12), or one medial keel (Fig. 2), to a medial keel with several lateral keels (Fig. 22). In some pentatomomorphs, phragmata have pairs of variously shaped fingerlike ventral apodemes (Fig. 30) and occasionally additional ventral medial lobes (Figs. 34, 35). Phragmata vary in cuticle thickness from thin (Fig. 33) to thick (Fig. 24). In some families, e.g., Belostomatidae, the phragmata sometimes had more than one thickness of cuticle. For example, in Belostoma sp. there was a medial arched window of extremely thin translucent cuticle.
2. Anterior mesothoracic phragma lateral keels (a ms ph lk)

Lateral keels were usually smaller keels flanking a larger medial keel on the anterior mesothoracic phragma (Fig. 22). Additional keels may be present, between the lateral keels and medial keel (Fig. 22). They possibly provide strengthening of the phragma and an additional insertion for $m$. mesonoti secundus. In aquatic heteropterans lateral keels were absent (Figs. 13, 14).
3. Anterior mesothoracic phragma medial keel (a ms ph mk )

This has an usually large medial keel on the anterior mesothoracic phragma (Fig. 33). It may provide support for m. mesonoti primus.
4. Anterior mesothoracic phragma, ventral apodemes (a ms ph vap)

There were fingerlike apodemes on the ventral edge of phragma and were common in Pentatomomorpha. They extend ventrally from the anterior mesothoracic phragma into the cervical opening between the pro-and mesothoraces. Variability of these apodemes ranged from absent (Fig. 28), hooked (Fig. 29), short-fingerlike (Fig. 30), crooked-fingerlike (Figs. 32, 33), to long-fingerlike (Fig. 34).
5. Anterior mesothoracic ventral bridge (a ms vb)

The ventral bridge was either a thickening of the cuticle (Fig. 20) or an invagination of the thoracic floor (Figs. 1, 36).
6. Anterior mesothoracic ventral bridge apodemes (a ms vb ap )

Highly variable apodemes were fused to the dorsal surface of the anterior mesothoracic ventral bridge. Shapes varied from absent (Figs. 21, 36), anvil-shaped (Figs. 33, 37), hooked (Fig. 32), spinelike (Figs. 15, 17, 26), peglike (Figs. 2, 14), fingerlike (Figs. 5, 7, 8), filamentous (Fig. 16), to square (Fig. 11).

Parsons (1960) and Lauck (1959) said that $m$. mesosterni primus originated on these apodemes and progressed along the thoracic floor to apodeme beta, depressing the prothorax. I suggest that other muscles, such as coxa I $m$. noto-trochanteralis and the smaller $m$. dorsoventralis, that raise the posterior prosternum, are also attached to their apodemes. Belostomatid bridge apodemes illustrate this well because of their unusually large size. Belostomatidae are large aquatic predators that seize prey with their forelegs. The large apodemes may provide additional support for large muscles used in grappling (Fig. 17).
7. Anterior mesothoracic shelf (a ms sh)

This was a posterior extension of the anterior mesothoracic ventral bridge, that paralleled the bridge as a lip. It was either absent (Figs. 2, 31) or present (Figs. 13, 33).
8. Apodeme alpha (apa)

This was the only intrasegmental structure in Heteroptera and usually were fused with ridge 3 (Figs. 20, 25, 35). In most Heteroptera it was associated with the dorsal thoracic wall, near the posterior mesothoracic phragma, but in some Auchenorrhyncha and Corixidae it was ventral (Figs. 14, 44-46). The apodeme was divided into base, stem, and head. The base was present in most families (Figs. 9, 11, 14, 22), but absent in some (Figs. 12, 13). Base shapes varied from C-shaped (Fig. 9), Y-shaped (Fig. 23), filamentous (Fig. 10), triangular (Figs. 14, 22), square (Fig. 21), broad (Figs. 29, 29, 30), to arched (Fig. 18 [unique]). The head was sometimes fused to ridge 3 and had no stem (Figs. 20, 26, 33, 37), or was fused with a stem to ridge 3 (Figs. 27, 36),

A usually short stem joined the base to the head (Figs. 14, 22, 27). Heads varied from absent (Figs. 6, 19), vestigial (Fig. 3), filamentous (Figs. 4, 10), short-fingerlike (Fig. 7), longfingerlike, (Figs. 8, 39), hooked (Fig. 9), bladelike (Figs. 15, 47), bicycle-saddleshaped (Fig. 13), bird-headshaped (Fig. 17), variously lobe-shaped (Figs. 18, 22, 26, 33, 35, 36, 41, 42), square (Fig. 21), discshaped (Figs. 24, 28, 29, 30, 32), ventrally spined (Figs. 35,41), hoodshaped (bonnet-shaped) (Figs. 44, 45, 46), featherlike (Fig. 48), spinelike (Fig. 2) to cupshaped (Fig. 14).

Attached to apodeme alpha was $m$. furca-plauralis, a minute muscle which joined the apodeme to the head of apodeme beta. Akbar (1957), Parsons (1960), and Lauck (1959) stated the function of this muscle is unknown. Goel (1967) said it might maintain body curvature. I
suggest it is involved in flight, because it and apodeme beta were reduced or absent in apterous species (Figs. 3, 7, 7a-b) and large in macropterous species (Figs. 22, 32,33, 35). Also originating with apodeme alpha was m. pleura-trochanteralis secundus, which inserted onto a tendon for moving the mesothoracic trochanter.

Table 2: 32 primary, intermediate, and secondary characters

| Primary characters | Intermediate characters | Secondary characters |
| :---: | :---: | :---: |
| 1 Anterior mesothoracic phragma | 23 Prothorax | 26 Palisades |
| 2 Anterior mesothoracic phragma lateral keel | 24 Thorax contour | 27 Keels |
| 3 Anterior mesothoracic phragma medial keel | 25 Coxae angles, separations, invagination | 28 Lobes |
| 4 Anterior mesothoracic phragma ventral apodeme |  | 29 Pits |
| 5 Anterior mesothoracic ventral bridge |  | 30 Pores |
| 6 Anterior mesothoracic ventral bridge apodeme |  | 31 Occipital condyle |
| 7 Anterior mesothoracic shelf |  | 32 Ridge 3 extension |
| 8 Apodeme alpha |  |  |
| 9 Apodeme beta |  |  |
| 10 Metathoracic ventral bridge |  |  |
| 11 Metathoracic ventral bridge apo | deme |  |
| 12 Metathoracic ventral bridge exte | sion |  |
| 13 Posterior mesothoracic phragma |  |  |
| 14 Posterior mesothoracic phragma | medial ridge |  |
| 15 Posterior mesothoracic ventral b | ridge |  |
| 16 Ridge 1 |  |  |
| 17 Ridge 2 |  |  |
| 18 Ridge 3 |  |  |
| 19 Spiracles |  |  |
| 20 Thoracic floor |  |  |
| 21 Thoracic wall |  |  |
| 22 Wing muscle opening |  |  |

9. Apodeme beta (ap.b)

This was the second most character-rich structure in Heteroptera. (The posterior mesothoracic phragma was the first.) Apodeme beta was ventral to the posterior mesothoracic phragma and lay opposite apodeme alpha. In species whose posterior mesothoracic phragma was large, either nearly touching, touching, or fusing with apodeme beta, it was a connection between the phragma and apodeme alpha, forming a loop of three interconnected structures (Figs. 29, 33, 34, 37). These three structures were either physically connected or connected via muscles (Figs. 33, 37).

Apodeme beta was made up of a base, stem, and head. The base was usually large (Fig. 28), its size and proportions directly related to the size and proportions of the posterior mesothoracic phragma (Figs. 7, 13, 14, 29). In gerrids (Figs. 3, 3a-b), it was completely fused with the phragma, making a column; in corixids, tessaratomids, scutellerids, and cydnids, et al., the dorsum of the base was concave to receive the phragma's foot (Figs. 27, 29, 31); in aradids and gelastocorids, et al., (Figs. 13, 26) both the dorsum of the apodeme and the foot of the phragma were flat, although they do not usually touch. Bases were variable, from absent/vestigial (Fig. 6), hooked (Fig. 2), fused with posterior mesothoracic phragma (Figs. 35, 37, 40, 42, 48), conical (Fig. 4), small fingerlike (Fig. 7), anvilshaped (Figs. 11, 12, 28, 31), columnar with flat dorsum (Figs. 13, [16 only observed specimen], 26), concave to receive the foot of the posterior mesothorcic phragma (Figs. 14, 29, 43), triangular usually narrowed to a stem (Figs. 17, 18, 19, 23, 47), boatshaped (Fig. 31, 33), fused with metathoracic ventral bridge apodeme (Fig. 32 [unique]), resting against metathoracic ventral bridge apodeme (Fig. 29a), with flat fins of cuticle (Fig. 34), to variously lobed (Figs. 25, 46). Stems were usually filamentous
extensions of the base that originated from the anterior surface of the base and progressed to the head (Figs. 30, 33, 37, etc.).

The head, a distal expansion of the stem, was normally located ventral to apodeme alpha. Sometimes the stem and head were missing (Figs. 13, 39), leaving only the base; all three may be fused either as a fingerlike process (Fig. 9) or as a filament (Fig. 2). Shape and size were important at the family level and, with a variety of surface features, may be useful for analysis. The head of apodeme beta can vary from absent (Figs. 19, 39), filamentous (Fig. 2), hooked (Fig. 4), tapered with longitudinal scallop shaped indentations (Fig. 5 [unique]), fingerlike (Fig. 9), featherlike (Figs. 11, 12, 18), fanlike (Figs. 14, 23), discshaped (Figs. 17, 24, 25, 27), coneshaped (Figs. 20, 26, 35), deeply cupped coneshaped (Fig. 34 [unique]), flat coneshaped (Fig. 31), starshaped (Fig. 24b), V-shaped with semicircular side (Fig. 24a), to funnelshaped (Figs. 40, 41, 42) (Appendix 5).

Apodeme beta was the site of several muscle insertions. M. dorso-ventralis secundus connected apodeme beta base dorsum to the posterior mesothoracic phragma and raised and depressed the meso and metathoraces. M. furca-pleuralis connected apodeme beta head and apodeme alpha for flight. M. mesosterni primus progressed along the thoracic floor from apodeme beta base to the anterior mesothoracic ventral bridge apodemes and depressed the prothorax. M. mesosterni secundus progressed along the thoracic floor from apodeme beta base to between the anterior mesothorcic ventral bridge apodemes and, also, depressed the prothorax; and $m$. furca-trochantinalis progressed from the posterior apodeme beta base to tendons on the medial metathoracic trochantin, which rotated coxa III and lifted the third leg.
10. Metathoracic ventral bridge (mt vb)

This was either an invagination of the exoskeleton (Fig. 35) or thickening of the cuticle (Fig. 32) on the metathoracic venter next to coxae III. The bridge strengthened the thoracic floor as well as connected the thorax and abdomen. In Cimicidae, the bridge was an attachment for a very large segma coria between the thorax and abdomen (Fig. 19). The phymatid bridge had a dorsal ridge (Fig. 25). The metathoracic ventral bridge often had dorsal apodemes (Figs. 13, 30, $34,35,36,41)$.
11. Metathoracic ventral bridge apodeme ( mt vb ap )

This apodeme was usually on the dorsum of the metathoracic ventral bridge close to coxa III; however, in corixids, saldids, tessaratomids, coreids, and largids the apodeme was anterior to and detached from the bridge (Figs. 14, 18, 31, 34, 38). Size varied from absent (Fig. 39), vestigial (Figs. 9, 16), to extremely large (Fig. 17). Its shape varied from triangular (Figs. 2, 22), short-fingerlike (Figs. 3, 7, 8, 24), long-fingerlike (Fig. 5), pointed (Fig. 4), anvil-shaped (Fig. 11), saddle-shaped with long posterior arms (Figs. 13, 12), rectangular (Fig. 14), toothlike (Fig. 15), C-shaped (Fig. 17 [unique]), knoblike (Figs. 18, 22, 35, 40), hooked (Figs. 20, 21, 27, 36), ring-shaped (Figs. 30, 34,41), to fused with apodeme beta (Fig. 32 [unique]). Attached to the apodeme were several muscles. M. ventralis abdominalis connected the posterior part of the apodeme to the second abdominal ventral segment and raised the abdomen; m. furcatrochanteralis connected the apodeme with trochanter tendon 70 to depress the trochanter; and m. dorsoventralis connected the tip of the apodeme with the posterior lateral midline of the posterior mesothoracic phragma to depress the posterior region of the metanotum.
12. Metathoracic ventral bridge extension (mt vbe)

The ventral bridge extension usually progressed dorsally along the thoracic wall from the metathoracic ventral bridge. Its shape varied from absent (Fig. 41), a ridge (Figs. 14, 23, 25), ridge fused with other abdominal ridges (Fig. 8), a wide band of pits (Fig. 9), a wide band of smooth cuticle (Fig. 36), lobed (Fig. 15), to folded and fused with a posterior segma coria (Figs. 19, 34). It connected the metathorax and the first abdominal segment.

## 13. Posterior mesothoracic phragma ( p ms ph )

This was the most character-rich structure in the heteropteran thorax. It was a variable sheet of cuticle that covered the posterior dorsal half of the mesothorax. The ventral half of the thorax was open for organs and muscles. In some families, there were two layers of cuticle (Fig. 11) which fused to form the phragma. The phragma was either very large (Figs. 22, 31, 41) or vestigial (Fig. 7). Shape and size were often consistent at the family level; for example, the Belostomatidae had a unique clubshaped phragma (Fig. 17), whereas the Miridae had a unique pair of openings called windows in the phragma's lateral arch (Fig. 22).

The posterior mesothoracic phragma was divided into crown, shaft, and foot. The lateral arch, when present, and crown were the dorsal third of the phragma, which was usually broad; the shaft was the medial third of the phragma and was necklike; and the foot was varied with numerous bulbous shapes. The phragma varied from absent (Figs. 4, 6, 19), bilobed (Fig. 2), a fused column with apodeme beta (Figs. 3, 5, 9, 10, 42), broadly triangular (Figs. 22, 31, 41), narrowly triangular, (Figs. 8, 14, 28, 33), hourglass-shaped (Fig. 11), tubular (Figs. 12, 26), divided (Figs. 15, 17), to nearly rectangular (Fig. 39 [unique]). The crown was either wide (Figs. 22, 31, 41), narrow (Figs. 28, 29,37), or with a lateral arch (Figs. 20, 33). In many families, the
arch progressed ventrally to spiracle 2 and/or the posterior mesothoracic ventral bridge extension (Figs. 29, 37). The arch and crown were usually fused (Fig. 22) but sometimes were divided by a ridge (Fig. 31). Ornamentation was sometimes present in the arch region, such as rugulae (Figs. 20, 37), dorsal lobes (Fig. 25), or dorsal ridge (Figs. 29, 38). The arch in mirids was unique, because it had two square anterior openings, here called the anterior and posterior windows. These windows fused ventrally with the posterior mesothoracic ventral bridge extension and spiracle 2 (Fig. 22). In this study, Nabidae was the only other family with a window (Fig. 21). Arches were sometimes absent (Fig. 40).

Although clearly visible in Anthocoridae, Corixidae, Naucoridae, etc., in many families the shaft was difficult to distinguish, being a continuation of the crown through to the foot.

The foot was character-rich and varied from absent (Fig. 2), spoonshaped (Fig. 8), boatshaped, ringed by a frill (Fig. 11), boatshaped (Figs. 14, 22), boatshaped with very convex venter (Figs. 28, 29, 41), an anterior semicircular lip with medial cavity (Fig. 12, 13), scallop shellshaped (Fig. 13b), footlike (Fig. 15), bulbous (Fig. 16), clubfooted (Fig. 17), hooked (Figs. 18, 20, 40), hooked and scoopshaped (Fig35), scoopshaped (Figs. 21, 25, 27, 31, 33), broadly scoopshaped (Fig. 34), blunt (Fig. 23), pointed (Fig. 24), rounded and flat (Fig. 24b), knobbed (Fig. 24a), flat with frill (Fig. 26), nearly flat (Fig. 32), to fused with apodeme beta (Figs. 37, 40).

Three muscles attached to the posterior mesothoracic phragma. M. dorsoventralis secundus connected the posterior arm of apodeme beta with the phragma foot and depressed the anterior metatergum and posterior mesotergum; m. mesonoti primus connected the posterior mesothoracic phragma to the anterior mesothoracic phragma and, as a large indirect flight muscle, depressed the forewings through antagonistic action; m. mesonoti secundus connected
the lateral surface of posterior mesothoracic phragma to the anterolateral region of mesoscutum and, as an indirect flight muscle, raised the forewings.
14. Posterior mesothoracic phragma medial ridge ( p ms ph mr )

A ridge that progressed dorsoventrally and divided the lateral arch and phragma. The shape varied from a trough (Fig. 18), finlike (Fig. 32), to a fold (Fig. 33). It may separate the $m$. mesonoti primus and m. mesonoti secundus.
15. Posterior mesothoracic ventral bridge ( p ms vb )

This was an invagination of either the integument (Figs. 36, 37), or thickening of the cuticle (Figs. 26, 27, 30) around coxa II. Its dorsal surface was usually fused with apodeme beta. Progressing along the bridge's dorsum was sometimes a trough (Fig. 18) or ridge (Fig. 27), and the bridge may at times extend dorsally to fuse with spiracle 2 (Fig. 40).
16. Ridge 1 (r1)

Lateral to the anterior mesothoracic phragma was a linear fold of integument, ridge 1
(Figs. 1, 34b, 38, 38a). It was the anterior ridge of a group of three ridges. It varied from absent (Figs. 7, 19), lobed (Figs. 4, 29, 33), linearly horizontal (Figs. 5, 11, 27), fused with ridges 2 and 3 (Figs. 3, 6, 9, 14), anterior arm of a 3-ridge "N" configuration (Figs. 13, 34, 34b, 38), parallel with the other 2 ridges (Fig. 10), anterior arm of a 3-ridge triangle formation (Fig. 12), curved (Figs. 16, 17, 18, 20), with an anterior hook (Figs. 22, 35, 36, 39), to an anterior arm of a 3 ridge fan configuration (Figs. 8, 23). It might serve as an insertion for $m$. mesonoti secundus, $m$. dorsoventalis primus, and $m$. noto-trochantinalis.
17. Ridge 2 (r2)

This was another fold of integument lateral to the anterior mesothoracic phragma
(Figs. 1,34b, 38, 38a). It was the medial ridge of a group of 3 ridges (Figs. 1, 34b, 38, 38a). It varied from absent (Figs. 7, 19), lobed (Fig. 4), fused with ridges 1 and 3 (Figs. 3, 6, 9, 14), medial arm of a 3-ridge " N " configuration (Figs. 13, 34, 34b, 38), parallel with the other 2 ridges (Fig. 10), posterior arm of a 3-ridge triangle formation (Fig. 12), to medial arm of a 3-ridge fan configuration (Figs. 8, 23). It might serve as an insertion for $m$. mesonoti secundus, $m$. dorsoventalis primus, and m. noto-trochantinalis.
18. Ridge 3 (r3)

This was the most posterior linear fold of the 3-ridge group (Figs. 1, 34a, 38, 38a). Apodeme alpha sometimes fused with this ridge (Figs. 20, 33, 34). It varied from absent (Figs. 7, 19), fused with ridges 1 and 2 (Figs. 3, 6, 9, 14), posterior arm of a 3-ridge " $N$ " configuration (Figs. 13, 34, 34b, 38), parallel with the other ridges (Fig. 10), ventral arm of a 3-ridge triangle formation (Fig. 12), bladelike (Fig. 11), curved (Figs. 17, 18), to posterior arm of a 3-ridge fan configuration (Figs. 8, 23). It might serve as an insertion for $m$. mesonoti secundus, $m$. dorsoventalis primus, and m. noto-trochantinalis. It had an extension in some families (Fig. 1). 19. Spiracles (sp)

Spiracle 1 may be found in one of three positions, the posterior prothorax (Figs. 3, 4, 39), the segma coria between the pro- and mesothoraces (Figs. 5, 10, 21, 22, 24), and the anterior mesothorax (Figs. 6, 14, 19, 20, 23, 25, 27, 29). It may be located either dorsally (Fig. 6), dorsolateral to lateral (Figs. 30, 31, 34, 40) or ventral (Figs. 20, 26). Size varied from absent (Figs. 15, 16, 17), small (Figs. 7, 8, 29, 30) to large (Figs. 22, 35, 36, 37). The shape was also variable, from oval (Figs. 22, 23), round (Figs. 6, 8, 20), rectangular with linear sutures of cuticle that radiated from the center (Fig. 14, 14b [unique]), to a tubular invagination of integument (Fig.

19 [unique]).
Spiracle 2 may be found on the lateral mesothoracic wall, ventral to the posterior mesothoracic phragma lateral arch. Orientation was either vertical (Figs. 29, 31, 32, 36, 39, 40), tilted (Figs. 27, 38, 41) or horizontal (Figs. 3,10). Size varied from absent (Figs. 15, 16, 17), small (Fig. 19), to large (Figs. 18, 29, 35, 36). Spiracle 2 may lie ventrally (Figs. 4, 22), laterally (Figs. 29, 33, 34), or dorsally (Fig. 3, 23, 47); and shape varied from oval (Figs. 3,10, 38, 40), round (Figs. 5, 47), balloonlike (Fig. 14 [unique]), coneshaped (Fig. 24, Stenopodinae [unique]), to a slit (Figs. 23, 25).

In some families, spiracle 2 had palisades (Figs. 29, 30, 34) (Glossary). Palisades were rarely observed around spiracle 1 unless also present with spiracle 2 (Fig. 40). There were incomplete palisades as sticklike structures (Figs. 36c-f [unique]).

Corixidae had a structure that was either a horizontal spiracle 3 or possibly a gland in the metathorax. It was ventrally located and was near an hourglass-shaped secondary ridge (Fig. 14).
20. Thoracic floor (tf)

This was the inner ventral surface of the thorax. In most Heteroptera, the integument of the thoracic floor was uniform in thickness, but the thickness varied in some cimicomorphs. Here it was usually thinner on the thoracic floor than the dorsum, with few or no cavities (Figs. 21, 23, 24). The curvature of the thoracic floor varied from nearly straight (Figs. 3, 14, 17, 39), slightly convex (Figs. 2, 34, 35, 40), to acutely convex (Figs. 12, 13, 19, 22, 25). Surface texture varied from smooth (Figs. 2, 3, 6, 22), smooth with pores (Figs. 7, 22e-i), smooth with pits (Figs. 24a, 37e), rough (Figs. 24b, 30, 30a, 34), rough with pores (Fig. 30), to rough with pits (Figs. 4, 9, 24a, 26, 26a-b, 34, 34a).

A single medial keel along the thoracic floor was common in Heteroptera. It connected the anterior mesothoracic ventral bridge to the base of apodeme beta (Figs. 2, 11, 12, 16, 17, 22), perhaps to enhance strength and flexibility of the thoracic floor and guide the ventral muscles. Corixidae were unique in that they had many thoracic floor keels (Fig. 14). Other structures on the thoracic floor varied from rectangular folds (Fig. 10 [unique]), large ventral lobes (Figs. 29, 32, 39, 39a,c, 41, 42), ventral troughs with bridges (Fig. 9 [unique]), to a tongue (Fig. 10 [unique]).
21. Thoracic wall (tw)

This was the lateral surface of the thorax. Surface textures and structures were like those of the thoracic floor. Surface textures varied from smooth (Figs. 2, 3, 6, 6a, 22a), smooth with pores (Figs. 22e-i), smooth with pits (Fig. 37e), rough (Figs. 24, 30a, 34, 34a), rough with pores (Fig. 30), pubescent patches of cuticle (Figs. 12, 47, 47a-d, 48, 48a), to rough with pits (Figs. 3, 9, 26a, 34, 35). Surface structures varied from lobes (Figs. 20, 39, 41, 42), linearly lobed (Figs. 32, 32a [unique]), cuticleous-tongued (Fig. 10 [unique]), with a posterior mesothoracic ventral bridge extension (Figs. 11, 25, 28), with a posterior mesothoracic ventral bridge extension with palisades (Fig. 30), S-curved lateral arch extension (Fig. 32 [unique]), with oval cavities (Fig. 14 [unique]), with large round lobe (Fig. 19 [unique]), glandular (Figs. 20, 20a-g [unique]), with palisades (Figs. 29, 30, 32, 40), palisades present in pro-, meso-, and metathoracic intersegmental regions (Figs. 34, 37), with posterior mesothoracic phragma lateral arch windows (Figs. 21, 22), variable dorsal lobes, ridges, and folds (Figs. 25, 38, 42), pronounced abdominal ridges (Fig. 30), enlarged anterior mesothoracic shelf (Fig. 34 [unique]), to extra ridge anterior to spiracle 2 (Fig. 36 [unique]).
22. Wing muscle opening (wmo)

This was a variably shaped opening in the thoracic wall through which the wing muscles passed. It was usually located dorsolaterally, anterior to the posterior mesothoracic phragma (Figs. 15, 17); sometimes very dorsal (Figs. 10, 18). Wing muscle openings vary in size from absent (Figs. 6, 19), to very small (Figs. 7, 35), to large (Figs. 28, 34). The shape may be oval (Fig. 28), round (Fig. 9), triangular (Fig. 13), square (Figs. 18, 34), concealed by other structures (Figs. 20, 21), or rectangular (Fig. 15).

## The intermediate characters:

23. Prothorax

The prothorax in Heteroptera varied in size and shape. Compared to the meso- and metathoraces, it was usually large in aquatic and predaceous heteropterans, and reduced in the terrestrial phytophagous insects. There were exceptions; for example, the hebrids, enicocephalids, and anthocorids, although predators, had small prothoraces. This may be because they hunt small prey such as Collembola and tiny invertebrates. In belostomatids, on the other hand, were voracious predators often hunting prey larger than themselves, the prothorax was very large with large anterior mesothoracic ventral bridge apodemes for coxa I muscle attachments. The plant-feeding coreids have small prothoraces. Their front legs are not used for grappling prey but for searching out and securing a foothold when walking across plants and for cleaning antennae and beak.

The prothorax was measured lengthwise relative to the size of the mesothorax. It varied from small (Figs. 36, 39), $1 / 4$ (Figs. 4, 6, 11), $1 / 3$ (Fig. 5), $1 / 2$ (Figs. 13, 14, 17, 18), 3/4 (Fig. 15), to
the same size as the mesothorax (Figs. 21a,b; 24a). Its shape varied from dorsoventrally rectangular (Figs. 3, 5), dorsoventrally compressed (Figs. 12, 13), necklike (Figs. 15, 16), square (Fig. 6, 21), round (Figs. 19, 24, 41), to flat-floored (Fig. 32 [unique]).

The prothorax had varied surfaces and structures, from smooth (Figs. 3, 10, 33), rough with pits (Fig. 4), lobed (Figs. 5, 6, 7, 8, 40, 42), with ridge(s) or ribbed (Figs. 10, 14, 15, 16, 41), with apodemes (Fig. 19), with palisades (Figs. 21, 23, 25, 36, 39), with fold(s) (Fig. 23), to those with an apophysis (Fig. 35 [unique]).

## 24. Thoracic contour

This was the overall shape or profile of the thorax, when looking inside, when it was cut in half. The profile of the heteropteran thorax was useful, because it indicated what kind of activities and environments the insects were encountering. The filiform contour, for example, was found in many aquatic families (Figs. 3, 6) and presumably streamlines the insects in water. The cunate shape was seen in many phytophagous and terrestrial families, and the pyriform shape occurs in some terrestrial predators. There were several forms of the thoracic contour from cunate (Fig. 27), filiform (Fig. 6), oval (Figs. 16, 20), round (Fig. 9), to pyriform (Figs. 12, 22). There was some variation within these shapes: the cunate shape may narrow posteriorly (Fig. 2), or acutely narrow posteriorly (Fig. 16), or broaden posteriorly (Fig. 14); the filiform may broaden posteriorly (Figs. 5, 17), or narrow anteriorly (Fig. 20).
25. Coxa angles, separations, invagination

Coxae enter the ventral thoracic cavity at various angles, from vertical (Fig. 31) to almost $90^{\circ}$ from vertical (Figs. 13, 17, 18). Coxal angles vary from nearly vertical (Figs. 6, 26), angled between 30 and $60^{\circ}$ (Fig. 4), angled between 60 and $90^{\circ}$ (Fig. 11, 14, 17), to a mixture of angles
between the coxae (Figs. 22, 23, 24). Spacing between the coxae was also variable, from coxa I separate from II and III, which were close together (Figs. 3, 20), coxa I separate from II and III which were closer together (Fig. 17), evenly spaced coxa (Figs. 4, 7, 8), to coxa I and II closer together while III was separate (Figs. 6,9).

Nearly all heteropteran coxae invaginate into the thoracic cavity. Cimicidae and partly so; Aradidae (Figs. 19,26), coxae were deeply invaginated which may be an adaptation for hiding in cracks and crevices. Coxal invagination was absent in many terrestrial families (Figs. 28, 33). In some aquatic families, coxa III was deeply invaginated (Fig. 17) for crawling and pushing through aquatic and/or semi-aquatic environments (Figs. 12, 13, 14, 18). Large hind coxae often provide support for powerful metathoracic coxal muscles, perhaps allowing these insects to live in physically challenging environments.

## The secondary characters:

26. Palisades

Present sporadically (except Pentatomomorpha) in the suborder, palisades maintain strength and flexibility while reducing the weight of the integument. They were mostly absent in Enicocephalomorpha, Gerromorpha, Leptopodomorpha, Nepomorpha, and Cimicomorpha. Exceptions were Nabidae (Fig. 21), Tingidae (Fig. 23), Veliidae (Fig. 4), Gerridae (Fig. 3), and Corixidae (Fig. 14). Palisades were common in Pentatomomorphs, usually surrounding spiracle 2 (Figs. 28, 29, 33, 37, 40) and in intersegmental regions between the pro- and mesothoraces, and meso- and metathoraces (Figs. 30, 32, 37). They may surround coxae, especially coxa II (Figs. $30,34,35,37$ ). Palisades may be incomplete sticklike structures rimming the spiracle 2 atrium
(Fig. 37 [unique]).
27. Keels

The keel, a thin fin of invaginated cuticle, was found in the anterior mesothoracic phragma and the mesothoracic floor. Keels were usually on large thin phragmata (Figs. 34, 38) and dorsal phragmata (Fig. 39). Thoraces that were deeply convex dorsally (Fig. 41) seemed to lack keels. There can be single medial keels (Figs. 14, 15, 40), single lateral keels (Fig. 42), or multiple keels (Figs. 9, 21, 22, 28, 34). If a phragma was short and small, keels were absent (Figs. 10, 17).

The ventral mesothoracic keel progressing from the base of apodeme beta along the mesothoracic floor to the anterior mesothoracic ventral bridge, was fairly common in Heteroptera. Flat thoracic floors tended not to have keels (Fig. 3), whereas slightly convex floors, did (Figs. 20, 22). In some families the convex thoracic floor was deep and short, and a keel may be not present (Figs. 25, 36, 41). Also, keels were not present in thoraces with thick rough walls (Figs. 4, 26, 34) or that were highly lobed (Fig. 20a, 36, 39), but were more common in insects with thinner smoother integuments (Figs. 16, 22).
28. Lobes

Lobes were rare in Enicocephalomorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, and Cimicomorpha. They were common in the Pentatomomorpha, either randomly across the inner mesothoracic wall (Figs. 29, 30, 36), or in very defined regions (Figs. 20, 39, 42). Their shapes varied from elongate (Fig. 32 [unique]) to round (Fig. 42). Lobes may also be present in the prothorax (Figs. 5, 6, 19).
29. Pits

Pits were random distribution of holes in the cuticle (Figs. 9, 30, 35). They were absent on phragmata. Pits may be found in specific regions: for example, either as defined bands (Fig. 9, 9a) or clustered near or in troughs between coxae (Figs. 7, 8, 26, 34).
30. Pores

Pores were not common in Heteroptera. They were seen in a few families (Figs. 4, 5 head, 22e-i, 25).
31. Occipital condyle

The occipital condyle was present in several families in the Gerromorpha and Nepomorpha (Figs. 3, 4, 5, 7, or Gelastocoridae [Parsons 1960]), and were rarely observed in the Pentatomomorpha (Fig. 34), Cimicomorpha, Leptopodomorpha, and Enicocephalomorpha. The occipital condyle had at least two muscles, the m. prosterni primus, which was inserted in the medial region of coxa I apodeme (Fig. 13), called by Parsons prothoracic furca (1960) and depressed, retracted, and rotated the head; and m. prosterni secundus, which was inserted in the lateral region of coxa I apodeme and did the same.
32. Ridge 3 extension (r3e)

This was a small secondary ridge either fused medially with ridge 3 (Fig. 34) or as an extension (Fig. 42). In Tingidae only, the extension had a funnel-shaped head in which ridges 1 , 2, and 3 were inserted (Fig. 23).

Table 3 showed some of the more important unique family level characters in heteropteran families. These unique characters were found only in a single family and not in other heteropteran families. For a more complete account of unique characters, see

Character/states coded by family.

## Character/states coded by family with some discussion:

Following are descriptions of the 32 characters and their states in the 39 heteropteran families and families from Auchenorrhyncha, Diptera and Hymenoptera. The order of the heteropteran families follows Appendix 1. When preparing specimens, thoraces were cut along the midline, thus wording in the text describes one half of each thorax. Drawings and scanning electron micrographs are in book two and should be used with text. Characters are identified by their abbreviations here and in book 2 .

Table. 3: The heteropteran endothoracic characters and abbreviations used is descriptions and
illustrations (Book 2).

| The characters | Character abb |
| :--- | :--- |
| 1 Anterior mesothoracic phragma | a ms ph |
| 2 Anterior mesothoracic phragma lateral keel | a ms ph lk |
| 3 Anterior mesothoracic phragma medial keel | a ms ph mk |
| 4 Anterior mesothoracic phragma ventral apodeme | a ms ph v ap |
| 5 Anterior mesothoracic ventral bridge | a ms vb |
| 6 Anterior mesothoracic ventral bridge apodeme | a ms vb ap |
| 7 Anterior mesothoracic shelf | a ms sh |
| 8 Apodeme alpha | ap a |
| 9 Apodeme beta | ap b |
| 10 Metathoracic ventral bridge | mt vb |
| 11 Metathoracic ventral bridge apodeme | mt vb ph |
| 12 Metathoracic ventral bridge extension | mt vb e |
| 13 Posterior mesothoracic phragma | p ms ph |
| 14 Posterior mesothoracic phragma medial ridge | p ms mr |
| 15 Posterior mesothoracic ventral bridge | p ms vb |
| 16 Ridge 1 | r 1 |
| 17 Ridge 2 | r 2 |
| 18 Ridge 3 | r 3 |
| 19 Ridge 3 extension | r 3 e |
| 20 Spiracles | sp |
| 21 Thoracic floor | tf |

22 Thoracic wall tw
23 Wing muscle opening wmo

## In group

## Heteroptera

## Enicocephalomorpha

## Enicocephalidae

Figures 2, 2a
Specimens examined:
Sp. (undetermined) Tanzania

Hymenocoris formicinia Uhler California

| Character | State |
| :--- | :--- |
|  |  |
| a ms ph | Small, ventral apodemes |
| a ms ph lk | Large, progressing vertically across phragma |
| a ms ph mk | Absent |
| a ms ph v ap | Small, filamentous |
| a ms vb | Square, dorsally round |
| a ms vb ap | Small, broad based lobes |
| a ms sh | Absent |
| ap a | Small filament |


| ap b | Short, hookshaped, with filament. Tanzania specimen, absent |
| :---: | :---: |
| mt vb | Vestigial |
| mt vb ap | Triangular, round at tip. Tanzania specimen, absent |
| mt vbe | Absent |
| p ms ph | Bilobed, smooth |
| p ms ph mr | California specimen, suture: Tanzania specimen, absent; shaft narrow, square; foot round |
| p ms vb | Vestigial |
| r1 | Dorsal, linear |
| r2 | Fused with ridge 3, progressing from anterior mesothoracic phragma to lobed region, posterior with apodeme alpha |
| r3 | Fused with ridge 2, progressing from anterior mesothoracic phragma to lobed region, posterior with apodeme alpha |
| r3e | Absent |
| sp | Spiracle 1, moderately large oval; spiracle 2 small, oval |
| ff | Smooth |
| tw | Smooth |
| wmo | Small, round |

## Comments

Prothorax small, square. Anterior mesothorascic phragma smooth, with large lateral keel, ventral apodemes. Mesothorax with large dorsomedial keel
progressing anteroposteriorly; narrow anteriorly, broad posteriorly (not illustrated). Ridge 1 linear, dorsal; ridges 2, 3 fused, progressing from anterior mesothoracic phragma to lobed region, posterior with apodeme alpha. Apodeme alpha filamentous. Apodeme beta base broad, narrowing to anterior hook with filament. Posterior mesothoracic phragma variable; H. formicinia: bilobed with medial ridge as suture; Tanzania specimen medial ridge absent, with square shaft narrowing to round foot. Anterior metathoracic ventral bridges with dorsal apodemes. Mesothorax with large medial anteroposterior ventral keel, divided, fused with anterior, posterior mesothoracic bridges. Thoracic wall, floor smooth. Spiracle 1 moderately large; spiracle 2 small. Coxal angles nearly vertical. Coxa I with anterior triangular lobed apodeme. Integument thin.

## Gerromorpha

## Gerridae

Figures 3, 3a-e
Specimens examined:
Gerrinae
Gerrini

Gerris insperatus Drake \& Hottes
Gerris nyctalis Drake \& Hottes
Aquarius remigis Say
Aquarius remigis Say
Limnoporus canaliculatus (Say)

Connecticut
Washington State
Minnesota, Connecticut, Wyoming apterous
California macropterous

Connecticut

| Limnoporus notabilis (Drake \& Hottes) | Washington State |
| :--- | :--- |
| Halobatinae |  |
| Halobates robustus Barber | Galápagos islands, Equador |
| Rhagodotarsinae |  |
| Rheumatobates palosi Blatchley | Minnesota |


| Character | State |
| :--- | :--- |
| a ms ph | Vestigial |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Small |
| a ms vb ap | Small, bi-lobed |
| a ms sh | Absent |
| ap a | Vestigial dorsal lobe; G. insperatus with filament |
| ap b | Absent |
| mt vb | Small, terminating in large coxa with fingerlike dorsal apodeme |
| mt vb ap | Fingerlike; fused with large coxa III wall |
| mt vb e | Broad, curved, progressing dorsally |
| p ms ph | Column; ventrally fused with coxa II dorsum, broadened dorsally to lateral arch |
| p ms ph mr | Medial trough |


| $\mathbf{p}$ ms vb | Small, fused with large coxa II wall |
| :--- | :--- |
| $\mathbf{r 1}$ | Fused with ridges 2, 3 |
| r2 | Fused with ridges 1, 3 |
| r3 | Fused with ridges 2, 3 |
| r3e | Absent |
| sp | Spiracle 1 large, surrounded by palisades; spiracle 2 large, horizontal |
| tf | Smooth |
| tw | Mostly smooth; metathoracic wall with area of small lobes arranged into |
|  | pentagons (Figs. 3-3e). Pentagon clusters of lobes in horizontal rows |
| wmo | Small, hidden by posterior mesothoracic phragma lateral arch |

## Comments

Thorax filiform. Dorsoventrally prothorax $25 \%$ wider than meso- metathoraces. Mesothorax very long, pro- metathoraces short. Head with very long filamentous occipital condyle. Anterior mesothoracic phragma vestigial. Ridges 1, 2, 3 fused. Apodeme alpha, vestigial lobe; apodeme beta absent. Posterior mesothoracic phragma column, fused ventrally with coxa II dorsum. Coxa II large, with anterior elongate lobe. Coxal angles variable. Coxa I vertical, coxa II $40^{\circ}$ from vertical, coxa III $85^{\circ}$ from vertical. Pro- mesothoracic walls, floors smooth. Metathoracic wall with numerous small lobes arranged into pentagons. Spiracle 1 surrounded by palisades; spiracle 2 horizontal. Integument moderately thick, with clustered oval cavities. Pronotal shield with numerous cavities.

## Veliidae

## Figures 4, 4a-d

Specimens examined:
Microveliinae
Microveliini

Microvelia americana (Uhler)
Microvelia californiensis McKinstry
Rhagoveliinae
Rhagovelia distincta Champion
Rhagovelia obesa Uhler

Connecticut

Oregon

Connecticut, Oregon
Connecticut
Character State
a ms ph Absent
a ms ph lk Absent
a ms ph mk Absent
a ms ph vap Absent
$\mathbf{a} \mathbf{m s} \mathbf{v b} \quad$ Ventrally divided; progressing dorsally fused with ridges $1,2,3$; with palisades
a ms vb ap Absent
a ms sh Absent
ap a Variable. M. americana: base conical; shaft narrow to filamentous, then broadened to bladelike head. Rhagovelia sp. shaft short, fingerlike, head absent

| ap b | Base round, tapered to short broad stem with small hooked head |
| :--- | :--- |
| mt vb | Broad, fused with coxa III wall |
| mt vb ap | Short; base broad; stem narrowed to pointed head |
| mt vb e | Broad, linear; with medial lobe, posterior with spiracle 2 |
| p ms ph | Absent |
| p ms ph mr | Absent |
| p ms vb | Linear, moderately broad, fused with coxa II wall |
| r1 | Broad, slightly crescentshaped with ventral lobe |
| r2 | Series of lobes |
| r3 | Straight, linear, progressing dorsally, ending with three lobes |
| r3e | Single lobe connecting ridges 2,3 |
| sp | Spiracles 1, 2 small, oval |
| tf | Large irregular pores, pits. Coxa walls, ventral bridges pits, pores absent |
| tw | Smooth, isolated pores; rough near ridges 1, 2, 3 |
| wmo | Apterous specimen, absent; macropterous specimen, small, round |

## Comments

Head with large triangular occipital condyle progressing through prothorax to anterior mesothorax (Fig. 4a). Prothorax vertically rectangular. Anterior mesothoracic phragma absent. Ridges 1, broad, slightly crescentshaped with ventral lobe; ridge 2 , series of lobes; ridge 3 broad with three dorsal lobes.

Apodeme alpha variable; M. americana with conical base; stem narrow,
filamentous, broadening to bladelike head. Rhagovelia spp. stem short, fingerlike with head absent. Posterior mesothoracic phragma absent. Anterior mesothoracic ventral bridge divided ventrally, progressing dorsally; with lateral palisades. Abdominal dorsal surface with pair of linear ridges progressing posteriorly with cross connections, like ladder rungs. Spiracles 1,2 small, oval. Coxal angles variable. Coxa I vertical; coxa II $35^{\circ}$ from vertical; coxa III $60^{\circ}$ from vertical. Integument very thick.

## Macroveliidae

Figures 5, 5a-b
Specimens examined:
Macrovelia hornii Uhler Oregon

| Character | State |
| :--- | :--- |
| a ms ph | Small, smooth |
| a ms ph lk | Large, bladelike; posterior leading edge dorsoventrally straight |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Small, narrow |
| a ms vb ap | Absent |
| a ms sh | Broad, with posterior palisades progressing dorsally to apodeme alpha |
| ap a | Fused with ridge 3, fingerlike |


| ap b | Base broad; stem broad, straight, slightly broadened to head; tapering to point; |
| :--- | :--- |
| mt vb | with longitudinal scallopshaped indentations |
| mt vb ap | Fingerlike; base broad; stem broad; head slightly bulbous |
| mt vb e | Broad, fused with first abdominal segment; deeply invaginated dorsally |
| p ms ph | Column; fused with coxa II dorsum; with medial anterior trough; crown broad; |
| p ms ph mr | Absent |
| p ms vb | Domeshaped with large surface pits |
| r1 | Anterior arm of "N" configuration with ridges 2, 3. " N " configuration tilted with |
| r2 fused with spiracle 2; foot with small anterior knob |  |

## Comments

Head with occipital condyle. Eye with apodeme, two large pores. Prothorax vertically rectangular. Coxa I with large triangular apodeme, anterior tooth; walls with large lobes. Anterior mesothoracic phragma small with large lateral keel. Anterior mesothoracic ventral bridge fused with anterior mesothoracic shelf; posterior palisades, numerous large ventral pits. Ridges $1,2,3$ in " N " configuration tilted with ridge 1 dorsal to others. Apodeme alpha small, fingerlike; apodeme beta base broad; stem broad, straight, slightly broadened to head; head narrowing to point, with longitudinal scallopshaped striae. Posterior mesothoracic phragma column, fused with coxa II dorsum; lateral arch fused with spiracle 2. Metathoracic ventral bridge with long fingerlike apodeme. Spiracle 1 small, oval, fused with segma coria; spiracle 2 round, fused with posterior mesothoracic phragma lateral arch. Coxal angles variable. Coxa I vertical, coxa II $30^{\circ}$ from vertical, coxa III $60^{\circ}$ from vertical. Integument thick, numerous dorsal oval cavities.

## Hydrometridae

## Figures 6, 6a

Specimens examined:
Hydrometrinae
Hydrometra martini Kirkaldy Connecticut
Hydrometra stagnorum (Linnaeus) England

tf Smooth, with few pits
tw Smooth, with few pits
vap a ms ph Absent
wmo Absent

## Comments

Thorax fusiform. Dorsoventrally, prothorax $25 \%$ wider than meso- and metathoraces. Metathorax very long, pro and mesothoraces short. Prothorax with dorsal lobes. Coxae with fingerlike apodemes. Thoracic wall, floor smooth with few pits. Spiracle 1 round with anterior palisades. Coxal angles $30^{\circ}$ from vertical. Integument moderately thick with dorsal long cavities

## Mesoveliidae

Specimens examined:
Mesoveliinae

| Mesovelia furcata Mulsant \& Rey | Italy | apterous |
| :--- | :--- | :--- |
| Mesovelia mulsanti White | Connecticut, Oregon | apterous |
| Mesovelia mulsanti White | Connecticut | macropterous |

Character State

## Apterous specimens

Figures 7, 7a-b
Specimens examined:

| Mesovelia mulsanti White (Mesoveliidae) |  |
| :---: | :---: |
| Mesovelia furcata Mulsant \& Rey (Mesoveliidae) |  |
| a ms ph | Absent |
| a ms ph Ik | Absent |
| a ms ph mk | Absent |
| a ms ph vap | Absent |
| a ms vb | Broad, with extension |
| a ms vb ap | Long, fingerlike |
| a ms sh | Narrow, fused with anterior coxa II; palisades variable |
| ap a | Short, fingerlike |
| ap b | Short, fingerlike |
| mt vb | Broad |
| mt vb ap | Fingerlike, with slight anterior bend |
| mt vbe | Broad, fused to dorsal region of thoracic wall |
| p ms ph | Vestigial; M. furcata, absent |
| p ms ph mr | Absent |
| p ms vb | Broad, with extension |
| r1 | Absent |
| r2 | Absent |
| r3 | Absent |
| r3e | Absent |
| sp | Spiracles small, round; spiracle 1 surrounded by anterior mesothoracic ventral |

bridge extension; spiracle 2, surrounded by posterior mesothoracic ventral bridge extension
tf Much pitting between ventral bridges, pitting absent from dorsal regions of bridges
tw Pits on lateral thoracic wall few, increasing number dorsally, with additional lobes
wmo Anterior with posterior mesothoracic phragma lateral arch

## Comments

Head with apodeme, short stem, coneshaped head. Eyes large; occipital condyle large. Prothorax vertically rectangular with large dorsal lobes. Anterior mesothoracic phragma absent. Apodeme alpha fingerlike. Apodeme beta fingerlike. Posterior mesothoracic phragma vestigial. All ventral bridges broad, with extensions. Thoracic wall, floor with pits, lobes. Wing muscle opening small. Spiracles small, round; fused with ventral bridge extensions. Coxa II with large cuplike walls; anterior palisades. Coxal angles $45^{\circ}$ from vertical.

Integument moderately thin.

## Macropterous specimens

Figures 8, 8a
Specimens examined:
Mesovelia mulsanti White

| Character | State |
| :---: | :---: |
| a ms ph | Small |
| a ms ph lk | Small, bladelike; same size as medial keel |
| a ms ph mk | Small, bladelike; same size as lateral keel |
| a ms phvap | Absent |
| a ms vb | Round |
| a ms vb ap | Base domelike, with thick fingerlike head |
| a ms sh | Absent |
| ap a | Straight, fingerlike, very long |
| ap b | Absent |
| mt vb | Broad |
| mt vb ap | Large, fingerlike, head slightly bulbous |
| mt vbe | Broad |
| p ms ph | Triangular; crown broad, flat; shaft broad, flat, broadening to spoonshaped foot; fused with posterior mesothoracic ventral bridge dorsum |
| p ms ph mr | Slight medial trough |
| p ms vb | Broad, flat with extension. Spiracle 2 fused with extension |
| r1 | Linear, straight; joined ventrally with ridges 2,3 ; fused with ridge 3 extension |
| r2 | Linear, curved dorsally; joined ventrally with ridges 1,3 ; fused with ridge 3 extension |
| r3 | Linear, curved dorsoposteriorly, fused with apodeme alpha; joined ventrally with |

ridges 1,2 ; fused with ridge 3 extension
r3e Broad with medial trough; dorsally joined with ridges $1,2,3$
$\mathbf{s p} \quad$ Spiracle 1 small, round, fused with segma coria; posteriorly fused with ridge 3 extension; spiracle 2 round, fused with posterior mesothoracic ventral bridge extension
tf Densely pitted; dorsal regions of bridges with few pits
tw Few evenly distributed pits
wmo
Rectangular, dorsally hidden by posterior mesothoracic phragma arch

## Comments

Head with anterior apodeme, thin stem, coneshaped head; eye small; occipital condyle absent. Prothorax vertically rectangular with large dorsal lobes. Anterior mesothoracic phragma small with medial, lateral keels. Ridges $1,2,3$ ventrally joined with ridge 3 extension, dorsally separating in fan configuration. Apodeme alpha fingerlike, very long. Apodeme beta absent. Posterior mesothoracic phragma crown broad, flat; shaft broad, flat, broadening to spoonshaped foot. Phragma fused with posterior mesothoracic ventral bridge dorsum. Metathoracic ventral bridge with large dorsal apodeme. Metathoracic wall with large dorsal lobes. Spiracles 1, 2 small, ventral, oval. Coxa II with anterior palisades. Coxal angles $45^{\circ}$ from vertical. Integument moderately thin.

## Hebridae

Figures 9, 9a-b
Specimens examined:
Hebrinae

| Hebrus buenoi | Drake \& Harris | Oregon |
| :--- | :--- | :--- |
| Hebrus burmeisteri | Lethierry \& Severin | Connecticut |

Character State
a ms ph Leading edge curled anteriorly with linear rugula
a ms ph lk Scimitarshaped; $3 / 4$ length of medial keel
a ms ph mk Scimitarshaped, progressing across whole phragma
amsphvap Absent
a ms vb Absent
a ms vb ap Absent
a ms sh Absent
ap a H. buenoi: short, fingerlike (Fig. 9a); H. burmeisteri: long, linear, with distal hook (Fig. 9)
ap b Base broad, narrowing to fingerlike head
mt vb Absent
mt vb ap Small, "Y"shaped; in large pit anterior to bridge; bridge crossing over long, deep, anteroposterior ventral trough

| mt vbe | Absent |
| :---: | :---: |
| p ms ph | Column, fused with coxa II, crown broad, large posterior mesothoracic lateral arch; |
|  | shaft with transverse suture, medial lobe, anterior ventral fin |
| p ms vb | Absent |
| p ms vb ap | Absent |
| r1 | Fused with ridges 2, 3 |
| r2 | Fused with ridges 1, 3 |
| r3 | Fused with ridges 1, 2 |
|  | H. burmeisteri: with small triangular spine; $H$. buenoi: spine absent |
| r3e | Absent |
| sp | Spiracle 1 fused with segma coria; spiracles 1, 2 round with triangular interior |
|  | spine, similar to "frog" in horse's hoof; H. buenoi: spiracle 2 fused with posterior |
|  | mesothoracic phragma lateral arch, with lobe, ventral fin; H. burmeisteri: spiracle 2 |
|  | more anterior, not fused with posterior mesothoracic phragma lateral arch; round |
|  | with inward spine; with rugose lobe. |
| tf | Many deep pores; large ventral trough progressing anteroposterior with variable |
|  | bridge numbers |
| tw | Smooth, few deep pores. |
| wmo | H. burmeisteri: dorsal to posterior mesothorascic phragma lateral arch; H. buenoi: |
|  | not observed |

## Comments

Prothorax small. Anterior mesothoracic phragma with rugose anterior curl.
Ridges 1, 2, 3 fused. Apodeme alpha variable; H. buenoi, spinelike, H. burmeisteri fingerlike, with distal hook. Apodeme beta base broad narrowing to point. Thoracic floor with large anteroposterior trough, bridges. Posterior mesothoracic phragma, column fused with coxa II; shaft with medial lobe, suture. Metathoracic ventral bridge with anterior "Y"shaped apodeme. Abdominal dorsal wall with paired circularlike patches of rough cuticle (Fig. 9b). Between metathorax abdomen band of large deep pits. Spiracle 1 fused with segma coria; spiracle 2 round, with interior "V"shaped invagination. Coxal angles variable. Coxa I vertical, coxae II, III $45^{\circ}$ from vertical. Integument moderately thick ventrally, thin dorsally.

## Nepomorpha

## Pleidae

## Figure 10

Specimens examined:
Neoplea striola (Fieber) Connecticut
Paraplea puella (Barber) Ohio
Sp. (undetermined) Connecticut
Character State
a ms ph Small to arch

| a ms ph lk | Absent |
| :--- | :--- |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Arched |
| a ms vb ap | Domeshaped base, dorsally reducing to filament |
| a ms sh | Absent |
| ap a | Filament |
| ap b | Absent |
| mt vb | Absent |
| mt vb ap | Absent |
| mt vb e | Absent |
| p ms ph | Column fused with coxa III; crown moderately broad, fused with wing muscle |
| pp ms vb | Small, positioned anteroventral to spiracle 1; or absent |
| p ms vb ap | Absent |
| r1 | Flat, fused with ridge 2 |
| r3 | Flat, fused with ridge 1 |
| r3 | Flat, progressing from anteroventral thoracic tongue to apodeme alpha. Tongue |
| rectangulai shaped flap. Thoracic wall with similarily shaped structure |  |

tf Series of ventral rectangular folds with thoracic tongue. Coxa II anteroventral to spiracle 1
tw Rough, with thoracic tongue
wmo Large, rectangular, fused with posterior mesothoracic lateral arch

## Comments

Large segma coria between head, prothorax. Prothorax vertically rectangular with anterior ridge. Anterior mesothoracic phragma small with arch. Ridges 1, 2 flat, fused; ridge 3 flat, progressing from anterior ventral thoracic tongue to apodeme alpha. Apodeme alpha filamentous; apodeme beta absent. Posterior mesothoracic phragma, column, fused with coxa III; crown moderately broad; shaft with several short troughs. Thoracic floor with series of rectangular folds, tongue; thoracic wall smooth with tongue. Tongues rectangular shaped, function undetermined. Spiracle 1 moderately large, almost rectangular, fused with segma coria; spiracle 2 between ventral, lateral thoracic tongues, horizontal, large, oval. Coxal angles variable. Coxae I, II vertical; coxa III $45^{\circ}$ from vertical. Coxa II anteroventral to spiracle 1. Integument moderately thick.

## Notonectidae

Figure 11
Specimens examined:
Notonecta meridionalis Hutchinson South Africa
Notoectinae

Notonectini

| Notonecta irrorata Uhler |  | Connecticut |
| :---: | :---: | :---: |
| Notonecta undulata Say |  | Connecticut |
| Character | State |  |
| a ms ph | Leading ed | posteriorly, wi |
| a ms ph lk | Fused late | hragma, prog |
| a ms ph mk | Absent |  |
| a msphvap | Absent |  |
| a ms vb | Small; bro | by square apo |
|  | keel |  |
| a ms vb ap | Square, fu | rly with large |
| a ms sh | Absent |  |
| ap a | Flat, squar | ed tongue; out |
| ap b | Anvilshap | ally; stem shor |
|  | edges, rug |  |
| mt vb | Broad, arc | d by large cox |
| mt vb ap | Anvilshap | all lateral anv |
|  | apodeme | filament, fea |
| mt vbe | Large, dog | d, progressing |
|  | angled par | oracic ridges |

pms ph Large, hourglass-shaped, with two layers of cuticle, large cavity; shaft narrow with wide boatshaped foot; foot ringed by dorsal frill
p ms vb Large, with several dorsal lobes including apodeme beta; progressing dorsally with large spoonshaped extension
p ms vb ap Absent
r1 Anteriorly large, long, double lobed, progressing to posterior mesothoracic phragma lateral arch. Medially narrow. Posterior third of ridge's dorsal edge fused with apodeme alpha ventrad
r2
Very short, anterior, "L"shaped
r3 Bladelike, very thin shelf or fin projecting into thoracic cavity progressing horizontally to dorsal region of posterior mesothoracic ventral bridge extension
r3e Absent
sp $\quad$ Spiracles small, hidden
tf Mesothoracic floor smooth with large medial keel
tw Mostly smooth
wmo Hidden by apodeme alpha

## Comments:

Prothorax vertically rectangular, fused with head. Anterior mesothoracic phragma dorsally smooth, leading edge curled posteriorly, with striations. Ridge 1 anteriorly large, elongate double lobe, progressing to posterior mesothoracic phragma lateral arch; medially narrow. Posterior third of ridge's dorsal edge fused
with apodeme alpha ventrad. Ridge 2, very short, anterior, "L"shaped. Ridge 3 bladelike as very thin shelf progressing horizontally to dorsal region of posterior mesothoracic ventral bridge extension. Posterior mesothoracic phragma large, hourglass-shaped, with two layers of cuticle, cavity; shaft narrow with wide boatshaped foot. Foot ringed by dorsal frill. Posterior mesothoracic ventral bridge with large spoonshaped extension. Metathorax with two parallel lateral ridges fused at each end. Posterior end of these two ridges progressing to abdomen. Metathoracic ventral bridge extension fused with ventral ridge of two metathoracic lateral ridges. Metathoracic bridge with anvilshaped apodeme fused with small identical companion apodeme; companion apodeme with anterior filament, featherlike head. Spiracles very small (not shown in figures). Coxal angles $45^{\circ}$ from vertical. Integument moderately thin.

## Naucoridae

## Figure 12

Specimens examined:

Pelocoris femoratus (Palisot) Connecticut, North Carolina

Character State
a ms ph Smooth, round with slight thickening of curled leading edge
a ms ph lk Very small
a ms ph mk Absent

## a ms ph vap Absent

a ms vb Broad, round, hidden by flattened dorsal apodeme
a ms vb ap Broad, flat, with posterior fingerlike head
a ms sh Narrow
ap a Flat round lobe with rugose ventral surface
ap b Anvilshaped; stem filamentous; head flat, with medial filament, frayed leading edge
mt vb Vestigial, with very large dorsal cupshaped coxa III hood covering bridge. Hood with anterior dorsal frill
mt vb ap Saddleshaped, base broad column. Posterior arm long, snakelike, with distal bend; anterior arm small
mt vbe Absent
pms ph Tubelar; crown slightly broad; shaft tubelike; foot slightly broad with semicircular anterior lip, cavity medioventral
pmsph mr Absent
p ms vb Small because of large coxa II
r1 Anterior arm of triangle formation with ridges 2, 3; proceeding along lateral edge of anterior mesothoracic phragma
r2
Posterior arm of triangle formation with ridges 1, 3. Dorsal region where ridges 1, 2 fused with patches of pubescent cuticle
r3
Horizontal ventral arm of triangle formation with ridges 1, 2. Anterior third of ridge lobed, with gap before progressing to apodeme alpha

| r3e | Absent |
| :--- | :--- |
| $\mathbf{s p}$ | Spiracle 1 small, fused with segma coria (not illustrated); spiracle 2 oval, fused |
|  | with posterior mesothoracic phragma lateral arch ventral ridges |
| tf | Smooth, with medial keel |
| tw | Dorsal prothorax slightly pitted. Meso- metathoracic pits smaller than prothoracic |
|  | pits. Mostly smooth, with slightly rugose patches |
|  | Smo |

## Comments

Head with occipital condyle. Prothorax small, half size of other thoracic segments.
Ventral mesothorax deeply concave, narrowing towards metathorax. Anterior mesothoracic phragma smooth, round with slight thickening of curled leading edge. Ridges 1, 2, 3 in triangle formation. Ridge 3 lobed anteriorly, with gap before progressing to apodeme alpha. At fusion of ridges 1,2 are pubescent patches. Apodeme alpha flat round lobe, with rugose ventral surface. Apodeme beta base anvilshaped; stem filamentous; head flat, with medial filament, frayed leading edge. Posterior mesothoracic phragma tubular with slightly broadening foot. Phragma with medial cavity. Metathoracic ventral bridge with large cupshaped coxa III hood covering bridge. Hood with dorsal frill. Metathoracic ventral bridge apodeme anterior to bridge; base broad with dorsal saddle; posterior arm long, snakelike, anterior arm small. Coxal angles variable. Coxa I vertical; coxa II $45^{\circ}$ from vertical; coxa III $85^{\circ}$ from vertical. Coxa III with large cupshaped
hood, dorsal anterior frill. Spiracle 1 small, fused with segma coria; spiracle 2
fused with ridges ventral to posterior mesothoracic phragma lateral arch.
Integument moderately thick, with long cavities dorsally.

## Gelastocoridae

## Figures 13, 13a-b

Specimens examined:

| Sp. (undetermined) | Connecticut |
| :--- | :--- |
| Gelastocorinae |  |
| Gelastocoris oculatus (Fabricius) | Oregon, New Jersey |
| Nerthrinae |  |
| Nerthra hapaeformis (Fabricius) | Brazil |


| Character | State |
| :--- | :--- |
| a ms ph | Small, smooth, slightly convex |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Broad; dorsally covered by large flat apodeme |
| a ms vb ap | Broad; covering bridge; flat, with small posterior lobes |
| a ms sh | Small |
| ap a | Bicycle-saddleshaped; posterior end fused with thoracic wall, anterior end jutting |
|  | out |


| ap b | Base broad, square; head flat overhanging base |
| :---: | :---: |
| mt vb | Fused with bases of metathoracic ventral bridge apodeme, cupshaped coxa III hood |
| mt vb ap | Saddleshaped, with tall base. Posterior arm long, snakelike, with distal square |
|  | lobes |
| mt vbe | Meandering. Extension progressing dorsally fusing with complex of dorsal |
|  | weaving ridges |
| p ms ph | Tubular; crown slightly broad; shaft tubelike; foot slightly broade, with |
|  | semicircular anterior lip. Phragma with inner cavity |
| p ms ph mr | Absent |
| p ms vb | Small, fused with coxa II hood, apodeme beta base |
| r1 | With anterior hook; progressing dorsally, turning $180^{\circ}$, forked; anterior arm of |
|  | inverted " N " configuration with ridges 2, 3. Three-ridge " N " configuration tilted |
| r2 | Fused with ridges 1,3 as inner diagonal of inverted "N" configuration |
| r3 | With ventral hook; progressing dorsally, then curving ventrally to apodeme alpha. |
|  | Posterior arm of inverted " N " configuration with ridges 1,2 |
| r3e | Absent |
| sp | Spiracle 1 small, fused with segma coria (not illustrated); spiracle 2 small, hidden |
|  | by posterior mesothoracic phragma (not illustrated) |
| tf | Smooth, with folds |
| tw | Smooth, with folds, rough areas |
| wmo | Small, triangular; dorsal with apodeme alpha |

## Comments

Prothorax about $30 \%$ smaller than other thoracic segments. Ventral mesothorax deeply convex. Anterior mesothoracic phragma small, smooth, domed. Ridges 1, 2, 3 as tilted inverted " N " configuration. Ridge 1 anterior arm of " N " configuration with anterior hook, posteriorly divided as inverted "Y". Ridge 2 diagonal medial arm of configuration. Ridge 3, posterior arm, with ventral hook, progressing dorsally then curving ventrally to apodeme alpha. Posterior mesothoracic phragma tubular; crown slightly broad; shaft tubelike; foot slightly broad, with semicircular anterior lip. Phragma with inner cavity. Apodeme alpha bicycle-saddleshaped. Apodeme beta base thick, square; head flat, overhanging base. Metathoracic abdominal wall with series of interconnected ridges. Coxal angles variable. Coxa I vertical, coxa II $30^{\circ}$ from vertical, coxa III $70^{\circ}$ from vertical. Coxa II with large cupshaped hood covering coxa; coxa III same, with dorsal frill. Anterior to coxa III is large apodeme. Spiracle 1 small, fused with segma coria (not illustrated); spiracle 2 small, hidden by posterior mesothoracic phragma (not illustrated). Integument moderately thin, dorsally with small elongate cavities.

## Corixidae

## Figures 14, 14a-c

Specimens examined:
Retrocorixa semistriata (Fieber) England
Corixinae
Corixini

| Callicorixa alaskensis Hungerford | Inner Hebrides, Scotland |
| :--- | :--- |
| Callicorixa wollastoni (Douglas \& Scott) | Inner Hebrides, Scotland |
| Hesperocorixa atopodonata (Hungerford) | Connecticut |
| Hesperocorixa interrupta (Say) | Connecticut |

Hesperocorixa sp. Kirkaldy California
Trichocorixa louisianae Jaczewski Florida
Tropocorixa meridonalis Hutchinson South Africa

| Character | State |
| :--- | :--- |
|  |  |
| a ms ph | Large, smooth, with horizontal ventral edge; arched dorsally fusing with posterior |
|  | mesothoracic phragma |
| a ms ph lk | Absent |
| a ms ph mk | Long, thin, scimitarshaped |
| a ms ph vap | Absent |
| a ms vb | Flat, fused with spiracle 1 |

a ms vb ap Large, rectangular with anterior lip, slightly curved
a ms sh Ventrally broad, narrow in lateral regions
apa Anteroventral, fused on thoracic floor ridge; stem short; head wide, flat, pointing posteriorly. Thoracic floor ridge dorsally ends in large oval cavity
ap b Base saddleshaped; stem narrow with fanshaped head. Posterior mesothoracic phragma foot resting on apodeme beta
mt vb Small; large coxa III cupshaped hood covering bridge
mt vb ap Anterior to coxa III hood opening. Large, rectangular, slightly hooked with posterior filament
mt vbe Ventrally triangular, progressing dorsally, narrowing to linear ridge
pms ph Triangular; crown broad, shaft narrow, foot scallop-shellshaped in H. atopodonata (Fig. 14b-c), boatshaped in H. interrupta, A. alaskensis (Fig. 14a); foot resting on apodeme beta
pms ph mr Absent
pms vb Vestigial
r1 Fused with ridges 2,3 as linear fold, dorsal to spiracle 1
r2
Fused with ridges 1, 3 as linear fold, dorsal to spiracle 1
r3
Fused with ridges 1, 2 as linear fold, dorsal to spiracle 1
r3e
Absent
sp
Spiracle 1 flat, rectangular with radiating rays of linear cuticle (Figs. 14, 14b-c) $H$. atopodonata, T. louisianae. Not present in other listed species. Spiracle 2 trachealike (Figs. 14, 14a-b). Possibly $3^{\text {rd }}$ metathoracic spiracle, large, horizontal
(Fig. 14)
With series of ventral linear anteroposterior finlike ridges; posterior ends fused with anterior wall of coxa II as palisades
tw Smooth, with varied structures. Anterior mesothorax with palisades, three ovalshaped cavities (Figs. 14, 14a). Metathorax with various fins, ridges, folds; "Y"shaped ridge between thorax, abdomen as extension of metathoracic ventral bridge extension (Fig. 14)
wmo Large, posterior with mesothoracic phragma lateral arch

## Comments

Prothorax moderately large, dorsoventrally rectangular, with thin cuticleous dorsoventral ridge. Anterior mesothoracic phragma large, smooth, with straight horizontal ventral edge, fusing posteriorly with posterior mesothoracic phragma.

Ridges 1,2,3 fused as linear fold. Apodeme alpha anteroventral, fused on thoracic floor finlike ridge; stem short; head wide, flat, pointing posteriorly; ridge dorsally ends with large oval cavity. Apodeme beta base saddleshaped; stem narrow; head fanshaped. Posterior mesothoracic phragma triangular; crown broad; shaft narrow; foot, scallop-shellshaped in H. atopodonata (Figs. 14b-c); boatshaped in H. interrupta, A. alaskensis (Figs. 14, 14a). Foot resting on apodeme beta. Metathoracic ventral bridge small, covered by coxa III hood. Anterior to hood is large rectangular metathoracic ventral bridge apodeme, with posterior filament. Anterior mesothoracic wall with palisades, three oval cavities. Metathoracic wall
with ridges, folds, fins, posterior "Y"shaped ridge (Fig. 14) fused to first abdominal segment. Mesothorax floor with long finlike ridges. Spiracle 1 rectangular, small with linear sutures of cuticle radiating from central opening; spiracle 2 large, trachealike; metathoracic spiracle 3, oval, horizontal. Coxae angles variable. Coxa I $25^{\circ}$ from vertical, coxa II $45^{\circ}$ from vertical, coxa III $85^{\circ}$ from vertical. Coxae I, III with large apodemes. Integument thin.

## Nepidae

Specimens examined:
Nepinae
Nepini
Nepa apiculata Uhler Minnesota
Ranatrinae
Ranatra fusca Palisot Minnesota
There are differences between these two species. Synapomorphies are ovate body form, large coxae; small anterior apodemes on coxa III; coxae II, III close together, coxa I separate; anterior mesothoracic phragma with $90^{\circ}$ bend; prothoraces elongate with internal ribs. Wing muscle openings small, round. Descriptions following are of each species.

## Ranatra fusca

Figures 15, 15a

| Character | State |
| :--- | :--- |
| $\mathbf{a ~ m s ~ p h}$ | Large, with $90^{\circ}$ bend |
| a ms ph lk | Absent |
| a ms ph mk | Long, thin, scimitarshaped |
| a ms ph v ap | Medial, deeply cupshaped, tapering to sharp point |
| a ms vb | Small; ending in double rings |
| a ms vb ap | Apodemes large, flat, medially fused with sheet of concave cuticle. Apodemes |
| a ms sh | Absent |
| ap a | Long, thin, bladelike fin; anterior end fused 2/3rds along Ridge 3 posteriorly as spines |
| ap b | Base square, fused with coxa II |
| mt vb | Vestigial, fused with large dorsal coxa III hood. Hood with several dorsal fins |
| mt vb ap | Small, toothlike or fingerlike; anterior surface sloped fusing with posterior wall of |
| p ms ph | Divided into two structures: 1) large medial structure with deep anteriorly cupped |
| m ms ph mr | Absent |
| mith folds, lobes |  |


| p ms vb | Absent, area covered by large coxa II |
| :---: | :---: |
|  | Coxa II wall large, dorsally square. Lateral side extended dorsally as column, |
|  | fusing with posterior mesothoracic phragma arch. Some specimens with thin |
|  | cuticleous sheet between column, thoracic wall |
| r1 | Curved anteriorly; progressing dorsally, narrowing |
| r2 | Very long, linear, progressing dorsally towards ridge 3 forming isosceles triangle |
|  | with ridge 3 ; lobe between ridges 2,3 |
| r3 | Large, linear, with anterior, posterior lobes. Posterior lobe separated from ridge, |
|  | between ridges 2, 3 |
| r3e | Absent |
| sp | Absent (respiration through abdominal siphon). Spiracle 1 as a cuticleous ventral |
|  | ring may be vestigial |
| tf | Smooth |
| tw | Ventral mesothoracic wall with $90^{\circ}$ bend, forming two sides of equilateral triangle |
| wmo | Externally small, round; internally, large, rectangular, dorsal with posterior |
|  | mesothoracic phragma lateral arch |

## Comments

Prothorax extremely elongate; goose-necklike, with internal ribbing. Anterior mesothoracic phragma with $90^{\circ}$ bend, large medial cupshaped apodeme. Anterior mesothoracic ventral bridge apodemes with medial sheet of cuticle between them, posteriorly pointed. Anterior mesothoracic ventral bridge ending with double
rings. Ridge 1 curved anteriorly, progressing dorsally, narrowing to point. Ridge 2 very long, linear, progressing dorsally towards ridge 3 , forming isosceles triangle with ridge 3. Ridge 3 large, linear, with anterior, posterior lobes. Posterior lobe detached from ridge 3. Lobe present between ridges 2, 3. Posterior mesothoracic phragma divided into two structures: 1) medial structure, deeply cupped sheet of cuticle, curled anteriorly: 2) small lateral column, broadening to humanlike foot. Mesothoracic ventral wall with $90^{\circ}$ angle. Coxa II with dorsal column fused with posterior mesothoracic lateral arch; some specimens with sheet of cuticle between column, thoracic wall. Spiracles absent; spiracle 1 may be present as a ventral vestigial ring. All coxal angles, nearly vertical. Coxa I seoartate from coxae II ,III. Coxa III hood with dorsal fins. Integument thin.

## Nepa apiculata

Figures 16, 16a
Character State
a ms ph Large, with $90^{\circ}$ angle, bilobed, rugose ventrally
a ms ph lk Absent
a ms ph mk Absent
a ms ph vap Fingerlike, lateral
a ms vb Vestigial
a ms vb ap Base small, progressing to long posterior filament

| a ms sh | Absent |
| :---: | :---: |
| ap a | Large rectangular fin next to coxa II |
| ap b | Base large, square, fused with coxa II; no stem or head |
| mt vb | Small |
| mt vb ap | Very small, filament, fused anteriorly with posterior coxa II |
| mt vbe | Absent |
| p ms ph | Triangular; crown broad, lobed; shaft short, narrow; foot bulbous with pointed tip. |
|  | Foot with lateral oval indentation, dorsal trough |
| p ms ph mr | Absent |
| p ms vb | Small, linear, with extension, fused with coxa II posterior wall, apodeme beta base |
| r1 | Curved anterodorsally, fused with dorsal ridge |
| r2 | Concave curve, anteriorly fused with anterior mesothoracic phragma ventral rugose |
|  | region |
| r3 | Slightly curved, progressing posteriorly to ribbed region dorsal to apodeme alpha |
| r3e | Absent |
| sp | Absent (respiration through abdominal siphon) |
| tf | Smooth, with small medial keel. Keel not finlike but round, forked anteriorly, |
|  | posteriorly fused with coxa II anterior wall |
| tw | Largely smooth. Posterior mesothoracic phragma arch with rectangular rugose |
|  | region |
| wmo | Small, hidden by apodeme alpha |

## Comments

Prothorax elongate. Coxa I with large dorsal apodeme. Prothorax wall with crosslike ridges. Anterior mesothoracic phragma with $90^{\circ}$ bend; ventral region rugose. Anterior mesothoracic ventral bridge with filamentous posterior apodeme. Apodeme alpha rectangular fin next to coxa II. Apodeme beta only as square base. Posterior mesothoracic phragma with broad crown, narrowing to short shaft; foot bulbous with pointed tip; lateral oval indentations with dorsal trough. Mesothoracic floor medial keel small, rounded; forked anteriorly, posteriorly fused with coxa II. Posterior mesothoracic phragma arch with dorsal rugose rectangular region. Wing muscle opening small, hidden by apodeme alpha. Spiracles absent because abdominal siphon respiration. Coxal angles almost vertical. Coxa I in prothorax more posterior than R. fusca: separate from coxae II, III. Coxa II large with sloping sides, flat dorsad. Coxa III hood with small filament apodeme. Integument thin.

## Belostomatidae

## Figures 17, 17a

Specimens examined:
Belostomatinae
Belostoma flumineum Say
Connecticut
Lethocerinae
Lethocerus griseus (Say) Connecticut
Lethocerus americanus (Leidy) Connecticut

| Character | State |
| :---: | :---: |
| a ms ph | Deeply convex, anteromedially rugose |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph vap | Absent |
| a ms vb | Vestigial, hidden by large dorsal apodemes |
| a ms vb ap | Extremely large (Fig. 17). Anterior arm with elevated flat head; posterior arm very |
|  | large, long, with pointed tip |
| a ms sh | Absent |
| ap a | Large, rectangular with birdlike head (Fig. 17) |
| ap b | Base with large pores, fused with anterior side of divided posterior mesothoracic |
|  | ventral bridge; stem long; head discshaped |
| mt vb | Arched with large pores, hidden by large dorsal apodemes |
| mt vb ap | Metathoracic ventral bridge apodeme extremely large "C" shape (Fig. 17a). |
|  | Anterior arm with large knob, posterior arm curved with sphere supported by flat |
|  | disc |
| mt vbe | Two interconnecting ridges with fold progressing to abdomen |
| p ms ph | Divided into two parts, fused in crown: 1) medial part curved sheet; 2) lateral part |
|  | broad shaft progressing to clubshaped foot |
| p ms ph mr | Absent |
| p ms vb | Two divided curvilinear ridges with medial cavity |

r1 Curved dorsally
Small, with $90^{\circ}$ medial bend. Ventrally fused with complex of secondary ridges, lobe, dorsal to ridge 3
r3 Progressing as wave from anterior mesothoracic phragma to apodeme alpha; dorsally fused with complex of secondary ridges, lobe, ventral with ridge 2
r3e Short, "S"shaped
sp Absent
tf Smooth, with large medial anteroposterior keel; keel with anterior hook
tw Smooth
wmo Large, oval, posterior with apodeme alpha

## Comments

Head with occipital condyle. Prothorax large. Anterior mesothoracic ventral bridge apodemes very large. Anterior mesothoracic phragma deeply convex, anteromedially rugose. Ridge 1 curved dorsally. Several secondary ridges, lobe are between ridges 2, 3. Apodeme alpha large, rectangular with birdlike head (Fig. 17). Apodeme beta base with large pores; stem long, thin; head discshaped.

Posterior mesothoracic ventral bridge divided as two ridges. Posterior mesothoracic phragma divided, fused in crown: 1) medial part curved sheet; 2) lateral part broad shaft progressing to clublike foot. Metathoracic ventral bridge apodeme extremely large,"C"shape, anterior arm with large knob, posterior arm
curved dorsally with sphere supported by flat disc; base with large pores (Fig. 17a). Wing muscle opening large, oval. Metathoracic ventral bridge extension with two interconnecting ridges, fold progressing to abdomen. Spiracles absent. All coxal angles $20^{\circ}$ from vertical. Integument moderately thin.

## Leptopodomorpha

## Saldidae

## Figures 18, 18a-b

Specimens examined:
Chiloxanthinae
Pentacora hirta (Say) Connecticut
Pentacora sphacelata (Uhler) Connecticut

## Saldula saltatoria (Linnaeus) Connecticut

Character State
a ms ph Moderately small, round, smooth
a ms ph lk Absent
a ms ph mk Side of keel fused with phragma, with straight angles, unattached side as crescent curve
a ms ph vap Small, fingerlike
a ms vb Very narrow, short

| a ms vb ap | Small, toothlike, lateral on bridge |
| :---: | :---: |
| a ms sh | Absent |
| ap a | Base arched; stem straight sided; head hooked with dorsal surface square, flat |
| ap b | With $45^{\circ}$ anterior tilt; base triangular; stem broad with basal lateral tooth, |
|  | narrowing to featherlike head |
| mt vb | Small, fused with coxa III |
| mt vb ap | With $45^{\circ}$ anterior tilt. Large; stem broad; head round with dorsal knob |
| mt vbe | Absent |
| p ms ph | Triangular; crown broad, convex; shaft narrow; foot hooked, with posterior hook |
| p ms ph mr | Trough progressing length of phragma |
| p ms vb | Small, medially fused with apodeme beta base, fused laterally with secondary |
|  | ridges |
| r1 | Broad, curved dorsally |
| r2 | Narrow, curved dorsally, fused ventrally with ridge 3 |
| r3 | Narrow, curved, broad dorsally, fused ventrally with ridge 2 |
| r3e | Absent |
| sp | Spiracle 1 small (not illustrated); spiracle 2 large, oval with many folds |
| tf | Deeply folded because of coxae; surface smooth |
| tw | Mostly smooth |
| wmo | Moderately large, square |

## Comments

Prothorax moderately large, with several lateral ridges. Coxa I with anterior apodeme, stem thin, head coneshaped. Anterior mesothoracic phragma moderately small, round, smooth with medial keel. Ridges $1,2,3$ dorsally curved, ridges 2,3 fused ventrally. Apodeme alpha with ventral arch, stem straight, head hooked with dorsal surface square, flat. Apodeme beta with $45^{\circ}$ anterior tilt; base triangular; stem broad with basal lateral tooth, head featherlike. Posterior mesothoracic phragma triangular, narrowing through shaft to hooked foot with posterior hook. Apodeme of metathoracic ventral bridge large with ventral linear folds. Abdomen with intersecting ridges. Spiracle 1 small (not illustrated); spiracle 2 large, oval with many folds. Coxae I, III very large, coxa II small. Coxal angles variable. Coxae I, III $75^{\circ}$ from vertical. Coxa II $30^{\circ}$ angle from vertical. Integument moderately thick.

## Cimicomorpha

## Cimicidae

## Figure 19

Specimens examined:
Cimicinae

Cimex lectularis Linnaeus
Oeciacus vicarious Horvath

Connecticut
California

| Character | State |
| :---: | :---: |
| a msph | Small, round, smooth |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph vap | Small, peglike |
| a ms vb | Absent |
| a ms vb ap | Absent |
| a ms sh | Absent |
| ap a | Short, bladelike |
| ap b | Small, base triangular; stem long snakelike, head absent |
| mt vb | Vestigial |
| mt vb ap | Long, fingerlike |
| mt vbe | Crescentshaped trough, with dorsal fold, progressing to spiracle 2 |
| p ms ph | Absent |
| p ms ph mr | Absent |
| p ms vb | Vestigial |
| r1 | Absent |
| r2 | Absent |
| r3 | Absent |
| r3e | Absent |
| sp | Spiracle 1 small, fused with segma coria; spiracle 2 small, oval |

tf
tw Smooth, with large deep, round lateral cavity in mesothorax
wmo Absent

## Comments

Prothorax $2 / 3$ size of mesothorax, with cervical constriction between two segments. Prothorax with dorsal lobes, anterior square, hooked apodeme. Coxae invaginated into thoracic cavity; coxa I $50 \%$, with large hooked apodeme, coxa II $75 \%$, coxa III $50 \%$. Mesothoracic wall with large outward domeshaped lobe. Anterior mesothoracic phragma small. Ridges 1, 2, 3 absent. Apodeme alpha small, fingerlike. Apodeme beta with snakelike stem; head absent. Posterior mesothoracic phragma absent. Posterior mesothoracic ventral bridge with fingerlike hooked apodeme. Metathoracic ventral bridge extension, as trough with dorsal fold progressing to spiracle 2. Between metathorax, abdomen is broad band of segma coria. Spiracle 1 fused with segma coria; spiracle 2 small, oval. Coxal angles variable. Coxae I, II almost vertical, coxa III $50^{\circ}$ from vertical. Integument thick.

## Anthocoridae

Figures 20, 20a-g
Specimens examined:
Sp. (undetermined) Israel
Anthocorinae
Sp. (undetermined) Nevada

Oriini
Orius insidiosus (Say) Massachusetts
Character State

| a ms ph | Large, with ventral arch, smooth, fused with posterior mesothoracic phragma |
| :--- | :--- |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Small, round |
| a ms vb ap | Absent |
| a ms sh | Absent |
| ap a | With short stem, head scoopshaped. Ventral surface of apodeme, with irregular |
| ap b | Base broad; stem filamentous; head coneshaped |
| mt vb | Broad, fused with coxa III |
| mt vb ap | Posterior pointing fingerlike hook 20, 20a) |
| mt vb e | Absent |
| p ms ph | Triangular; crown broad with dorsal rugose region; shaft short, broad; foot hooked, |
| p ms ph mr | Series of small intertwining folds |

p ms vb Broad, with dorsal ridge
r1 Vertical, curved slightly dorsoposteriorly. Between ridges 1,2 are glands (Figs. $20 \mathrm{~b}-\mathrm{f}$ ), with stalk, round head. Figure 20 g shows glands as high-walled openings
r2 Ventrally fused with ridge 3, progressing dorsally. Between ridges 1,2 are glands (Figs. 20b-f), with stalk, round head. Figure 20 g shows glands as high-walled openings
r3 Ventrally fused with ridge 2, progressing diagonally to apodeme alpha r3e Absent
sp $\quad$ Spiracle 1 ventral, round, fused with segma coria; spiracle 2 oval, fused with posterior mesothoracic phragma lateral arch
tf Mesothoracic floor with large keel, broad posteriorly, narrow anteriorly
tw Prothoracic wall smooth. Mesothorax smooth with large lateral lobes; $O$. insidiosus mesothorax wall rough with no lobes
wmo Hidden by posterior mesothoracic phragma lateral arch

## Comments

Rectangular prothorax small, smooth, dorsoventrally narrow. Anterior mesothoracic phragma large, fusing with posterior mesothoracic phragma. Ridge 1 vertical; ridges 2,3 ventrally fused as "Y"shaped configuration. Between ridges 1 and 2 are glands (Figs. 20a-f). Each gland with dark porelike base, stalk, round head (Figs. 20e-f). Figure 20 g shows glands as high-walled openings. Some specimens with secondary gland area, dorsal to posterior mesothoracic phragma
lateral arch. Posterior mesothoracic phragma triangular, with dorsal rugose region (Figs. 20, 20a); crown broad; shaft narrow, short; foot hooked, with large posterior hook. Thoracic floor with keel. Mesothoracic wall with large lobes. Apodeme alpha with short stem; head scoopshaped, with ventral irregular teeth, pits (Figs. 20, 20a). (Nevada specimen apodeme alpha fused to large anterior spine).

Apodeme beta base broad; stem narrow; head coneshaped. Coxal angles nearly vertical. Integument moderately thick; ventral external surface with ornamented plates (Fig. 20a).

Nabidae
Figures 21, 21a-b
Specimen examined:
Nabinae
Nabiini

| Nabis americoferus Carayon | Canada |
| :--- | :--- |
| Nabis rufusculus Reuter | Connecticut |
| Nabicula subcoleoptrata Kirby | Connecticut |


| Character | State |
| :--- | :--- |
|  |  |
| a ms ph | Large, with smooth ventral arch, fusing with posterior mesothoracic phragma |
| a ms ph lk | Scimitar-shaped, with medial $90^{\circ}$ bend |
| a ms ph mk | Scimitar-shaped, with medial $90^{\circ}$ bend |


| a ms ph vap | Absent |
| :---: | :---: |
| a ms vb | Absent |
| a ms vb ap | Absent |
| a ms sh | Absent |
| ap a | Square peglike |
| ap b | Base triangular, with dorsal tooth; filamentous stem fused with base anterior; head |
|  | coneshaped |
| mt vb | Broad |
| mt vb ap | With posterior facing fingerlike hook |
| mt vbe | Progressing dorsally, broadening into triangular region |
| p ms ph | Triangular; crown broad, with squareshaped opening (window) in posterior |
|  | mesothoracic lateral arch (Fig. 21, 21a-b); shaft flat progressing to scoopshaped |
|  | foot |
| p ms ph mr | Absent |
| p ms vb | Broad |
| r1 | Anterior arm of three-ridge " N " configuration; short, thin with anterior ventral |
|  | hook |
| r2 | Medial arm of three-ridge " N " configuration; short, broad |
| r3 | Posterior arm of three-ridge " N " configuration; short, thin |
| r3e | Absent |
| sp | Spiracle 1 ventral, fused with very large segma coria; spiracle 2 small, oval |
| tf | Smooth |

tw Mostly smooth with rough areas
wmo Small, hidden by apodeme alpha

## Comments

Prothorax large, smooth, with anterior extension. Threadlike palisades in prothorax, with very large segma coria. Palisades on coxa I anterior. Large hollow spine covering prothoracic floor. Segma coria constriction between pro-and mesothoraces. Anterior mesothoracic phragma large, with smooth ventral arch, fusing with posterior mesothoracic phragma. Ridges $1,2,3$ in " N " configuration. Apodeme alpha square peglike. Apodeme beta base triangular with dorsal tooth; filamentous stem fused with base anterior, head coneshaped. Posterior mesothoracic phragma triangular; crown broad, with squareshaped opening (window) (Figs. 21, 21a); shaft flat progressing to scoopshaped foot. Metathoracic ventral bridge with large posterior apodeme. Spiracle 1 ventral, fused with very large segma coria; spiracle 2 small, oval. Coxal angles variable. Coxa I $50^{\circ}$ from vertical, coxae II, III, $20^{\circ}$ from vertical. Coxae II, III close together, coxa I separate. Integument moderately thin, with oval cavities.

## Miridae

Figures 22, 22a-j
Specimens examined:
Mirinae

Mirini

| Adelphocoris lineolatus (Goeze) | Connecticut |
| :---: | :---: |
| Capsus ater (Linnaeus) | Connecticut |
| Coccobaphes frontifer Walker | Connecticut |
| Lygidea mendax Reuter | Connecticut |
| Lygidea rosacea Reuter | Minnesota |
| Lygocoris pabulinus Linnaeus | Connecticut |
| Lygocoris quercalbae Knight | Connecticut |
| Lygus lineolaris Palisot de Beauvois | Connecticut |
| Poecilocapsus lineatus Fabricius | Connecticut |
| Tropidosteptes amoenus Reuter | Connecticut |
| Tropidosteptes cardinalis Uhler | Connecticut |
| Tropidosteptes palmeri Reuter | Connecticut |
| Resthenini |  |
| Prepops fraternus Knight | Pennsylvania |
| Prepops insitivus Say | Connecticut |
| Prepops nigricollis Reuter | Connecticut |
| Stenodemini |  |
| Collaria oculata Reuter | Connecticut |
| Leptopterna dolabrata Linnaeus | Connecticut |
| Trigonotylus ruficornis Geoffroy | Connecticut |
| Orthotylinae |  |

Orthotylini

| Ilnacora malina Uhler | Connecticut |
| :--- | :--- |
| Ceratocapsus modestus Uhler | Connecticut |
| Lopidea caesar Reuter | Connecticut |
| Lopidea media Say | Connecticut |
| Lopidea robiniae Uhler | Connecticut |
| Melanotrichus flavosparsus Sahlberg | Connecticut |
| Pseudoxenetus regalis Uhler | Connecticut |
| Orthotylus cruciatus Van Duzee | Connecticut |
| Slaterocoris atritibialis (Knight) | Connecticut |
| Bryocorinae |  |
| Dicyphini | Massachusetts, Connecticut |
| Dicyphus rubi Knight |  |
| Bryocorini | Connecticut |
| Monalocoris americanus Wagner \& Slater | Connecticut |
| Phylinae | Connecticut |
| Phylini | Connecticut |
| Plagactotomus mali Meyer-Dür | Clagiognathus albatus Van Duzee |


| Microphylellus flavipes Provancher | Connecticut |
| :--- | ---: |
| Hallodapini |  |
| Orectoderus obliquus Uhler | Connecticut |
| Pilophorini |  |
| Pilophorus laetus Heidemann | Connecticut |

Character State
a ms ph Large, smooth, progressing to dorsal star ridge configuration
a ms ph lk Usually straight, with anterior "Z"shaped curve (Fig. 22)
a ms ph mk Scimitarshaped (Fig. 22). Usually with extra keel or linear thinning of phragma, between it, lateral keels
a ms ph vap Absent
a ms vb Absent
a ms vb ap Absent
a ms sh Absent
ap a Base very broad, covering half laterodorsal mesothorax surface; square, three corners elongated as secondary ridges, first progressing ventrally to coxa II, second progressing anteriorly to pro- mesothoraces segma coria, third progressing dorsally to ridges 2,3 . Stem very short, thick; head discshaped, with rough edges, round ventrally (Figs. 22, 22a).
ap b Usually anvilshaped, with posterior arm knoblike, anterior arm progressing to long
filamentous stem with small coneshaped head. Some specimens (L. dolabrata, I malina, P. fraternus [Figs. 22a-d]) stem broad near head
mt vb Small
mt vb ap Usually posterior curled fingerlike hook, fused with coxa III
mt vbe Absent
pms ph Triangular; crown extremely wide, narrowing through shaft to usually shallow boatshaped foot (Fig. 22b); phragma edges curled; lateral arch with two square interior openings (windows), (Figs. 22, 22a-b). Openings surrounded by twisted folds of cuticle
p ms ph mr Absent; present only in A. lineolatus (Goeze)
$\mathbf{p} \mathbf{m s} \mathbf{v b} \quad$ With large extension fused with spiracle 2, lateral arch openings
$\mathbf{r 1}$ Progressing dorsally, with anterior hook
r2
Fused with ridge 3, dorsal cuticleous fold
$\mathbf{r 3}$ Fused with ridge 2, dorsal cuticleous fold
r3e Absent
sp Spiracle 1 ventral, large, fused with large segma coria; spiracle 2 ventral, large, next to posterior mesothoracic phragma foot
tf Smooth, with keel (Figs. 22b, 22e-f)
tw Smooth, with pores in many species (Figs. 22e-j)
wmo Hidden by rectangular fold

## Comments

Prothorax 50\% smaller than other thoracic segments; prothorax wall and floor smooth with coxa I anterior. Anterior mesothoracic phragma large, smooth, progressing to dorsal star ridge configuration; number of keels variable. Ridge 1 progressing dorsally, with anterior hook; ridges 2,3 fused with dorsal fold. Apodeme alpha base square, very broad, covering half dorsolateral mesothorax surface; base with three corners elongated as secondary ridges, first progressing to coxa II, second progressing anteriorly to pro- mesothoraces segma coria, third progressing dorsally to ridges 2,3 ; stem very short, thick; head discshaped, with rough edges, round ventrad (Figs. 22c-d). Apodeme beta with large anvilshaped base, thin stem, coneshaped head. Posterior mesothoracic phragma very large, triangular; crown extremely broad; shaft narrow progressing to usually boatshaped foot (Fig. 22b); phragma edges curled; lateral arch with anterior, posterior openings (windows), (Figs. 22, 22a). Anterior opening larger, with dorsal corner fused to dorsal starlike formation of radiating ridges. Lateral arch, twisted folds between openings. Broad band of segma coria between metathorax, abdomen. Usually keeled mesothorax with deeply concave floor. Thoracic floor smooth with many species with pores (Figs. 22e-j). Spiracles 1, 2 large, oval, ventral. Coxal angles variable. Integument thin.

## Tingidae

Figures 23, 23a-b
Specimens examined:

| Tinginae |  |
| :--- | :--- |
| Tingini | Massachusetts |
| Corythucha caryae Bailey | Connecticut |
| Corythucha marmorata (Uhler) | Massachusetts |
| Corythucha pergandei Heidemann | Massachusetts |
| Gargaphia angulata Heidemann | Connecticut |
| Melanorhopala clavata (Stå) |  |


| Character | State |
| :--- | :--- |
| a ms ph | Small |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Small, narrow |
| a ms vb ap | Absent |
| a ms sh | Absent |
| ap a | Variable. C. marmorata: base "Y"shaped, arched; stem short, broad; head |
|  | bonnetshaped with rough ventral surface, (Figs. 23, 23a). M. clavata: rectangular |
|  | lobe (Fig. 23b) |
| ap b | Base triangular, fused with dorsal surface of coxa II; stem broad; head fanshaped |
| mt vb | Very broad dome |

mt vb ap Long, posterior curled hook
mt vbe Linear, meandering, progressing to posterior mesothoracic phragma dorsoposterior pms ph Triangular; crown moderately broad; shaft narrow, progressing to blunt round foot pmsph mr Absent
pms vb Small
$\mathbf{r 1}$ Ridges 1, 2, 3 in fan configuration, with ventral ends inserted into funnelshaped head of ridge 3 extension. Ridge 1 narrow, progressing vertically
r2 Broad, posterior side straight, anterior side meandering; progressing posteriorly at $20^{\circ}$ slant
r3 Moderately narrow, progressing posteriorly at $45^{\circ}$ slant
r3e Moderately wide with dorsal funnelshaped head which ridges 1, 2, 3 insert
sp $\quad$ Spiracle 1 ventral, oval, fused with large segma coria (Figs. 23, 23a); spiracle 2 small, oval
tf
Slightly rough with sparse deep pores
tw Slightly rough with sparse pores. C. marmorata with four large metathoracic lobes (Fig. 23a)
wmo Oval, anterior to posterior mesothoracic phragma lateral arch

## Comments

Broad band of segma coria between head, prothorax. Prothorax smooth with palisades, ventral pits; coxa I large, with dorsal apodeme. Anterior mesothoracic phragma small. Ridges 1, 2, 3 fanning out from extension funnelshaped head of
ridge 3. Apodeme alpha variable. C. marmorata base "Y"shaped, arched; stem short, broad; head bonnetshaped with rough ventral surface (Figs. 23, 23a); M. clavata apodeme alpha rectangular lobe (Fig. 23b). Apodeme beta base, triangular, fused with coxa II; stem broad; head fanshaped. Posterior mesothoracic phragma moderately small, triangular, thick with blunt edges. Metathoracic ventral bridge broad dome, with posteriorly curled dorsal fingerlike apodeme, extension meandering. Spiracle 1 fused with segma coria, moderately large; spiracle 2 small, oval. Coxal angles $20^{\circ}$ from vertical. Dorsal integument very thick, with large oval cavities; ventrally moderately thin, with external ornamentation.

## Reduviidae

Figures 24, 24a-h
Specimens examined:
Harpactorinae

| Acholla multispinosa (DeGeer) | Connecticut |
| :--- | :--- |
| Arilus cristatus (Linnaeus) | Connecticut |
| Pselliopus cinctus (Fabricius) | Connecticut |
| Sinea diadema (Fabricius) | Connecticut |
| Zelus exsanguis Stål | Connecticut |
| Peiratinae |  |
| Melanolestes picipes (Herrich-Schaeffer) | Connecticut |
| Reduviinae |  |
| Reduvius personatus (Linnaeus) | North Carolina |

Stenopodainae
Sp. (undertermined)Amyot \& Serville Florida
Triatominae

| Triatoma dimidiata Latreille | Guatemala |
| :--- | :--- |
| Rhodnius prolixus Stål | Guatemala |

Character State
a ms ph Small, with ventral arch
a ms ph lk Very small, dorsal
a ms ph mk Broad anteriorly, tapered posteriorly
a ms ph vap Absent
a ms vb Large, broad, with flat dorsal surface
a ms vb ap Anvilshaped, with anteroposterior elongate arms, curved ventrally
a ms sh Absent
ap a Stem thick, fused laterally with head; head discshaped, ventral surface domed (Figs. 24, 24a)
ap b Variable. Stenopodainae: base small, triangular; stem filamentous; head discshaped (Figs. 24d, 24e); Harpactocorinae: A. cristatus: base square; stem broad; head three cornered starshaped (Fig. 24b); Harpactocorinae: $S$. diadema:base small, triangular; stem broad, flat; head "V"shaped, semicircular sides (Fig. 24a)

| mt vb | Flat, broad |
| :---: | :---: |
| mt vb ap | Small, fingerlike |
| mt vbe | Broad, poor definition |
| p ms ph | Variable. Triangular; crown broad, shaft narrow progressing to usually pointed foot (Figs. 24a,d,e,h); A. cristatus: foot rounded, flat (Fig. 24b); R. prolixus: foot triangular, dorsal knob (Fig. 24c) |
| p ms ph mr | Absent |
| p ms vb | Moderately broad, dorsal ridge. S. diadema: lateral indentations on each side of ridge (Figs. 24, 24a) |
| r1 | Fused with ridges 2, 3 as anterodorsal folded plate |
| r2 | Fused with ridges 1, 3 as anterodorsal folded plate |
| r3 | Fused with ridges 1, 2 as anterodorsal folded plate |
| r3e | Absent |
| sp | Spiracle 1 large, oval, fused with segma coria; spiracle 2 usually oval; |
|  | Stenopodainae: small dorsal spiracle 2 , coneshaped, with central round opening <br> (Figs. 24d,e): A. cristatus: spiracle 1 small, ventral (Fig. 24b) |
| tf | Slightly rough |
| tw | Slightly rough, sparse pits |
| wmo | Hidden by apodeme alpha |

## Comments

Prothorax large, with segma coria between pro- and mesothoraces; coxa I large, with lateral ridge extension. Anterior mesothoracic phragma small. Anterior mesothoracic ventral bridge apodeme anvilshaped, anteroposterior arms elongate, curved ventrally. Ridges $1,2,3$ fused as plate. Apodeme alpha stem broad, fused laterally with head; head discshaped, ventral surface domed (Figs. 24, 24a). Apodeme beta variable; Stenopodinae: base small, triangular; stem filamentous; head discshaped (Figs. 24d,e); $A$. cristatus: base square; stem broad; head three cornered-starshaped (Fig. 24b); S. diadema: base small, triangular; stem, broad, flat; head, "V"shaped with semicircular sides, like Venus fly trap (Fig. 24a). Posterior mesothoracic phragma variable, usually triangular; crown broad, tapering through shaft to usually pointed foot (Figs. 24a,d,e); S. diadema: foot flat (Fig. 24a); A. cristatus: foot triangular with distal knob (Fig. 24b). R. prolixus foot triangular with dorsal knob (Fig. 24c). Posterior mesothoracic ventral bridge moderately broad, dorsal ridge; S. diadema: lateral indentations on ridge sides (Fig. 24). Thoracic wall with sparse deep pits (Fig. 24). Spiracle 1 large, oval, fused with segma coria; spiracle 2 usually oval; Triatominae: spiracle 2 coneshaped, with central round opening (Figs. 24, 24a). Coxal angles variable. Coxa I vertical, coxae II, III $45^{\circ}$ from vertical. Coxae II, III close together, coxa I separate. Integument thick with cavities of varying sizes; exoskeleton rough.

## Phymatidae

Figures 25, 25a
Specimens examined:

| Sp. (undetermined) | Brazil |
| :--- | :--- |
| Sp. (undetermined) | Texas |
| Sp. (undetermined) | Massachusetts |

Character State
a ms ph Moderately large; straight, with $90^{\circ}$ bend, dorsal ridge
a ms ph lk Absent
a ms ph mk Triangular, bladelike, broad, narrowing to dorsal pointed tip; dorsal trough; phragma ventral arch curved to meet keel tip
a ms ph vap Absent
a ms vb Broad, flat, with thin medial trough
a ms vb ap Fingerlike apodeme anterior with bridge, curving posteriorly, partially fused with coxa I
a ms sh Narrow, progressing dorsally, fused with apodeme alpha
ap a Fused with ridge 3 forming single structure; flat, clublike head, with ventral striations
ap b Anvilshaped, with extra anterior arm; posterior arm fingerlike; anterior primary arm filamentous, progressing to small discshaped head; secondary anterior arm
small, progressing to frayed featherlike head; base broad
mt vb Slightly broad dome, dorsal ridge
mt vb ap Absent
mt vbe Meandering dorsally
pms ph Triangular, narrow; crown broad, shaft narrow progressing to scoopshaped foot (Fig. 25a); foot resting on apodeme beta; posterior mesothoracic phragma lateral arch with two dorsal lobes
p ms ph mr Dorsal, short
p ms vb Broad, square
r1 Broad dorsally, narrow medially, broad ventrally
r2 Broad dorsally, inserted between ridge 1, thoracic wall, broad ventrally
r3 Narrow, linear, fused dorsally with apodeme alpha
r3e Absent
sp $\quad$ Spiracle 1 ventral, small, oval; spiracle 2 ventral, oval
tf Smooth
tw Smooth, with dorsal lobes, sparse pits
wmo Hidden by curved triangular lobe triangular lobe

## Comments

Prothorax moderately large, rectangular; coxa I with ridge extension; palisades. Anterior mesothoracic phragma with $90^{\circ}$ bend, lateral rectangular cavity; broad dorsally with ridge, narrowing to ventral point; medial keel triangular; ventral arch
curved, meeting medial keel ventral tip. Ridges 1,2 broad, ridge 2 dorsally inserted between ridge 1 , thoracic wall. Ridge 3 narrow, linear, fused dorsally with apodeme alpha. Three ridges exhibiting proto-" N " configuration of pentamomomorphs. Apodeme alpha fused with ridge 3, forming single structure; head flat, clublike with ventral striations. Apodeme beta base, broad, proto- anvilshaped with two anterior arms, posterior arm; posterior arm fingerlike; primary anterior arm filamentous progressing to small discshaped head, secondary arm filamentous with frayed featherlike head. Posterior mesothoracic phragma triangular, crown broad, shaft narrowing to scooplike foot, resting on apodeme beta (Fig. 25a); lateral arch with two dorsal lobes. Spiracles 1, 2 ventral, small, narrowly oval. Coxal angles $20^{\circ}$ from vertical. Integument thick with exoskeletal lobes.

## Pentatomomorpha

## Aradidae

Figures 26, 26a-c
Specimens examined:
Aradinae
Aradus sp. Spinola Costa Rica
Aradus crenatus Say Indianna
Aradus quadrilineatus Say Texas, Connecticut
Aradus robustus robustus Uhler Connecticut

mt vb ap Toothlike
mt vb e Small
p ms ph Variable. A. robustus robustus (Fig. 26b), Aradus sp. (Fig. 26c): triangular; crown usually broad, shaft narrow progressing to pointed or round foot; $A$. quadrileatus (Figs. 26, 26a): phragma tubelike, crown slightly broad, with ventrally flat frilled foot, resting on coxa II dorsum
pmsph mr Absent
p ms vb Arched, with thick cuticle
$r 1$ Vertical, ventrally inserted between ridge 3 extension, thoracic wall
r2 "V"shaped; pointing ventrally, broad dorsally
r3 Slightly curved dorsally, fused with apodeme alpha
r3e Hourglass-shaped
sp $\quad$ Spiracle 1 slightly oval with irregular edges; spiracle 2 ventral, oval
tf Smooth, with deep sparse pits
tw Smooth, with deep sparse pits
wmo Dorsoanterior, with apodeme alpha

## Comments

Head large rectangular. Prothorax small. Anterior mesothoracic phragma small, with variable keels (not illustrated); lateral keel variable; A. quadrilineatus:, $A$. robustus robustus: thin, long (Figs. 26a-b); Aradus sp: large (Fig. 26c). Medial keel variable; A. quadrilineatus, $A$. robustus robustus: thin long; Aradus sp: large (Fig. 26c). Costa Rican specimen, medial keel absent. Ridge 1 vertical, ventrally
inserted between ridge 3 extension, thoracic wall. Ridge 2 " $V$ "shaped; pointed ventrally, broad dorsally. Ridge 3 slightly curved dorsally, fused with apodeme alpha. Apodeme alpha variable; A. quadrilineatus: head fused with thoracic wall, ridge 3, forming single structure; dorsally flat, and round ventrally (Figs. 26, 26a); Aradus sp: filament (Fig. 26c). Apodeme beta base fused with anterolateral coxa II; stem straight, narrow; head coneshaped. Posterior mesothoracic phragma triangular, variable in form. A. robustus robustus (Fig. 26b), Aradus sp. (Fig. 26 c ): crown usually broad, with narrow shaft progressing to pointed or round foot; A. quadrilineatus (Figs. 26, 26a): crown slightly broad, columnlike with frilled ventrally flat foot. Phragma resting on coxa II. A. quadrilineatus: coxa II very large with circular flat dorsum; A. robustus robustus: coxa II large, domed. In Aradus sp. (Fig. 26c): coxa II small, with dorsal apodeme beta; base saddleshaped, with posterior tooth; stem moderately broad with featherlike head. Thoracic floor, wall with deep pits. Spiracle 1 slightly oval with irregular edges; spiracle 2 ventral, oval. Coxal angles $20^{\circ}$ from vertical. Integument moderately thick with numerous exoskeletal lobes.

NB. Posterior mesothoracic phragma in Costa Rican Aradus sp. similar to that of Brazilian Nerthra hapaeformis (Gelastocoridae).

## Cydnidae

Figures 27, 27a
Specimens examined:
Amnestus sp.
Florida

| Sp. (undetermined) | Brazil |
| :--- | :--- |
| Sp. (undetermined) $\quad$ North Carolina |  |
| Character | State |
| a ms ph | Large with ventral anterior curl; ventral edge straight |
| a ms ph lk | Small, scimitarshaped |
| a ms ph mk | Long, scimitarshaped |
| a ms ph v ap | Absent |
| a ms vb | Vestigial |
| a ms vb ap | Anvilshaped, with toothlike anterior arm, fingerlike posterior arm |
| a ms sh | Broad |
| ap a | Apodeme anterior with spiracle 2. Base fused with posterior mesothoracic ventral |

p ms ph mr Linear narrow fold
$\mathbf{p m s} \mathbf{~ v b} \quad$ Very thick cuticle. Bridge triangular, with large dorsal straight ridge. Ridge progressing to apodeme beta. Bridge extension with complex folds, fused to posterior mesothoracic phragma lateral arch, apodeme alpha, spiracle 2
r1 Fused with ridges 2, 3; narrow, very straight with matching opposing hooks divided by break, progressing to posterior mesothoracic phragma
r2 Fused with ridges 1, 3; narrow, very straight with matching opposing hooks divided by break, progressing to posterior mesothoracic phragma
r3 Fused with ridges 1, 2; narrow, very straight with matching opposing hooks divided by break, progressing to posterior mesothoracic phragma
r3e Thick linear fold posterior with spiracle 1
sp
Spiracle 1 ventral, narrowly oval; posterior of spiracle fused with ridge 3 extension; spiracle 2 fused with posterior mesothoracic ventral bridge extension; moderately large
tf Smooth, with large domed lobes
tw Smooth, with domed lobes
wmo Small

## Comments

Cunate thorax at $45^{\circ}$ slant, with prothorax small broadening to posterior mesothoracic phragma. Prothorax with large domed lobes. Anterior mesothoracic phragma large with scimitar keels. Ridges 1, 2, 3 fused as single
ridge; ridge, narrow, very straight with matching opposing hooks divided by break, progressing to posterior mesothoracic phragma. Apodeme alpha base fused with posterior mesothoracic ventral bridge extension; stem short progressing to large discshaped head. Apodeme beta anvilshaped, base, tall, broad, cupped to fit posterior mesothoracic phragma foot; stem with small ventral lobe, thin, long; head coneshaped. Thoracic floor with lobes, "S"shaped ventral ridge progressing from coxa II to posterior mesothoracic ventral bridge. Posterior mesothoracic ventral bridge with very thick cuticle; triangular with large dorsal straight ridge progressing to apodeme beta; extension, with complex folds, fused to posterior mesothoracic phragma lateral arch. Apodeme alpha, spiracle 2 fused with extension. Posterior mesothoracic phragma, triangular, narrow; crown moderately broad; shaft narrow progressing to round, broad scoopshaped foot with square anterior edge, resting on apodeme beta. Metathoracic ventral bridge fused with coxa III; posteriorly invaginated loop of integument fused to first abdominal segment. Posterior metathoracic ventral bridge extension, complex of braided segma coria folds with ridge. Spiracle 1 ventral, oval, fused posteriorly with ridge 3 extension; moderately large spiracle 2 fused with posterior mesothoracic ventral bridge extension. Coxal angles $45^{\circ}$ from vertical. Integument moderately thick with posterior mesothoracic ventral bridge very thick

## Pentatomidae

Figures 28, 28a,b
Specimens examined:
Edessinae
Edessa sp. Fabricius Brazil
Pentatominae
Halyini
Brochymena arborea (Say) Connecticut
Pentatomini
Acrosternum hilare (Say) Connecticut
Codophila sp. Mulsanti \& Rey Turkey
Mormidea lugens (Fabricius) Connecticut
Character State
a ms ph Anterodorsal, progressing to dorsal transverse ridge anterior with posterior mesothoracic phragma; anterior $10 \%$ with almost transparent square arch of thin cuticle.
a ms ph lk Very small, scimitar-shaped, with additional lateral keel
a ms ph mk Thin, long, scimitar-shaped with additional lateral keel
ams phvap Absent
a ms vb Smooth, round

| a ms vb ap | Base large, domed, with posterior curled fingerlike head |
| :---: | :---: |
| a ms sh | Laterally broad, medially narrow, hour-glass shaped |
| ap a | Base broad, stem narrow broadening to large discshaped head with dorsal medial |
|  | dome (Figs. 28, 28a) |
| ap b | Anvilshaped with pointed posterior arm, anterior arm progressing to filamentous |
|  | stem, flat coneshaped heah; base dorsum slightly cupshaped to fit posterior |
|  | mesothoracic phragma foot |
| mt vb | Vestigial |
| mt vb ap | Anteriorly fused with coxa III; hooked, curling posteriorly |
| mt vbe | Large, oval with raised walls, fused with segma coria (Figs. 28, 28a) |
| p ms ph | Triangular; crown broad with dorsal trough; shaft narrow with inwardly curled |
|  | edges, progressing to rimmed foot with ventral hollow lobe, deeply boatshaped, |
|  | resting on apodeme beta |
| p ms ph mr | Linear |
| p ms vb | Vestigial |
| r1 | Narrow, nearly horizontal |
| r2 | Large, crescentshaped trough |
| r3 | Narrow, dorsal with wing muscle opening |
| r3e | Absent |
| sp | Spiracle 1 (not illustrated) fused with segma coria; spiracle 2 oval, with anterior |
|  | palisades (Fig. 28) |
| tf | Lobed |


| tw | Lobed |
| :--- | :--- |
| wmo | Large, oval |

## Comments

Prothorax small (not illustrated). Anterior mesothoracic phragma dorsal, with medial, extra, lateral keels, straight ventral arch. Dorsal position of anterior mesothroacic phragma, rotated ridges $1,2,3$ horizontal. Ridges 1,3 nearly horizontal, 2 crescentshaped trough. Apodeme alpha base broad, stem broad, progressing to large discshaped head with dorsal medial dome (Figs. 28, 28a). Apodeme beta anvilshaped with pointed posterior arm, anterior arm progressing to thin stem, flat coneshaped head; base cupped, for posterior mesothoracic phragma foot. Posterior mesothoracic phragma triangular, with dorsal trough; crown broad, narrowing to long shaft with inwardly curled edges, progressing to rimmed foot with ventral hollow lobe, deeply boatshaped. Wing muscle opening large, oval. Metathoracic ventral bridge extension large, oval, fused with segma coria; sides raised. Wall, floor of thorax, lobed. Spiracle 1 ventral, fused with segma coria; spiracle 2 oval, with anterior palisades. Coxal angles vertical. Integument moderately thick.

## Scutelleridae

Figures 29, 29a-b
Specimens examined:
Eurygastrinae
Eurygaster alternata (Say) Connecticut
Pachycorinae
Homaemus aeneifrons (Say) Connecticut
Character State
a ms ph Dorsal; anteriorly, cuticle very thin
a ms ph lk Absent
a ms ph mk Broad; posterior edge straight, anterior edge curving with phragma
a ms ph vap Straight sided hook curling posteriorly (Figs. 29, 29a)
a ms vb Arched
a ms vb ap Absent
a ms sh Absent
ap a Base very broad, stem slightly narrower, fused with large discshaped head (Figs. 29, 29a-b)
ap b Anvil-shaped, posterior arm bilobed, anterior arm filamentous stem progressing to flat coneshaped head; dorsally cupped to receive posterior mesothoracic phragma foot

| mt vb | Small, arched |
| :--- | :--- |
| mt vb ap | Absent |
| mt vb e | Linear, meandering, fused with segma coria |
| p ms ph | Triangular; crown broad, shaft narrow, linear with inwardly curled edges, |
|  | progressing to rimmed foot with ventral hollow lobe, deeply boatshaped; foot |
| p ms ph mr | Very large, separating posterior mesothoracic phragma from lateral arch (Figs. 29, |
| p ms vb | Vestigial |
| r1 | Small, fingerlike lobe |
| r2 | Short, horizontal |
| r3 | Ventral to ridge 2; short crescent with ventral edge straight, dorsal edge curved |
| r3e | Short, separated from ridge 3, fused with anterior mesothoracic ventral bridge |
| sp | Spiracle 1 ventral, small, fused with ridge 3 extension; spiracle 2 large, oval, with |
| wmo | palisades |
| tf | Mostly smooth, with medial keel by apodeme alpha |
| tw (Figs. 29, 29b) |  |

## Comments

Prothorax small (not illustrated). Anterior mesothoracic phragma dorsal with very thin cuticle anteriorly; ventral apodeme hooked. Ridges $1,2,3$ very small. Ridge

3 extension separate, fused with anterior mesothoracic ventral bridge. Spiracle 1 anteriorly fused with ridge 3 extension. Apodeme alpha dorsal, with very broad stem, discshaped head. Posterior mesothoracic phragma lateral arch with broad dorsal ridge, fused to transverse dorsal ridge (Figs. 29, 29a-b). Posterior mesothoracic phragma triangular, with broad medial ridge dividing phragma from lateral arch; crown broad; shaft narrow, long with inwardly curled edges, progressing to rimmed foot with ventral hollow lobe, deeply cupped into apodeme beta. Spiracle 1 ventral, small, fused with ridge 3 extension; spiracle 2, large, oval, with palisades. Thoracic floor with medial keel. Thoracic wall lobed.

Coxal angles vertical. Integument moderately thick.

## Acanthosomatidae

Figures 30, 30a
Specimens examined:
Acanthosomatinae
Elasmostethus cruciatus (Say) Connecticut, New Hampshire
Elasmucha lateralis (Say)
Alaska
Character State
a ms ph Anterodorsal, with anterior thinning of cuticle
a ms ph Ik Absent
a ms ph mk Anteriorly broad, progressing to $90^{\circ}$ bend in phragma, reducing to very thin,
bladelike

| a ms ph vap | Short, fingerlike |
| :---: | :---: |
| a ms vb | Moderately large, round |
| a ms vb ap | Small; curved fingerlike head. Apodemes on ventral bridge curled inward, like |
|  | open jaws of feeding Manta Ray who smoked cigars and made false promises |
| a ms sh | Broad medially, narrow laterally, with posterior palisades |
| ap a | Stem short, broad; head very large, discshaped |
| ap b | Anvilshaped; posterior arm either pointed (Fig. 30) or lobed (observed with |
|  | dissecting scope, not SEM), anterior arm progressing as filament to coneshaped |
|  | head. Base cupped dorsally for posterior mesothoracic phragma foot |
| mt vb | Broad, flat |
| mt vb ap | Ring fused with posterior apodeme beta base; ventral palisades |
| mt vbe | Broad ventrally, narrow dorsally; anterior palisades |
| p ms ph | Triangular; crown broad, shaft narrow progressing to very deep boatshaped foot, |
|  | cupped in apodeme beta. Lateral arch large with dorsal ridge |
| p ms ph mr | Linear, large, fused with posterior mesothoracic phragma lateral arch dorsal ridge |
| p ms vb | Cuticle very thick, arched |
| r1 | Fused with ridges 2, 3, bilobed; dorsal lobe triangular, with anterior hook, ventral |
|  | lobe triangular, round, fused with spiracle 1, dorsally inserted between dorsal |
|  | lobe, thoracic wall |
| r2 | Fused with ridges 1, 3, bilobed; dorsal lobe triangular, with anterior hook, ventral |
|  | lobe triangular, round, fused with spiracle 1, dorsally inserted between dorsal |

lobe, thoracic wall
r3 Fused with ridges 1, 2, bilobed; dorsal lobe triangular, with anterior hook, ventral lobe triangular, round, fused with spiracle 1 , dorsally inserted between dorsal lobe, thoracic wall
r3e
sp
tf
tw Prothorax, mesothorax heavily lobed
wmo Hidden by large apodeme alpha

## Comments

Eye with anteroventral crescent fin. Prothorax small. Pro- mesothoracic walls with lobes, pits. Intersegmental palisades. Anterior mesothoracic phragma dorsal with anterior thinning, ventral apodeme. Ridges 1, 23 fused, bilobed; dorsal lobe triangular, with anterior hook, ventral lobe triangular, round, fused with spiracle 1, dorsally inserted between dorsal lobe, thoracic wall. Apodeme alpha dorsal, with large discshaped head. Apodeme beta anvilshaped, posterior arm either pointed (Fig. 30) or lobed, anterior arm filamentous, progressing to coneshaped head; base cupped dorsally for posterior mesothoracic phragma foot. Posterior mesothoracic phragma triangular; lateral arch with dorsal ridge fused to posterior mesthoracic phragma medial ridge; crown broad, shaft narrow with inwardly curled edges,
progressing to deeply boatshaped rimmed foot with ventral hollow lobe, cupped in apodeme beta. Metathoracic ventral bridge apodeme ring with ventral palisades, fused anteriorly with posterior apodeme bata base. Posterior mesothoracic ventral bridge very thick. Metathoracic ventral bridge extension with anterior palisades. Abdominal segments with pronounced ridges. Spiracle 1 small; spiracle 2 large. Spiracles with palisades, oval. Coxa II with anterior palisades. Coxal angles $20^{\circ}$ from vertical. Integument moderately thick.

## Tessaratomidae

Figures 31, 31a
Specimens examined:
Tessaratoma javanica (Thunberg) India

| Character | State |
| :--- | :--- |
|  |  |
| a ms ph | Anterodorsal with ventral edge curled anteriorly |
| a ms ph lk | Scimitar-shaped, short |
| a ms ph mk | Scimitar-shaped, long |
| a ms ph v ap | Large anterior curved lobe |
| a ms vb | Posterior with spiracle 1, progressing to apodeme alpha |
| a ms vb ap | Anvil-shaped; posterior arm angled dorsally to flat posterior head, anterior arm |
| a ms sh | Absent |
| ap a | Dorsal, with short broad stem, large discshaped head |

ap b Saddle-shaped for posterior mesothoracic phragma foot; base broad, flared with lateral folds; stem filamentous broadening to flat cone-shaped head
mt vb Slightly domed
mt vb ap Absent
mt vbe Segma coria folds progressing dorsally
$\mathbf{p m s}$ ph Wide triangle; crown very broad, lateral arch large with ventral extension; shaft narrow, progressing to flat scoopshaped foot, lateral edges curled ventrally (Figs. 31, 31a); foot cupped into apodeme beta. With dorsal ridge progressing to fused ridges $1,2,3$
pmsph mr Linear, dividing phragma from lateral arch
p ms vb Slightly arched
$\mathbf{r 1}$ Fused with ridges 2, 3, bilobed; dorsal lobe triangular, with anterior hook, progressing dorsally, meandering. Ventral lobe triangular, round, fused with spiracle 1, dorsal region inserted between dorsal lobe, thoracic wall Fused with ridges 1, 3. bilobed; dorsal lobe triangular, with anterior hook, progressing dorsally, meandering. Ventral lobe triangular, round, fused with spiracle 1, dorsal region inserted between dorsal lobe, thoracic wall Fused with ridges 1, 2. bilobed; dorsal lobe triangular, with anterior hook, progressing dorsally, meandering. Ventral lobe triangular, round, fused with spiracle 1, dorsal region inserted between dorsal lobe, thoracic wall r3e Absent

Spiracle 1 oval, fused with anterior mesothoracic bridge, segma coria; spiracle 2
large, oval, posterior to posterior mesothoracic phragma lateral arch extension
tf
tw
wmo Smooth

Smooth

Anterodorsal with apodeme alpha

## Comments

Prothorax large. Anterior mesothoracic phragma, anterodorsal with ventral edge curled anteriorly; keels scimitarshaped. Anterior mesothoracic ventral bridge apodeme moderately large. Ridges 1, 2, 3 fused, bilobed, dorsal lobe triangular, with anterior hook, progressing dorsally, meandering. Ventral lobe triangular, round, fused with spiracle 1, dorsal region inserted between dorsal lobe, thoracic wall. Apodeme alpha dorsal, with short broad stem, large discshaped head. Apodeme beta boatshaped with dorsum cupped for posterior mesothoracic phragma foot. Posterior mesothroacic phragma large triangular, with lateral arch, progressing ventrally as extension to posterior mesothoracic ventral bridge; crown broad, shaft narrow, progressing to flat spoonshaped foot resting on apodeme beta. Phragma with dorsal ridge progressing to fused ridges $1,2,3$. Coxa III with large hooked apodeme. Metathoracic ventral bridge extension, segma coria folds progressing dorsally. Spiracle 1 oval, fused with anterior mesothoracic bridge, segma coria; spiracle 2 large, oval, posterior with posterior mesothoracic phragma lateral arch extension. Coxal angles $10^{\circ}$ from vertical. Integument somewhat thick.

## Thyreocoridae

Figures 32, 32a
Specimens examined:
Galgupha aterrima Malloch Connecticut
Galgupha atra Amyot \& Serville Connecticut
Galgupha sp . (undetermined) Florida
Galgupha sp. (undetermined) Colorado
Character State

| a ms ph | Anterodorsal; anteriorly with thin cuticle |
| :--- | :--- |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Small, fingerlike |
| a ms vb | Arched |

a ms vb ap Base broad, vertical, with $90^{\circ}$ hook; broad fingerlike head a ms sh Absent
ap a Stem short, thick; head large, discshaped, tilted dorsally to show scalloped ventral surface with outer ringlike smooth edge (Figs. 32, 32a)
ap b Anvilshaped; posterior arm fused with metathoracic ventral bridge apodeme (Figs. 32, 32a), anterior arm progressing to filamentous stem, broadening to coneshaped head. Base covering coxa II, split, posterior extension fused to metathoracic
ventral bridge, anterior extension progressing into mesothoracic floor; base dorsum concave for posterior mesothoracic phragma foot
mt vb Small, covered by large apodeme, narrow laterally, curving around coxa III wall, fused to large extension
mt vb ap Base large covering metathoracic ventral bridge; posterior base with buttress partially fused with coxa III; stem short progressing to short bulbous head with slight flare. Stem anteriorly fused with apodeme beta base posterior arm. G. aterrima: touching apodeme beta base posterior arm, not fused
mt vber Round, ventrally linear, broadening dorsally to posterior dorsal lobe; with anterior rectangular palisades
p ms ph Triangular; phragma, crown, shaft all narrow, with medial ridge progressing to shallow scoopshaped foot. Foot is medial ridge of posterior mesothoracic phragma rotated $90^{\circ}$, resting on apodeme beta (not illustrated because phragma foot pulled away from apodeme beta in drying of specimen). Lateral arch fused ventrally with " $S$ " shaped posterior mesothoracic ventral bridge extension; spiracle 2 inside extension
$\mathbf{p} \mathbf{m s} \mathbf{p h} \mathbf{~ m r} \quad$ Very large, square, dorsally fused with posterior mesothoracic phragma lateral arch dorsal ridge; ventrally rotated $90^{\circ}$ as flat scoopshaped foot
p ms vb Small, slightly arched
r1 Anteriorly narrow, broadening slightly, progressing to apodeme alpha
Triangular lobe between ridges 1,3
r3 Linear, narrow, inserted dorsally between ridge 1, thoracic wall

| r3e | Absent |
| :--- | :--- |
| sp | Spiracle 1 large, oval, ventral; spiracle 2 large, broad, oval, inside posterior |
| mesothoracic ventral bridge extension |  |
| tf | Large lobes |
| tw | Prothorax smooth; mesothorax with linear lobes in vertical rows (Figs. 32, 32a); |
|  | metathorax smooth |
| wmo | Dorsal with apodeme alpha |

## Comments

Prothorax $1 / 3$ size of other thoracic segments. Prothorax smooth, floor flat. Anterior mesothoracic phragma with small ventral apodeme. Anterior mesothoracic ventral bridge apodeme large, broad, with $90^{\circ}$ bend to head. Apodeme alpha stem short, broad; head large, discshaped, tilted dorsally to show scallop ventrad with outer smooth ringlike edge (Fig. 32). Mesothoracic wall with row of linear lobes. Mesothorax floor lobed. Apodeme beta anvilshaped; posterior arm fused with metathoracic ventral bridge apodeme (Figs. 32, 32a), anterior arm progressing to filamentous stem broadening to coneshaped head; base ventrad split, posterior extension fused with metathoracic ventral bridge, anterior arm progressing into mesothoracic floor. Apodeme beta covering coxa II; base concave for posterior mesothoracic phragma foot. Triangular posterior mesothoracic phragma, crown, shaft narrow, progressing to shallow scoopshaped foot. Posterior mesothroacic phragma medial ridge turned $90^{\circ}$ into flat cupshaped
foot to fit apodeme beta (not illustrated because phragma foot pulled away from apodeme beta in drying of specimen). Lateral arch fused ventrally with " S "shaped posterior mesothoracic ventral bridge extension (Figs. 32, 32a). Spiracle 2 inside mesothoracic ventral bridge extension. Metathoracic ventral bridge extension large, with anterior palisades. Mesothoracic wall with linear, domed lobes. Spiracle 1 large, oval, ventral; spiracle 2 large, broad, oval, fused with posterior mesothoracic ventral bridge extension. Coxal angles, vertical. Abdominal wall with large lobes. Integument moderately thick.

## Parastrachiidae

Figures 33, 33a
Specimens examined:
Parastrachia japonensis (Scott) Japan
Character State
a ms ph Small, progressing to ridges 1,2 dorsal lobes; ventral anterior arch very arched each side of ventral apodeme
a ms ph lk Bladelike
a ms ph mk Absent
a ms ph vap Fingerlike; ventral arch very arched each side of apodeme
a ms vb Covering invaginated coxa I
a ms vb ap Absent
ams sh Broad
ap a Stem long; head discshaped with ventral lobe, anteroposterior edges curved ventrally
ap b Saddleshaped; base fused with domed posterior mesothoracic ventral bridge, covering invaginated coxa II; posterior arm, large, square; anterior arm progressing to long filamentous stem with flat coneshaped head; head anteroposterior edges curled ventrally (Fig. 33a), with central apophysis (Appendix 1, Fig. 17)
mt vb Small, slightly arched over non invaginate coxa III
mt vb ap Fingerlike, fused with coxa III
mt vbe Absent
pmsh Triangular, narrow with curled edges; lateral arch absent; crown with dorsal "Y", "L"shaped ridges; shaft narrow progressing to deep boatshaped foot, resting on apodeme beta
pmsph mr Absent
p ms vb Arched, with extension, palisades, posterior to spiracle 2; extension fused to fan structure with posterior half fused to metathoracic wall, anterior half fused to apodeme alpha; "Y, "L"shaped ridges dorsally Small, as dorsal lobe, fused with ridge 2 lobe
r2 Narrow, anteriorly slightly curved, posterior lobe fused to ridge 1 lobe
Dorsoventral, short, anteriorly fused with apodeme alpha stem; posteriorly broadening as sheet
r3e Crescent, progressing anteroventrally along edge of anterior mesothoracic

|  | phragma |
| :--- | :--- |
| sp | Spiracle 1 very small, ventral, hidden (not illustrated); spiracle 2 very small, |
|  | ventral, oval |
| tf | Smooth |
| tw | Prothorax smooth, with horizontal parallel ridges |
| wmo | Hidden by apodeme alpha |

## Comments

Prothorax smooth with horizontal parallel ridges. Anterior mesothoracic phragma with ventral apodeme, dorsally fused with ridge 1 lobe. Ridge 2 with posterior lobe fused to ridge 1 lobe, progressing anteriorly as narrow, slightly dorsally curved ridge; ridge 3 ventral with ridge 2, fused to apodeme alpha stem, broadening as sheet posteriorly. Apodeme alpha, stem long; head discshaped with anteroposterior edges curled ventrally, with medial ventral lobe. Apodeme beta base boatshaped, fused with domed posterior mesothoracic ventral bridge, covering deeply invaginated coxa II; posterior arm large, square, anterior arm long filamentous stem with flat coneshaped head; head anterior, posterior edges ventrally curled (Fig. 33a), with central apophysis (Appendix 1, Fig. 17). Posterior mesothoracic phragma triangular, narrow with curled edges; lateral arch absent; shaft narrow progressing to deeply boatshaped foot, resting on apodeme beta. Crown with dorsal "Y", "L"shaped ridges. Posterior mesothoracic ventral bridge arched, with extension, palisades; extension fused with fan structure,
posterior half fused with metathoracic wall, anterior half fused with apodeme alpha. Spiracles small. Coxae invaginations variable. Coxa I invaginate 45\%; coxa II invaginate $25 \%$; coxa III not invaginate with fingerlike apodeme. Coxal angles $30^{\circ}$ from vertical. Integument moderately thin.

## Coreidae

Figures 34, 34a-b
Specimens examined:
Coreinae
Acanthocephala terminalis (Dallas)
Ohio, Maryland
Anisoscelidini
Hygia opaca Uhler Japan
Leptoglossus corculus (Say)
North Carolina
Leptoglossus occidentalis Heidemann
Connecticut
Leptoglossus phyllopus (Linnaeus)
Connecticut
Petillia calcar Dallas
Arizona

Coreini
Anasa tristis (DeGeer)
Connecticut
Nematopodini
Thasus gigas (Klug)
Arizona
Thasus neocalifornicus Brailovsky \& Barrera
California
Character State
a ms ph Large, with medial trapezoid thinning of cuticle; ventral lobes, apodeme; with medial triangular cross lateral lobe
a ms ph Ik Scimitarshaped, with ventral $90^{\circ}$ bend at medial triangular cross lateral lobe
a ms ph mk Scimitarshaped; very large, progressing from ventral lobes dorsally through cross lateral lobe to dorsal edge of phragma; with dorsal dark scleratization
a ms ph vap Long, fingerlike
a ms vb Vestigial
a ms vb ap Anvilshaped; posterior arm long, with curved hook, anterior arm long, linear with small anterior distal split
a ms sh Very broad, progressing dorsally to apodeme alpha
ap a Stem fused with ridge 3; head cunate with flat dorsad; ventral dark medial patch; small lobe inside head
ap b Variable among species. Base usually broad with anterior extension, either with thin stem, L. occidentalis, (Fig. 34) or straight sided curving abruptly into stem, $A$. tristis (Fig. 34); stem filamentous; head coneshaped
$\mathbf{m t} \mathbf{v b} \quad$ Medially, very narrow, abruptly broadening to large lobe posterior with coxa III, narrowing to extension
mt vb ap Ring with broad base; base progressing anteriorly to mesothoracic ventral bridge, not touching
mt vb e Narrow ventrally, progressing dorsally, broadening, with medial linear trough;

|  | large pore dorsally |
| :---: | :---: |
| p ms ph | Triangular, large; crown broad with large lateral arch; shaft narrowing to flat |
|  | scoopshaped foot |
| p ms $\mathrm{ph}_{\text {mr }}$ | Linear, ventrally rotated into foot (Fig. 34) |
| p ms vb | Broad, arched, dorsal ridge; with anterior extension of apodeme beta |
| r1 | Anterior arm of " N " configuration with ridges 2, 3; anterior hook (Fig. 34) |
| r2 | Medial arm of " N " configuration with ridges 1,3 ; progressing ventrally to anterior |
|  | mesothoracic phragma ventral apodeme |
| r3 | Posterior arm of " N " configuration with ridges 1,2 ; fused dorsally with apodeme |
|  | alpha |
| r3e | Narrow, vertical, slightly meandering |
| sp | Spiracle 1 lateral, moderately large, oval; spiracle 2 large, oval with anterior row |
|  | of palisades |
| tf | Smooth with few pits |
| tw | Smooth with few pits |
| wmo | Large, inside posterior mesothoracic phragma lateral arch |
| Comments |  |
|  | Prothorax small, smooth. Anterior mesothoracic phragma large, with medial |
|  | trapezoid thinning of cuticle; ventral lobes, apodemes, with triangular cross lateral |
|  | lobe; medial keel large with dorsal dark sclerotization. Anterior mesothoracic |
|  | ventral bridge anvilshaped apodeme with posterior arm hooked, anterior arm |

fingerlike. Anterior arm distally divided. Ridges 1, 2, 3 in " N " configuration (Fig. 34). Ridge 2 progressing ventrally to anterior mesothoracic phragma ventral apodeme. Ridge 3 with narrow slightly meandering extension. Apodeme alpha stem fused with ridge 3; head cunate with flat dorsad; ventral dark medial patch; small lobe inside head. Anterodorsal with apodeme alpha is small lobe. Apodeme beta variable. Base usually broad, either narrowing to stem, $L$. corculus or straight sided, curved abruptly to stem, A. tristis (Fig. 34); stem filamentous; head coneshaped. Anterior extension of apodeme beta base progressing ventrally across posterior mesothoracic ventral bridge. Posterior mesothoracic phragma triangular, large. Crown broad; shaft narrow ing to flat scoopshaped foot. Lateral arch large, fused with wing muscle opening. Posterior mesothoracic ventral bridge arched, with dorsal ridge. Metathoracic ventral bridge apodeme as ring, with broad base, progressing anteriorly to mesothoracic ventral bridge, not touching. Metathoracic ventral bridge, extension large, round; extension with large dorsal pore. Spiracle 1, lateral, moderately large, oval; spiracle 2 large, oval with anterior row of palisades. Coxa II with anterior palisades. Coxal angles nearly vertical. Integument moderately thin.

## Alydidae

Figures 35, 35a-e
Specimens examined:
Alydinae

Alydus eurinus (Say)

Connecticut

Alydus pilosulus Herrich-Schaeffer Connecticut<br>Megalotomus quinquespinosus (Say) Connecticut

Character State
a ms ph Large, with large ventral medial lobe
a ms ph lk Absent
a ms ph mk Scimitarshaped, thin, long, progressing into large ventral medial lobe a ms ph vap Thin, fingerlike, crooked
a ms vb Small, linear, progressing around spiracle 1, to anterior mesothoracic phragma ventral apodeme
a ms vb ap Fused with coxa I posterior lip, hooked
a ms sh Broad, with ragged posterior edge, progressing dorsally to apodeme alpha
ap a Stem fused with ridge 3; head large disc, with coneshaped ventral lobe narrowing to rough sided apophysis with jagged diagonal tip. Apophysis deeply inserted into head of modified apodeme beta (Figs. 35, 35a-e)
ap b Base broad with small posterior tooth, stem narrow progressing to deep coneshaped head. Posterior mesothoracic phragma foot resting on base
mt vb Broad with anterior crescent trough, progressing to large extension with surface tongue, posterior segma coria wall; dorsal region of extension with large anterior lobe
mt vb ap Anterior to bridge, short, fingerlike, with bulbous head
mt vb e Fused with bridge as one structure, with surface tongue, posterior segma coria
wall; dorsal with large lobe
pms ph Triangular; crown broad, narrowing through short shaft to broad scoopshaped foot, resting on apodeme beta (Fig. 35a)
p ms ph mr Slight fold
$\mathbf{p} \mathbf{m s} \mathbf{v b} \quad$ Small, short with linear ridge
$\mathbf{r 1}$ Anterior arm of " N " configuration with ridges 2, 3; anterior hook; dorsal end fused with ridge 2 making triangular extension
r2 Medial arm of " N " configuration with ridges 1,3
r3 Posterior arm of " N " configuration with ridges 1, 2, fused dorsally with apodeme alpha
r3e
Absent
sp
Spiracles 1, 2 large, oval. Spiracle 1 ventral, spiracle 2 dorsal
tf Somewhat smooth, with large pits especially in metathorax (Figs. 35, 35a,e)
tw Somewhat smooth, with moderately sized pits (Figs. 35a,e)
wmo Square, with small ventral tooth on side wall

## Comments

Head with occipital condyle. Head, prothorax fused with segma coria. Prothorax small. Coxa I fused with anterior mesothoracic ventral bridge apodeme. Ridges $1,2,3$ in " N " configuration. Anterior mesothoracic shelf broad progressing dorsally to apodeme alpha. Apodeme alpha stem fused with ridge 3; head large disc with coneshaped ventral lobe narrowing to rough sided apophysis, jagged diagonal tip. Apophysis deeply inserted into head of apodeme
beta (Fig. 35, 35a-e). Apodeme alpha in Figs. 35b,c shows ventral apophysis rubbing inner wall of apodeme beta's head which may be result of injury, because abrasion occurs no where else. Posterior mesothoracic phragma broadly triangular; crown broad; shaft very short, progressing to flat scoopshaped foot. Posterior mesothoracic phragma medial ridge diagonally crossing ventral region of phragma, curving anteriorly to inner edge of foot (Figs. 35d,e). Metathoracic ventral bridge apodeme anterior with bridge; short, fingerlike with bulbous head. Metathoracic ventral bridge broad with anterior crescent trough, progressing to large extension with surface tongue, posterior segma coria wall; with large dorsal lobe. Posterior with metathoracic ventral bridge, extension is large rugose abdominal region. Spiracles large, oval. Coxa I fused with anterior mesothoracic ventral bridge, crooked apodeme. Coxal angles nearly vertical. Thoracic wall, floor mostly smooth with some large pits. Integument moderately thick.

## Rhopalidae

## Figures 36, 36a-b

Specimens examined:
Rhopalini

| Liorhyssus hyalinus (Fabricius) | Korea |
| :--- | :--- |
| Liorhyssus hyalinus (Fabricius) | Arizona |

Character State
$\begin{array}{ll}\text { a ms ph } & \text { Large, evenly thick cuticle, progressing to dorsal ridge (Figs. 36, 36a-b); ventral } \\ & \text { arch anteriorly curled edge }\end{array}$

| a ms ph lk | Absent |
| :---: | :---: |
| a ms ph mk | Absent |
| a ms phvap | Absent |
| a ms vb | Small, round |
| a ms vb ap | Absent |
| a ms sh | Absent |
| ap a | Stem fused with ridge 3; head square with one side tapering into stem: flat |
|  | posterior, straight sides, narrowing to ridge 3. Edges curled ventrally (Figs. 36, |
|  | 36b) |
| ap b | Base slightly flared, narrowing to filamentous stem, progressing to broad flat |
|  | coneshaped head |
| mt vb | Broad, anteriorly fused with coxa III |
| mt vb ap | Anterior with bridge; small, broad, hooked with palisades |
| mt vbe | Meandering dorsally with folds |
| p ms ph | Triangular; crown, lateral arch very broad, shaft narrow progressing to hooked |
|  | scoopshaped foot; medial ridge as lateral rugose arch fold (Figs. 36a,b) |
| p ms ph mr | As posterior mesothoracic phragma lateral arch fold progressing ventrally to foot |
|  | (Figs. 36a,b) |
| p ms vb | Deep narrow invagination of integument (Figs. 36, 36a) |
| r1 | Anterior arm of " N " configuration with ridges 2, 3; with anterior hook. Dorsal |
|  | end of ridge covering ridge 2 |
| r2 | Medial arm of " N " configuration with ridges 1, 3. Dorsal end between ridge 1, |

thoracic wall
r3 Posterior arm of " N " configuration with ridges 1, 2, fused dorsally with apodeme alpha; medial region slightly broad before narrowing to small anterior hook (Figs. 36, 36b)
r3e Narrow bladelike, with broad medial crescent sheet, progressing to apodeme alpha (Fig. 36)
sp Both extremely large, medial; atrium valves very large; openings narrowly oval (Figs. 36, 36b). Spiracle 2 with extra anterior ridge
tf Pro and mesothoraces with either many lobes or smooth. Metathorax with palisades (Figs. 36, 35a,b)

Many large lobes. Prothorax with medial apophysis; anterior to spiracle 2 is additional ridge
wmo Small, square, partly hidden by apodeme alpha

## Comments

Prothorax small, dorsoventrally rectangular, with apophysis, large lobes. Anterior mesothoracic phragma progressing dorsally to dorsal ridge. Ridges $1,2,3$ in " N " configuration. Ridge 2 dorsally between ridge 1 , thoracic wall. Ridge 3 with short extension. Apodeme alpha stem fused with ridge 3; head with posterior straight, sides straight, narrowing to ridge 3 ; edges curled ventrally (Figs. 36, 36b). Apodeme beta base flared, stem filamentous progressing to broad flat coneshaped head. Posterior mesothorascic phragma, triangular; crown, lateral
arch very broad, shaft short, narrow progressing to hooked scoopshaped foot (Fig. 36a); medial ridge is lateral arch fold, slightly rugose, progressing ventrally to foot. Metathoracic ventral bridge apodeme detached, with anterior palisades. Spiracles extremely large, medial; atrium valves very large; opening, narrowly oval (Figs. 36, 36a) Spiracle 2 with extra anterior ridge. Thoracic floor, walls with lobes. Coxal angles nearly vertical; with palisades. Integument with large cavities, especially pronotum, scutellum; moderately thick.

The two specimens from Korea and Arizona, USA were compared. Exoskeletons were identical, but the endoskeletons were differenct. The Korean specimen has a squarer metathoracic ventral bridge dorsal apodeme, the spaces between posterior palisades of coxa II are reduced, and the thoracic lobes are contiguous (Fig. 36b). The Arizona specimen has a rounder metathoracic ventral bridge dorsal apodeme, the spaces between posterior palisades of coxa II are large, and the thoracic lobes are separated (Fig. 36a). Most important, spiracle 2 anterior ridge (unique to the family) is broad in the Korean and narrow in the Arizona specimens. On the other hand, two nearly contiguous Connecticut populations of Anasa tristis (Coreidae) show no intraspecific differences (Figs. 34, $34 \mathrm{a}-\mathrm{c}$ ).

## Pyrrhocoridae

Figures 37, 37a-f
Specimens examined:

Odontopus nigricornis Stål
Dysdercus sp. Guérin-Méneville (undetermined) Arizona
Dysdercus sp. Guérin-Méneville (undetermined) California
Character State
a ms ph Small, with lateral lobe, with twist; dividing before fusing with anterior metathoracic wall
a ms ph lk Absent
a ms ph mk Absent
a ms ph vap Absent
a ms vb Narrow, arched
a ms vb ap Anvilshaped; base covering bridge; posterior arm large bulbous, anterior arm short with ventrally pointed tip
a ms sh Absent
ap a Stem long; head discshaped, rim slightly wavy, with medial ventral lobe ap $\mathbf{b} \quad$ Base dorsally flat with arms, fused (Fig. 37) or touching posterior mesothoracic phragma foot (Figs. 37e,f); anterior arm mouthlike with medial linear cavity, posterior arm small lobe; stem on outer lateral side of base (Fig. 37), very long filamentous stem, head coneshaped (Fig. 37a)
mt vb Small, with dorsal ridge
mt vb ap Apodeme, large hook, covering metathoracic bridge, progressing dorsally as extension
mt vbe Fused ventrally with metathoracic ventral bridge apodeme, with anterior palisades

| p ms ph | Narrow triangle; crown narrow fused with small lateral arch, progressing through |
| :---: | :---: |
|  | narrow shaft to scoopshaped foot, fused with apodeme beta (Fig. 37) or touching |
|  | apodeme beta (Figs. 37e,f) |
| p ms ph mr | Absent |
| p ms vb | Narrow, arched |
| r1 | Anterior arm of " N " configuration with ridges 2, 3; with small anterior hook, |
|  | dorsal lobe |
| r2 | Medial arm of " N " configuration with ridges 1, 3 |
| r3 | Posterior arm of " N " configuration with ridges 1, 2, fused dorsally with stem of |
|  | apodeme alpha; medial region slightly broad, ends narrow |
| r3e | Linear. California, Arizona specimens with lobes (Fig. 37e) |
| sp | Spiracle 1 large, oval; spiracle 2 dorsal, narrowly oval with large anterior row of |
|  | palisades |
| tf | Smooth with ventral keel (Fig. 37e) |
| tw | Smooth |
| wmo | Small, oval; directly dorsal with spiracle 2 ; anterior with opening is rugose |
|  | rectangular region |

## Comments

Prothorax smooth with row of anterior palisades; floor is coxa I. Anterior mesothoracic phragma small; lateral lobe, with twist progressing to mesothoracic wall, dividing as "Y". Anterior mesothoracic ventral bridge apodeme
anvilshaped; base covering bridge; posterior arm large, bulbous, anterior arm short with pointed tip. Ridges $1,2,3$ in " N " configuration. Ridge 3 with extension. Apodeme alpha stem long; head discshaped, with medial ventral lobe, wavy rim. Dorsal to apodeme alpha and wing muscle opening, is a rugose rectangular area. Apodeme beta base with two arms, dorsally flat, fused with posterior mesothoracic phragma foot; anterior arm mouthlike with medial linear cavity (Fig. 37), posterior arm as small lobe; stem on lateral side of base (Fig. 37), thin, long; head, coneshaped. Posterior mesothoracic phragma narrow triangle; crown narrow fused with small lateral arch, progressing through narrow shaft to scoopshaped foot, fused with apodeme beta (Fig. 37) or touching apodeme beta (Figs. 37e,f). Metathoracic ventral bridge apodeme hooked. Anterior side of metathoracic ventral bridge extension with palisades. Thoracic wall, floor smooth. Spiracle 1 large, oval; spiracle 2 dorsal, narrowly oval with large anterior row of palisades. Spiracle 2 in California, Arizona specimens with filamentous palisades, distally unattached, fingerlike (Figs. 36a-d). Coxal angles nearly vertical, with palisades. Integument moderately thick.

## Largidae

## Figures 38, 38a-f

Specimens examined:
Larginae
Largus sp. Hahn Texas, North Carolina
Largus sp. Hahn (undetermined) Arizona

| Largus sp. Hahn (undetermined) | California |
| :--- | :--- |
| Physopeita analis (Signoret) | Ghana |

Character State
a ms ph Thick; ventral arch round, folded laterally into anterior mesothoracic bridge a ms ph lk Ventrally, inside triangular lobe, short; dorsally pointed
a ms ph mk Scimitarshaped; large; ventral tip following phragma curve; dorsally pointed a ms phvap Absent
a ms vb Broad, fused with large anterior segma coria, large spiracle 1; dorsal end crescent lobe, fused with lateral edge of anterior mesothorascic phragma
a ms vb ap Absent
a ms sh Crescentshaped; fused with ridge 3 extension; progressing dorsally to ridge 3
ap a Stem filamentous, fused with ridge 3; head rhombusshaped with ventral pits
ap b Anvilshaped; fused with posterior mesothoracic phragma (Figs. 38a-f), anterior arm progressing as long filamentous stem to deeply coneshaped head
mt vb Broad, narrow dorsally
mt vb ap Anteriorly separated, with small connection to metathoracic ventral bridge; hooked fingerlike, fused with coxa III
mt vb e Wider than bridge, fused completely into dorsal thoracic wall
pms ph Triangular; crown broad, lateral arch fused with dorsal linear ridge, complex of dorsal folds, ridges, lobes; shaft, short progressing to foot fused with apodeme beta (Figs. 38, 38a); outer lateral side of shaft with rugose cuticleous sheet, fused
with posterior mesothoracic ventral bridge anterodorsal surface

| p ms ph mr | Linear, with irregular rugose surface, slightly wavy while progressing ventrally |
| :---: | :---: |
| p ms vb | Broad, arched, with medial trough; extension progressing dorsally, dividing |
|  | around spiracle 2, with large anterior, posterior palisades |
| r1 | Anterior arm of " N " configuration with ridges 2, 3; no anterior hook |
| r2 | Medial arm of " N " configuration with ridges 1,3 |
| r3 | Posterior arm of " N " configuration with ridges 1,2 ; fused dorsally with apodeme |
|  | alpha stem, curving ventrally, fused with anterior mesothoracic ventral bridge |
| r3e | Progressing across dorsal surface of anterior mesothoracic ventral shelf, as |
|  | bladelike keel |
| sp | Spiracle 1 large, with straight sides, round ends; spiracle 2 large, oval, surrounded |
|  | by posterior mesothoracic ventral bridge extension and palisades |
| tf | Smooth |
| tw | Smooth with sparse small lobes |
| wmo | Oval, hidden by apodeme alpha |

## Comments

Prothorax small. Anterior mesothoracic phragma thick, broad; ventral arch round, folding laterally into anterior mesothoracic bridge. Anterior mesothoracic fasia lateral keel ventrally inside triangular lobe, dorsally pointed; medial keel scimitarshaped, large with ventral tip following curve of phragma, dorsally pointed. Anterior mesothoracic ventral bridge complex of several fused
structures, broad fused with large spiracle 1 , large segma coria; dorsal end as crescent lobe fused with lateral edge of anterior mesothorascic phragma. Ridges 1,2,3 in " N " configuration. Ridge 1, no anterior hook. Anterior mesothoracic ventral shelf, ridge 3 extension fused as twist. Dorsal with apodeme alpha, anterior with the wing muscle opening is complex of folds, ridges, lobes. Posterior mesothoracic phragma triangular; crown broad, lateral arch fused with dorsal linear ridge, complex of dorsal folds, ridges, lobes; shaft short, narrow, progressing to foot fused with apodeme beta. Shaft lateral side with rugose cuticleous sheet (Figs. 38, 38a), fused with anterodorsal surface of posterior mesothoracic ventral bridge. Posterior mesothoracic ventral bridge with medial dorsal trough; extension, with large anterior, posterior palisades. Metathoracic ventral bridge apodeme hooked, anteriorly separated from bridge, fused with coxa III; extension broader than bridge, completely fused into dorsal thoracic wall. Spiracle 1 large, with straight sides, round ends; spiracle 2 large, oval, surrounded by posterior mesothoracic ventral bridge extension and palisades. Coxal angles $30^{\circ}$ from vertical. Integument moderately thick, with very thick region near posterior mesothoracic ventral bridge. Thoracic contours of Old World (Figs. 38, 38a,b), New World specimens (Fig. 38c) similar.

Largidae indicate interspecific variability in subfamilies. Physopelta analis (Signoret) from Ghana, and the two Largus sp., from the United States possess common characters: spiracle 2 palisades, three ridge" $N$ " configuration, dorsoventrally fused posterior mesothoracic phragmata, anvilshaped apodeme beta
with filamentous stem, coneshaped head and apodeme alpha with stemlike base and spined triangular head. Differences are in the posterior mesothoracic phragmata. The Largus phragmata are narrow and curved with scoopshaped feet, whereas the Physopelta analis phragma is wide, crescentshaped, with a pointed foot (Figs. Physopelta analis 38a; Largus sp. 38c).

## Berytidae

## Figures, 39, 39a-e

Specimens examined:
Jalysus sp. Stål Florida
Jalysus spinosus (Say) Connecticut
Jalysus wickhami Van Duzee Connecticut
Berytinus sp. Kirkaldy Michigan
Character State

| a ms ph | Very large, progressing to dorsal ridge with square fold (Figs. 39, 39a,c); ventral |
| :--- | :--- |
|  | arch rugose |
| a ms ph lk | When present, small |
| a ms ph mk | When present, small |
| a ms ph v ap | Absent |
| a ms vb | Absent |
| a ms vb ap | Base broad, with thick anterior hooked head, fused with coxa I |
| a ms sh | Absent |

ap a Base with three cavities (Fig. 39), stem short, head linear, fingerlike ap b Base broad, fused with coxa II; stem short, head broad, dorsally flat, with $80^{\circ}$ incline; spinelike posterior extension (Figs. 39, 39a,b); dorsal surface with cuticleous pubescence (Fig. 39e)

## mt vb Absent

mt vb ap Absent. J. wickhami: apodeme, present, hooked
mt vbe Absent
p ms ph Nearly rectangular, thick, very broad; lateral arch, crown, stem, foot as one sheet, with foot as slight anterior scoopshaped lobe; lateral edge, rugose
pmsph mr Absent
pms vb Absent
r1 Anterior arm of " N " configuration with ridges 2, 3; with very long anterior hook.
Between ridges 1,2 , partially 3 , segma coria like region
r2 Medial arm of " N " configuration with ridges 1, 3, short. Between ridges 1, 2, partially 3, segma corialike region
r3 Posterior arm of " N " configuration with ridges 1, 2. Ridge very long, fused dorsally with apodeme alpha stem. Between ridges 1,2 , partially 3 , segma corialike region
r3e
Absent
sp $\quad$ Spiracle 1 fused with segma coria, small, ventral; spiracle 2 oval
tf Slightly rough
tw Wall with large triangular area of spaced lobes (Figs. 39, 39a,c)
wmo Hidden by dorsal square fold

## Comments


#### Abstract

Prothorax small. Anterior mesothoracic phragma very large, progressing to dorsal ridge with square lobe(Figs. 39, 39a); ventral arch rugose. Phragma large, ridges 1,3 very long. Ridges $1,2,3$ as " N " configuration with segma corialike region between ridges 1,2 , much of 3 . Apodeme alpha long, fingerlike; base with cavities (Fig. 39). Apodeme beta, base broad, fused with coxa II.; stem broad; head dorsally flat, with anterior $80^{\circ}$ incline; spinelike posterior arm, dorsal surface with cuticleous velvetlike pad of pubescence (Figs. 39b,e); pubescence perhaps reducing slippage, when posterior mesothoracic phragma foot rests on the dorsal surface of the apodeme. Posterior mesothoracic phragma thick, almost rectangular; lateral arch, crown, stem, foot as single structure; foot as anterior lobe with rugose lateral edge. Thoracic wall with triangular region of large lobes. Spiracle 1 oval, fused with segma coria. Spiracle 2 oval. Coxal angles vertical. Coxa II with some anterior palisades (Fig. 39a). Integument moderately thick.


## Lygaeidae

## Figures 40, 40a-c

Specimens examined:

| Lygaeus kalmii Stål | North Carolina, Connecticut |
| :--- | :--- |
| Oncopeltus phragmatus (Dallas) | North Carolina, Connecticut |


| Character | State |
| :---: | :---: |
| a ms ph | Small, with linear striations on arch |
| a ms ph Ik | Absent |
| a ms ph mk | Scimitarshaped; ventral half bladelike, dorsally pointed |
| a msphvap | Absent |
| a ms vb | Small, arched |
| a ms vb ap | Very small lobe fused with coxa I |
| a ms sh | Absent |
| ap a | Stem fused with ridge 3; head scoopshaped; ventral surface straight, lateral walls |
|  | semicircular in"V"shape (Venus fly traplike) (Fig. 40) |
| ap b | Base dorsally flat, fused with posterior mesothoracic phragma lateral foot (Figs. |
|  | 40, 40a-c); base anterior arm, straight-sided fin narrowing into stem; stem, |
|  | moderately broad progressing to coneshaped head |
| mt vb | Arched |
| mt vb ap | Anteriorly separated from metathoracic ventral bridge, fused with coxa III. Base |
|  | with cavities, stem hooked, head bulbous, pointing posteriorly |
| mt vbe | Linear, progressing dorsally, curving towards posterior mesothoracic phragma, |
|  | with anterior palisades |
| pmsph | Triangular; crown broad with dorsal ridge (Fig. 40), shaft narrow progressing to |
|  | foot fused with apodeme beta; lateral arch fused with complex of dorsal folds, ridges, fingerlike lobes; arch folded across phragma as medial ridge |

pms ph mr As extension of posterior mesothoracic phragma lateral arch p ms vb Arched
$r 1$ Anterior arm of " N " configuration with ridges 2, 3 with small anterior hook
r2 Medial arm of " N " configuration with ridges 1,3
r3 Posterior arm of " N " configuration with ridges 1,2 , fused dorsally with apodeme alpha stem
r3e Progressing from ridge 3, around spiracle 1 posterior edge to ventral loop
Spiracle 1 moderately large, oval, with ventral palisades; spiracle 2 moderately large, with row of large anterior palisades
tf
Slightly rough
tw Smooth
wmo Hidden by complex of lobes, ridges, folds

## Comments

Head with posterior circular cluster of minute lobes; keel by eye. Prothorax small. Anterior mesothoracic phragma small with large medial keel, rugose arch. Ridges $1,2,3$ in " N " configuration. Ridge 3 extension, crescent with ventral loop. Apodeme alpha stem fused with ridge 3 , head scoopshaped; head ventral surface straight, lateral walls semicircular in "V"shape (Venus fly traplike) ( Fig. 40). Dorsal to apodeme alpha is a complex of fingerlike lobes, ridges, folds. Apodeme beta base dorsum is flat and fused with lateral side of posterior mesothoracic phragma foot; anterior arm with straight sided fin narrowing to stem; stem
moderately broad progressing to coneshaped head (Figs. 40, 40a-c). Posterior mesothoracic phragma triangular; crown broad with dorsal ridge (Fig. 40); shaft narrow progressing to foot fused with apodeme beta; lateral arch fused with complex of folds, ridges, fingerlike lobes; arch folding ventrally across phragma as medial ridge. Metathoracic ventral bridge apodeme anterior with bridge, bulbous. Posterior margins of all thoracic segments with rows of large palisades. Thoracic wall, floor smooth. Spiracles 1,2 moderately large. Coxae $30^{\circ}$ from vertical. Coxa II with anterior palisades. Integument moderately thick.

## Rhyparochromidae

Figures 41, 41a-b
Specimens examined:
Myodocha serripes Oliver
Connecticut
Character State
a ms ph Arched
a ms ph lk Absent
a ms ph mk Absent
a ms phvap Absent
a ms vb Broad, arched, progressing dorsally to apodeme alpha, fused with anterior mesothoracic shelf
a ms vb ap Very small lobe fused with posterior wall of coxa I

| a ms sh | Broad, fused with anterior mesothoracic ventral bridge |
| :---: | :---: |
| ap a | Stem absent; fused with ridge 3 ; head round progressing to large rough sided |
|  | spine (Figs. 41, 41a,b); small crescent ridge dorsal to apodeme alpha (Figs. 41, |
|  | 41a) |
| ap b | Base domed, progressing to short thin stem, broadening to deep, narrow |
|  | funnelshaped head for large apodeme alpha ventral spine (Fig. 41) |
| mt vb | Arched |
| mt vb ap | Ring, anterior with metathoracic ventral bridge, fused with coxa III; base |
|  | progressing posteriorly across thoracic floor to metathoracic ventral bridge |
| mt vbe | Absent |
| p ms ph | Triangular, very broad; crown extremely broad, with vestigial lateral arch; shaft |
|  | not obvious; foot small, hooked |
| p ms ph mr | Absent |
| p ms vb | Arched |
| r1 | Anterior arm of " N " configuration with ridges 2,3 with small anterior, posterior |
|  | hooks |
| r2 | Medial arm of " N " configuration with ridges 1, 3 |
| r3 | Posterior arm of " N " configuration with ridges 1,2 , fused apodeme alpha |
| r3e | Absent |
| sp | Spiracles 1, 2 moderately small, oval |
| tf | Many domed lobes |
| tw | Domed lobes, fewer than on thoracic floor |

wmo Hidden by crescent ridge, dorsal with apodeme alpha

## Comments

Head gooselike, with very long cervix. Prothorax large, semi-oval with some domed lobes. Anterior mesothoracic phragma small, smooth. Ridges 1, 2, 3 in " N " configuration. Ridge 1 with small anterior, posterior hooks. Anterior mesothoracic bridge, ventral shelf fused. Apodeme alpha with no stem; head with very large ventral spine, fused with ridge 3. Apodeme beta base domed, progressing to short narrow stem, broadening to deep narrow funnelshaped head for large apodeme alpha ventral spine Posterior mesothoracic phragma triangular; crown extremely broad with vestigial lateral arch, narrowing to small hooked foot. Metathoracic ventral bridge apodeme, ring with base progressing posteriorly across thoracic floor to posterior mesothoracic ventral bridge. Coxa III with long, posterior curled, fingerlike apodeme. Spiracles moderately small, oval. Coxal angles $30^{\circ}$ from vertical. Integument moderately thin.

## Blissidae

Figures 42, 42a-b
Specimens examined:
Ischnodemus bosqui (Slater \& Wilcox) Brazil
Character State
a ms ph Small, smooth

| a ms ph lk | Small (Fig. 42) |
| :---: | :---: |
| a ms ph mk | Absent |
| a ms ph vap | Absent |
| a ms vb | Small, arched |
| a ms vb ap | Absent |
| a ms sh | Absent or possibly present as region with no thoracic wall, with floor lobes |
| ap a | Fused with ridge 3; head horizontal, pointed posteriorly; dorsally flat, ventrally |
|  | round; dorsal with apodeme alpha, complex of folds |
| ap b | Base extremely large, domed, fused with posterior mesothoracic phragma foot; |
|  | stem moderately long with broad funnelshaped head; head rugose, with anterior |
|  | lip more elongate, than posterior lip |
| mt vb | Small, fused with Coxa III |
| mt vb ap | Usually absent |
| mt vbe | Short, dorsally curved |
| p ms ph | Column; crown very broad, rough with lateral arch fused with lateral segma coria |
|  | (Figs. 42, 42a), progressing through shaft to foot, fused with apodeme beta (Fig. |
|  | 42b) |
| p ms ph mr | Absent |
| p ms vb | Arched, fused with very large apodeme beta base |
| r1 | Anterior arm of " N " configuration with ridges 2,3 with small almost cryptic |
|  | anterior hook; curved |
| r2 | Medial arm of " N " configuration with ridges 1,3 , almost vertical; fused ventrally |

with ridge 3 , progressing to spiracle 1 posterior
r3 Posterior arm of " N " configuration with ridges 1, 2, fused dorsally with apodeme alpha
r3e Absent
sp Spiracle 1 small, oval, tilted anteriorly, fused with large segma coria. Segma coria progressing dorsally between ridges 1,2 ; dog-boneshaped ridge dorsal with spiracle 1 . Spiracle 2 small, narrowly oval, fused with lateral segma coria. Ventral with segma coria, several fingerlike apodemes (Fig. 42)
tf With many large domed lobes (Figs. 42, 42a)
tw With numerous large domed lobes. Region parallel with ridge 3 smooth. This may be anterior mesothoracic shelf. Prothorax with row of ladyfinger shaped pubescent cuticle (Figs. 42, 42a)
wmo Small, dorsal with apodeme alpha

## Comments

Prothorax large, cunate (narrow anteriorly, broad posteriorly), with many lobes; medially row of ladyfinger-shaped pubescent cuticle. Between prothorax and mesothorax, large segma coria. Ridges $1,2,3$ in " N " configuration, ridges 2,3 fused ventrally as " Y ", progressing to spiracle 1 posterior. Area between ridges 1, 2 with segma coria. Anterior mesothoracic phragma small. Anterior mesothoracic shelf, probably region lacking lobes and parallel with ridge 3 . Apodeme alpha fused with ridge 3, horizontal and posterior pointing (Figs. 42,

42a), dorsally flat, ventrally round. Dorsal with apodeme, complex of folds. Apodeme beta with large domed base, dorsum fused with posterior mesothoracic phragma foot; stem broad, progressing to funnelshaped head with anterior lip elongated. Head sides, rugose. Posterior mesothoracic phragma, column, fused ventrally with apodeme beta. Lateral arch fused with lateral segma coria, several fingerlike apodemes ventrally. Thoracic wall, floor with many lobes. Spiracle 1 small, oval, tilted anteriorly, fused with large segma coria. Segma coria progressing dorsally between ridges 1,2 . dog-boneshaped ridge dorsal with spiracle 1 (Fig. 42). Spiracle 2 small, narrowly oval, fused with lateral segma coria. Coxae I, II nearly vertical, coxa III $45^{\circ}$ from vertical. Coxa II with anterior palisades. Integument thick with dorsal cavities.

## Out group

## Auchenorrhyncha

## Cercopidae

Figures 43, 43a
Specimens examined:
Philaenus spumaria (Linnaeus) Connecticut
Character State
a ms ph Small, with rugose arch
a ms ph lk Bladelike with flat posterior surface (Figs. 43, 43a)
a ms ph mk Absent
a ms ph vap Absent
a ms vb Fused with coxa I
a ms vb ap Fused with coxa I, anterior pointing, fingerlike, curled dorsally
a ms sh Small, fused with posterior ventral edge of coxa I
ap a Stem absent, head round, deeply cupped, with posterior edge progressing to point. Ventral surface convex with medial ridge, fused with ridge 3
ap b Base anvilshaped; anterior, posterior arms small, fingerlike; stem thick, fused with dorsomedial area of base, curved dorsally; head, unobserved
mt vb Small, fused with large metathoracic cuticleous bladder. Dorsal with bladder is
long thin apodeme, broadening slightly to bulbous head. Ventral with apodeme is opening to evagination, seen as lateral external lobe, ventral on thorax.

Illustration with abdomen cutaway showing lobe (Figs. 43, 43a)
mt vb ap
Small anterior lobe, fused with anterior wall of coxa III
mt vbe Absent
pms ph Narrow; crown fused with lateral arch as one structure; spiracle 2 surrounded by lateral arch. Fingerlike apodeme with"Y"shaped base dorsal with arch; lateral arch with extension, progressing ventrally as " S " curved column fused with apodeme beta base posterior. Hooked apodeme where arch turns ventrally; shaft same width throughout length, curving anteriorly to round tipped foot, with small medial trough
pms ph mr Absent
pms vb Small
pms vb ap Absent
$\mathbf{r 1}$ Linear, fused posteriorly with tongueshaped lobe of ridge 2
r2
Parallel with ridge 1 , progressing posteriorly to tongueshaped lobe. Medial ridge 2 an extension progressing ventrally around posterior edge of spiracle1

Short, ventral with ridge 2 tongueshaped lobe, progressing to apodeme alpha
r3e Continuation of ridge 3 ventrally to coxa I
sp Spiracle 1 large, vertical, anterior with ridge 2 extension; broad dorsally, narrow ventrally, fused with segma coria. Spiracle $2,45^{\circ}$ from vertical, $50 \%$ smaller than spiracle 1 ; oval, surrounded by posterior mesothoracic phragma lateral arch

| tf | Smooth |
| :--- | :--- |
| tw | Slightly rough |
| wmo | Lateral, with spiracle 2 |

## Comments

Eye with anterior filamentous apodeme. 25\% of eye ventrally hidden by crescent eye phragma. Clypeus with arched bridge, bridge apodeme. Anterior mesothoracic phragma small, with rugose arch, lateral keel. Ridges 1, 2 parallel; ridge 2 with extension, posterior tongueshaped lobe. Ridge 3 vertical, fused with ridge 2 tongueshaped lobe; progressing ventrally to apodeme alpha as extension fused with coxa I posterior. Apodeme alpha stem absent; head round, deeply cupped, with posterior edge progressing to point. Ventral surface of apodeme convex with medial ridge. Apodeme beta anvilshaped; anterior, posterior arms small, fingerlike; stem thick, fused with dorsomedial area of base, curving dorsally; head may be present and trumpetshaped, but broken off (Fig. 43). Anterior mesothoracic ventral bridge with fingerlike apodeme fused with coxa I. All ventral bridges small. Posterior mesothoracic phragma narrow; crown fused with lateral arch; spiracle 2 surrounded by lateral arch; fingerlike " $Y$ "shaped apodeme and anterior hooklike apodeme dorsal to arch; arch with extension progressing ventrally as " $S$ " curved column fused with apodeme beta base posterior; shaft same width throughout length, curved anteriorly to round tipped foot with small dorsomedial trough. Metathorax with large cuticleous bladder,
external lobe, filmentous apodeme. Spiracle 1 large, vertical, fused with segma coria; spiracle $250 \%$ smaller than spiracle $1,45^{\circ}$ from vertical. Coxal angles variable, coxa I vertical, coxa II $30^{\circ}$ from vertical, coxa III $70^{\circ}$ from vertical. Integument thin.

## Cicadidae

Figures 44, 44a
Specimens examined:
Tibicen canicularis (Harris) Connecticut

| Character | State |
| :--- | :--- |
| a ms ph | Fused with scutellum; small, domed, with clubshaped ridge paralleling arch; |
|  | dorsally slightly rugose |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Deeply invaginate with double arches; triangular evaginated lobe anterior to |
|  | bridge |
| a ms vb ap | Fused between arches; square angled, hookshaped pointing anteriorly |
| a ms sh | Small, linear |
| ap a | Medially on ridge $3 ;$ medial region of ridge 3 narrow, then broadening as |
|  | buttresslike stem of apodeme alpha. Proximal to stem, but not fused, two ridges, |

clockwise one at $60^{\circ}$, other at $240^{\circ}$ to stem; head hoodshaped

| ap b | Very broad, triangular; dorsad flat triangular, with three fingerlike horizontal arms at each corner; posterior arm longest |
| :---: | :---: |
| mt vb | Small |
| mt vb ap | Absent |
| mt vbe | Small |
| p ms ph | Triangular; crown broad with dorsal ridge, narrowing through shaft to cupped pointed foot; lateral arch, arched dorsally over spiracle 2 |
| p ms ph mr | Absent |
| p ms vb | Small with shallow invaginated double arches progressing dorsally around spiracle 2; with anterior "Y"shaped parallel ridge |
| p ms vb ap | Absent |
| r1 | Progressing anteroposteriorly following lateral margin of scutellum, with small hook |
| r2 | Hookshaped, as inverted question mark |
| r3 | Ventral with ridge 2 ; progressing dorsoventrally; broad fin narrowing into buttresslike stem of apodeme alpha, then ventrally divided around coxa II. Close to stem, but not fused, two ridges, clockwise one at $60^{\circ}$, other at $240^{\circ}$ |
| r3e | Absent |
| sp | Spiracle 1 small, oval, vertical; spiracle $260^{\circ}$ from vertical |
| tf | Smooth |
| tw | Slightly rough |

## wmo $\quad$ Hidden by ridge 2

## Comments

Head large; ventral with eye is square loop of cuticle. Posterior head with pair of fingerlike apodemes in "L" configuration. Ventral with "L" configuration apodemes a cuticleous connection, joining head to small prothorax, connection medially straight, curved distally; prothoracic end fused with small fingerlike apodeme. Prothoracic cavity large enough for coxa I insertion. Anterior mesothoracic phragma small with clubshaped ridge. Notum, scutellum with dorsal medial ridges, these broadening posteriorly. (Fig 44 shows notum, scutellum lifted to illustrate dorsal medial ridges; flat natural position, not seen). Anterior mesothoracic ventral bridge with large anterior hooked anterior mesothoracic ventral bridge apodeme. Ridge 1 posteriorly following lateral margin of scutellum to small dorsal hook, ridge 2 hook as inverted question mark, ridge 3 ventral with ridge 2 , progressing dorsoventrally as broad fin narrowing to buttresslike stem of apodeme alpha, then ventrally divided around coxa II. Apodeme alpha medial on ridge 3; medial region of ridge 3 narrow, then broadening as buttresslike stem of apodeme alpha; near apodeme alpha stem, but not fused, two ridges, clockwise one at $60^{\circ}$, other at $240^{\circ}$; head hoodshaped. Apodeme beta very broad, triangular; dorsal surface flat, triangular with three fingerlike horizontal arms at each corner; posterior arm longest. Posterior mesothoracic ventral bridge small with shallow invaginated double arches,
progressing dorsally around spiracle 2 , with anterior " Y "shaped parallel ridge. Posterior mesothoracic phragma triangular; crown broad with dorsal ridge, narrowing through shaft to cupshaped pointed foot. Lateral arch curved dorsally over spiracle 2 . Coxa III with secondary ridge progressing dorsally. Spiracle 1 small, oval, vertical; spiracle $2,60^{\circ}$ from vertical. Coxal angles $45^{\circ}$ from vertical. Integument moderately thick.

## Cicadellidae

Figures 45, 45a
Specimens examined:

| Graphocephala coccinea (Forster) | Connecticut |
| :--- | :--- |
| Helochara communis Fitch | Connecticut |


| Character | State |
| :--- | :--- |
|  |  |
| a ms ph | Dorsal, with flat half crescent anterolateral lobe |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Small |
| a ms vb ap | Absent |
| a ms sh | Absent |
| ap a | Fused with ridge 3; base wide, divided as ring, progressing around edge of |

mesothoracic floor; head very large, hoodshaped

| ap b | Broad; base dorsad flat, curved edges, with two variably shaped anterior arms; |
| :--- | :--- |
|  | primary arm progressing as stem with flat arrowshaped head, inserted laterally |
| mt vb | into apodeme alpha's hoodshaped head; secondary arm, small, fingerlike |
| mt vb ap | Absent |
| mt vb e | Fused with series of anterior cross ridges on metathoracic wall |
| p ms ph | Triangular, slightly concave posteriorly; crown board, narrowing through shaft to |
| p ms ph mr | Absent |
| p ms vb | Vestigial scoopshaped foot; lateral arch with discshaped lobe; posterior mesothoracic |
| p ms vb ap | Absent |
| r1 | Fused with ridge 2 as overlying flat cuticleous sheets, with dorsal posterior |

narrowly oval
tf Lobed
tw Lobed
wmo
Unobserved

## Comments

Head large. Ring apodeme anterior to eye. Prothorax small with room for coxa I opening. Segma coria between pro and mesothoraces large, fused with small spiracle 1. Anterior mesothoracic phragma dorsal, progressing to external scutellum, with flat half crescent anterolateral lobe. Ridges 1,2 fused as overlapping cuticleous sheets, with dorsal fingerlike apodeme. Ridge 3 complex, meandering dorsoventrally, fused with apodeme alpha stem, progressing ventrally as ring circling mesothoracic floor. Dorsoposterior with ridge 3 posterior mesothoracic phragma lateral arch discshaped lobe. Apodeme alpha fused with ridge 3 ; stem wide, head very large, hoodshaped. Apodeme beta broad, base dorsum flat, with curved edges, two anterior arms; primary anterior arm as flat stem with flat arrowshaped head inserted into apodeme alpha hoodshaped head; secondary arm small, fingerlike. Posterior mesothoracic phragma triangular, slightly concave posteriorly; crown broad, narrowing through shaft to flat scoopshaped foot; lateral arch with discshaped apodeme. Metathoracic wall with network of cross ridges. Spiracles1, 2 small; spiracle 1 narrowly oval, fused with segma coria; spiracle 2 narrowly oval. Coxae angles $45^{\circ}$ from vertical.

Integument moderately thick.

## Membracidae

Figures 46, 46a
Specimens examined:

| Campylenchia latipes (Say) | Connecticut |
| :--- | :--- |
| Stictocephala lutea Kopp \& Yonke | Connecticut |
| Ceresa bubalis Fabricius | Connecticut |


| Character | State |
| :--- | :--- |
| a ms ph | Domed, smooth, with posterior medial dorsal ridge |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms ph v ap | Absent |
| a ms vb | Vestigial |
| a ms vb ap | Variable. C. latipes: with anterior hook; S. lutea: anvilshaped, stem tall, thick with |
|  | posterior, anterior fingerlike apodemes, anterior arm fused to head (Fig. 46) |
| a ms sh | Absent |
| ap a | Vertical, fused with ridge 3; stem as small buttress progressing to hoodshaped |
| ap b | head |
|  | Very broad triangular; dorsal surface of base flat with three arms variably shaped |
| at each corner; anterior arm, stem with small featherlike head, posterior arm |  |

square lobe, medial arm small pointed lobe (Fig. 46).

| mt vb | Vestigial |
| :---: | :---: |
| mt vb ap | Absent |
| mt vbe | Absent |
| p msph | Phragma round with slight anterior curve into scoopshaped foot; slightly cupped; cuticle almost transparent. Phragma with posterior apodeme |
| p ms ph mr | Absent |
| p ms vb | Broad, flat |
| p ms vb ap | Absent |
| r1 | Paralleling lateral margin of anterior mesothoracic phragma, with dorsal square |
|  | hook; ventral region with $90^{\circ}$ bend, broad, narrowing to point, fused with base of ridge 2 apodeme |
| r2 | Progressing dorsoventrally; ventrally, fused with anterior mesothoracic bridge, |
|  | thoracic floor ridge; dorsally fused with dorsal apodeme. S. lutea: apodeme stem |
|  | thin, moderately short; head flat, coneshaped; C. latipes: apodeme very small, |
|  | with very short flat stem, vestigial cupped head |
| r3 | Dorsoventral, thin, ventrally fused with apodeme beta, dorsally with round dorsal |
|  | lobes. Apodeme alpha base fused with medial region. Between ridge 3 dorsal |
|  | lobes, posterior mesothoracic phragma lateral arch is domed region of thin cuticle |
| r3e | Absent |
| sp | Spiracle 1 small, fused with segma coria; spiracle 2 small |
| tf | With some small lobes |

tw With some lobes. C. latipes with more lobes
wmo Not observed

## Comments

Thorax compressed anteroposteriorly while dorsoventrally elongate; small, fitting coxa I insertion; fused with very large pronotum. Anterior mesothoracic ventral bridge apodeme large. Anterior mesothoracic phragma domed, smooth, with posterior medial dorsal ridge. Ridges $1,2,3$ separated. Ridge 1 progressing anteroposteriorly paralleling lateral margin of anterior mesothoracic phragma, ending with square dorsal hook; ventrally with $90^{\circ}$ bend; broad, then narrowing to point, fused with ridge 2 apodeme stem. Ridge 2 dorsoventral; ventrally fused with anterior mesothoracic bridge, thoracic floor ridge; dorsally fused with apodeme; S. lutea: apodeme stem thin, moderately short; head, flat, coneshaped; C. latipes: apodeme very small, with very short flat stem, very small cupped head. Ridge 3 separated from other ridges, dorsoventral, thin, fused with apodeme alpha. Apodeme alpha stem fused with medial region of ridge 3. Ridge with dorsal lobes. Between ridge 3 dorsal lobes and posterior mesothoracic phragma lateral arch is domed region of thin cuticle. Apodeme alpha fused with ridge 3; stem finlike, progressing to hoodshaped head. Apodeme beta very broad, triangular; base dorsum flat with three variably shaped arms, one at each corner; anterior arm as stem with small featherlike head, posterior arm as square lobe, medial arm as small pointed lobe. Posterior mesothoracic phragma round (not
illustrated) with slight anterior curve to scoopshaped foot; slightly cupped, cuticle almost transparent; lateral arch deeply curved; phragma posterior with posterior apodeme. Thoracic wall, floor with few lobes. Spiracles very small. Spiracle 1 fused within segma coria. Coxal angles tilted anteriorly to $70^{\circ}$ from vertical. Integument moderately thin.

## Hymenoptera

## Anthophoridae

Specimen examined:
Xylocopa virginica (Linnaeus) $\ddagger$ Connecticut

## Vespidae

Figures 47, 47a-d
Specimens examined:
Polistes sp. 우 Connecticut

Vespula maculifrons Brysson $\mp$ Connecticut

| Character | State |
| :--- | :--- |
|  |  |
| a ms ph | Fused entirely with scutum |
| a ms ph lk | Absent |
| a ms ph mk | Absent |
| a ms phvap | Absent |


| a ms vb | Finlike; dividing pro and mesothroaces, progressing dorsally to anterodorsal |
| :--- | :--- |
|  | spiracle 1. Anterior with bridge is segma coria, small anterior cavity for coxa I; |
|  | ventrally bridge fused with "V"shaped dorsal apodemes, rotating posteriorly as |
| thoracic floor keel, progressing to apodeme beta base |  |
| a ms vb ap | Ventrally, apodemes fused with anterior mesothoracic ventral bridge in |
| a ms sh | "V"shaped configuration |
| ap a | Finshapent with three basal plumose filaments; head, with apodeme beta head |
|  | inserted; posterior straight cuticleous filaments form channel for guiding wing |
|  |  |

ap b Base very broad, anterior surface narrow, fused with thoracic floor keel, anterior mesothoracic ventral bridge; dorsally narrowing to stem with basal anterior tooth; head featherlike inserted between apodeme alpha, thoracic wall. Between stem, thoracic wall, several dorsoventral straight cuticleous filaments. Posterior to apodeme thin ring of cuticle starting at coxa III, progressing in circle, around thorax
mt vb Absent
mt vb ap Absent
mt vbe Absent
p ms ph Angled at $120^{\circ}$ to $300^{\circ}$ from vertical. Same width from crown through shaft with slight narrowing at foot; foot slightly curved, anteriorly flat, scoopshaped. Posterior mesothoracic phragma lateral arch small. Surface mostly smooth with
ladyfingerlike cuticleous pubescence (Fig. 47a)

| p ms ph mr | Absent |
| :---: | :---: |
| p ms vb | Vestigial |
| p ms vb ap | Absent |
| r1 | Progressing between anterior mesothoracic phragma (scutum), prothorax, ending |
|  | posteriorly as knob |
| r2 | Dorsal with apodeme alpha progressing dorsally to posterior scutum; shaped like |
|  | smokers pipe, with anterior bowl, posterior stem |
| r3 | Flat inverted "L"shaped lobe anterodorsal with apodeme alpha |
| r3e | Absent |
| sp | Spiracle 1 small, round, in dorsal prothorax; spiracle 2 small, round, ventral with |
|  | posterior mesothoracic phragma lateral arch. Posterior to spiracle 2, plumose |
|  | filament; spiracle 3, small, round, in dorsal propodeum |
| ff | Numerous pits for setae insertions |
| tw | With rows of ladyfinger-shaped cuticleous pubescence (Figs. 47, 47a-d); |
|  | numerous pits for setae insertions |
| wmo | Posterior with apodeme alpha, where ridges 2, 3 fuse. Apodeme alpha, posterior |
|  | straight cuticleous filaments for guiding wing muscles |

## Comments

Posterior prothorax triangular wedge inserted into mesothorax. Anterior mesothoracic phragma (scutum) dorsal with inserted prothorax. Anterior
prothorax, small cavity for coxa I insertion. Prothorax posterior edge bordered by finlike anterior mesothoracic ventral bridge. Spiracle 1 in dorsal prothoracic corner where ridge 1 , anterior mesothoracic ventral bridge fuse. Anterior mesothoracic ventral bridge with "V"shaped dorsal apodemes; bridge progressing posteriorly to ventral thoracic keel, base of apodeme beta, creating single large circular ring starting at ridge 1 , ending at apodeme beta. Ridge 1 curved dorsally, with posterior knob dorsal to apodeme alpha. Ridge 2 more posterior, with anterior disclike lobe progressing dorsally to posterior scutum, smokers pipeshaped. Ridge 3 flat inverted "L"shaped lobes, dorsoanterior with apodeme alpha. Apodeme alpha finshaped with three basal plumose filaments. Featherlike head of apodeme beta inserted between apodeme alpha, thoracic wall. Apodeme beta base very broad; anterior surface narrowing, fused with thoracic floor keel, anterior mesothoracic ventral bridge; stem with basal anterior tooth progressing to featherlike head inserted between apodeme alpha, thoracic wall. Between stem, thoracic wall, several dorsoventral straight cuticleous filaments. Posterior with apodeme beta, thin ring of cuticle starting at coxa III, forming ring around thorax. Posterior mesothoracic phragma steeply angled, smooth with ladyfinger-shaped cuticleous pubescence (Fig. 47a), small lateral arch; width from crown through shaft to foot is the same, slight narrowing with foot; foot slightly curved anteriorly flat, scoopshaped. Spiracle 1 small, round, in dorsum of prothorax; spiracle 2 small, round, ventral with posterior mesothoracic phragma lateral arch; posterior with spiracle 2 , plumose filament; spiracle 3 small, round, in dorsal propodeum.

Wing muscle opening, directly posterior with apodeme alpha where ridges 2,3 fuse; apodeme alpha, posterior straight cuticleous filaments forming channel to guide wing muscles. Thoracic floor with medial keel. Thoracic wall with rows of ladyfinger-shaped pubescence (Figs. 47, 47a-d). Coxal angles mixed; coxa I nearly vertical; coxae II, III $40^{\circ}$ from vertical. Integument moderately thin.

## Diptera

## Tabanidae

Figures 48, 48a-b
Specimen examined:
Tabanus sulcifrons Macquart
New York State
Character State
a ms ph Small; thin cuticleous anterior region in isosceles trapezoid shape; ventral edge with thick rim
a ms ph lk Absent
a ms ph mk Absent
a ms phvap Absent
a ms vb Bladelike, thick
a ms vb ap Fingerlike, tapering to small round tip with filament
a ms sh Absent
ap a Coneshaped, with lateral linear fins tapering to point, stem with two lateral plumose appendages; distal third of apodeme plumose
ap b Horn of plenty shaped, opening posteriorly, with dorsal edge curled anteriorly forming lip with feathering along length; ventral surface fused to thoracic floor; anterior end progressing to triangular point with small crooked ventral anterior keel, fused with anterior mesothoracic ventral bridge. Chininous arch looped over keel. Outer lateral wall of apodeme narrowing to broad ridge progressing dorsally, curling posteriorly as round hook with lateral knob. Knob fused with posterior mesothoracic phragma lateral arch dorsal ridge. Posterior with knob two plumose headed apodemes. Inner lateral wall of apodeme progressing to short ridge, divided around coxa II opening. Apodeme with several small posterior ridges (not illustrated, because of large ventral keel)
mt vb Broad, with complex of folds fused anteriorly with posterior mesothoracic ventral bridge
mt vb ap Large, covering bridge, flat, thin, broadly arrowhead shaped, paralleling bridge (not illustrated)
mt vbe Unobserved
$\mathbf{p}$ ms ph Broadly triangular; crown with dorsal ridge; narrow ventrally, progressing through shaft is a half twist, rotating posterior facing of discshaped foot $180^{\circ}$; fused with thoracic triangular buttress; lateral arch progressing ventrally as sheet of cuticle, fused with triangular thoracic buttress. Phragma, lateral arch combined to form church-windowlike opening; arch with large dorsal ridge distally broadening;
ridge anterior fused with apodeme beta lateral knob
p ms ph mr Absent; phragma with some rugose areas
p ms vb Broad, fused posteriorly with metathoracic ventral bridge
p ms vb ap Absent
r1 Fused with ridge 2. Origin at anterior mesothoracic phragma rim, progressing in curve to complex of small fingerlike apodemes, continuing dorsally around posterior edge of dorsal domed lobe; dorsal region with small posterior fingerlike hooked apodeme, plumose tip. Ridges terminating in dorsal thoracic region with several different angled surfaces of mesonotum

Completely fused with ridge 1 ; between fused ridges 1,2 ; separate ridge 3 rugose thin cuticleous region
r3 Anteriorly fused with triangular lobe, progressing $45^{\circ}$ posteriorly to apodeme alpha
r3e Progressing from triangular lobe ventrally, divided as "Y" with anterior arm as small fin, posterior arm as small cuticleous loop crossing over anterior end of small crooked ventral thoracic keel (not illustrated)

Spiracle 1 two dorsoventral cuticleous plates, opening two millimeters into thoracic cavity, narrowly oval; spiracle 2 small, posterior with posterior mesothoracic phragma foot, horizontal, oval
tf With large medial keel, flat anvilshaped dorsal apodeme; anterior arm fingerlike, posterior arm pointed, with tiny dense pits for setae insertions
tw Mostly smooth; dorsal to fused ridges 1,2, rows of ladyfinger-shaped pubescence;
also in dorsal mesonotum, domed lobe region
wmo
Large, rectangular

## Comments

Prothorax small, fitting coxa I opening. Anterior mesothoracic phragma small, thin cuticleous anterior region with isosceles trapezoid shape; ventral edge with thick rim; phragma smooth fused with mesonotum, several angled surfaces converging to dorsal starlike point. Ridges 1, 2 fused originating at anterior mesothoracic phragma rim, progressing in curve to complex of small fingerlike apodemes, continuing dorsally around posterior edge of dorsal domed lobe. Dorsal region with fingerlike hooked apodeme, plumose tip. Ridges terminating in dorsal thoracic region. Ridge 3 ventral to ridges 1, 2; starting with small anterior triangular lobe, progressing to apodeme alpha. Apodeme alpha coneshaped with lateral linear fins, progressing to point; base with two lateral plumose appendages; apodeme distal third, plumose. Apodeme beta Horn of Plenty-shaped, opening posteriorly, with dorsal edge curled forming lip with feathering along anterior edge; ventral surface fused to thoracic floor; anterior progressing to triangular point with small crooked ventral anterior keel; keel fused with anterior mesothoracic ventral bridge. Cuticle arch looping over keel. Outer lateral wall of apodeme narrowed to broad ridge progressing dorsally, curling as round hook with lateral knob, fused with posterior mesothoracic phragma lateral arch dorsal ridge. Posterior to knob two plumose headed apodemes. Inner lateral
wall of apodeme beta progressing to short ridge, divided around coxa II opening; with several small posterior ridges (not illustrated because of large ventral keel). Posterior mesothoracic phragma broadly triangular; crown with dorsal ridge; narrowing ventrally through shaft in half twist rotating posterior facing discshaped foot $180^{\circ}$; fused with thoracic triangular buttress; lateral arch with dorsal ridge, secondary ridges, progressing ventrally as sheet of cuticle, fused with triangular thoracic buttress. Phragma, lateral arch forming church-windowlike opening. Posterior mesothoracic ventral bridge, metathoracic ventral bridge fused. Metathoracic ventral bridge broad, with complex of folds; covering bridge flat, thin, broadly arrowhead-shaped apodeme paralleling bridge. Thoracic floor with large medial keel with flat anvilshaped dorsal apodeme; anterior arm fingerlike, posterior arm pointed. Floor with tiny dense pits for setae insertions. Thoracic wall mostly smooth with dorsal rows of ladyfinger-shaped pubescence; found also in dorsal mesonotum, dorsal domed lobe region of fused ridges 1, 2. Spiracle 1 made of two dorsoventral cuticleous plates with opening two millimeters into thoracic cavity, (flat tubelike), narrowly oval; spiracle 2 small. Coxal angles variable; coxa I , $30^{\circ}$ from vertical, coxa II, $60^{\circ}$ from vertical, coxa III, 85 to $90^{\circ}$ from vertical. Integument moderately thin

## Calliphoridae

Figure 49
Specimen examined:
Phormia regina (Meigan) Connecticut
Specimen not discussed.

## Morphological analysis of character data:

The most character-rich segment in Heteroptera is the mesothorax, with 23 primary, 3 intermediate, and 6 secondary structures and features (Table 2). These characters are categorized into three groups based on degree of commonality and variability. The 23 primary structures are very common and highly variable; the 3 intermediate structures, also common, provide unique family level characters, but lack variability; and the 6 secondary characters are uncommon, but considered important because they are unique to families. The 32 characters yielded 403 states (Appendix 2). Unique family-level characters are common in Heteroptera; some are listed in Table 4.

The phenogram shows (Fig. 50) most infraorders intact and their phenetic arrangement agreeing with current literature except for two families, Reduviidae and Mesoveliidae. There is interspecific variability in Reduviidae, and Mesoveliidae are pterygopolymorphic. For these diverse families, combinations of diagnostic characters are necessary. For example, Nepomorpha and Pentatomomorpha both have posterior mesothoracic phragmata touching ventral surfaces, but nepomorphs have large anterior mesothoracic ventral bridge apodemes that pentatotomids
lack. This as well as other characters can diagnose groups of species.

## Enicocephalomorpha and Gerromorpha (Appendix 4, Figs. 2-9)

The Enicocephalomorpha and Leptopodomorpha were each represented by one family, so results are preliminary. Enicocephalomorpha are represented by two species.

Table 4: Unique family level characters of some heteropteran families

| Family | Unique characters |
| :---: | :---: |
| Gerridae | Very long occipital condyle (Fig.3) |
| Hebridae | Ventral trough with multiple bridges (Fig. 9) |
| Pleidae | Thoracic wall tongues; rectangular scalloped floor (Fig. 10) |
| Notonectidae | Apodeme alpha rectangular, tonguelike (Fig. 11) |
| Naucoridae | Pubescent patches between ridges 1 and 2 (Fig. 12) |
| Gelastocoridae | Apodeme alpha bicycle-saddleshaped (Fig. 13) |
| Corixidae | Apodeme alpha anteroventral; Spiracle 2, balloonlike; many thoracic floor keels; metathoracic spiracle? (Fig. 14) |
| Belostomatidae | Very large ventral bridge apodemes; apodeme alpha birdheadshaped (Fig. 17) |
| Saldidae | Apodeme alpha base arched (Fig. 18) |
| Cimicidae | Severe constriction between pro- mesothoraces; lobes in abdomen (Fig. 19) |
| Anthocoridae | Anterodorsal hyphaelike glands between ridges 1 and 2 (Fig. 20) |
| Nabidae | Large square prothorax with filamentous palisades (Fig. 21) |
| Miridae | Posterior mesothoracic phragma lateral arch with two square openings (windows); small domed lobes on mesothoracic wall (Fig. 22) |
| Phymatidae | Apodeme beta with extra stem and head (Fig. 25) |
| Thyrecoridae | Apodeme beta fused with mt vb apodeme (Fig. 32) |
| Coreidae | a ms ph with transverse linear lobe (Fig. 34) |
| Rhopalidae | Spiracle 2 with anterior ridge (Fig. 36) |
| Pyrrhocoridae | Spiracle 2 with unusually detached palisades (Fig. 37d) |
| Berytidae | Rectangular posterior mesothoracic phragma; pubescence on apodeme beta dorsum (Fig. 39) |
| Rhyparochromidae | Myodocha serripes: head with posterior region elongate, (gooseneck) (Fig. 41) |

family (Enicocephalidae) and had simple endothoraces. Enicocephalomorpha and Gerromorpha
both had small, smooth, thin anterior mesothoracic phragmata; anterior mesothoracic ventral bridge small with apodemes; apodemes alpha, beta small if present; posterior mesothoracic phragma with narrow crown if present; ridges $1,2,3$ small; thoracic floor, wall smooth; coxae I separated from II, III; spiracles oval, spiracle 1 fused in segma coria (see glossary); posterior mesothoracic ventral bridges small; and prothorax small. Enicocphalomorpha, but not Gerromorpha, had cunate thorax; anterior mesothoracic ventral bridge square; metathoracic ventral bridge with extension; posterior mesothoracic phragma with arch; no occipital condyle; posterior meso- and metathoracic ventral bridges small or vestigial.

Most gerromorphs had filiform thoraces with simple endothoraces that lack many characters. Species within families show interspecific similarity and families were mostly intact, except Mesoveliidae, because of ptergyopolymorphism. Pterygopolymorphism was common in gerromorphs, e. g., Veliidae, Hydrometridae, Hebridae, and Gerridae. Results (Fig. 50) showed the macropterous mesoveliid similar to Macroveliidae (between pleids and notonectids), whereas the apterous mesoveliid is similar to Veliidae.

In Gerromorpha, families were grouped as Veliidae/apterous Mesovelidae with Gerridae; Hydrometridae/Hebridae with Pleidae; and Macroveliidae with macropterous mesoveliids. Characters that linked the Veliidae/apterousMesoveliidae branch to the Gerridae were the occipital condyle; no anterior mesothoracic phragma; anterior mesothoracic shelf; metathoracic ventral bridge with apodeme; thoracic wall, floor lobed; anterior mesothoracic ventral bridge small with apodeme; spiracles oval; and palisades.

The coxal spacing of Gerridae may indicate adaptation for movement on water. Coxae II, III were close together, I is separate, putting additional strength posteriorly (Fig. 3). On the other
hand, Hebridae live in semi-aquatic environments, their coxae I and II were close together, whereas III is separate (Fig. 9), putting additional strength anteriorly. Both families had moderately thick integuments, and $30 \%$ coxal invagination with a $30^{\circ}-60^{\circ}$ angle tilt that may assist movement in viscous environments.

Characters that linked the Hydrometridae/Hebridae branch to the Pleidae were no metathoracic ventral bridge; anterior mesothoracic ventral bridge with apodeme; apodeme alpha small (sometimes absent); columnlike posterior mesothoracic phragma; ridges 1, 2, 3 fused; some thoracic wall lobes, pores, or pits; nearly vertical coxal angles with up to $30 \%$ invagination; and moderately thick integument.

Characters that linked the Macroveliidae with the macropterous Mesoveliidae branch were posterior mesothoracic phragma fused to thoracic floor; apodeme alpha fingerlike; metathoracic ventral bridge with apodeme; prothoracic lobes; spiracle 1 fused in segma coria; coxae with up to $30 \%$ invagination.

In Gerromorpha, single character states occur only a few families. Gerromorpha families in general had moderately high levels of interspecific variability and less intraspecific variability. Nepomorpha (Appendix 4, Figs. 10-17)

Nepomorpha characters were: large anterior mesothoracic ventral bridge apodemes; posterior mesothoracic phragma touching ventral surfaces, with lateral arch; smooth thoracic wall, floor; small ridge 2 ; small spiracle 1 fused in segma coria; and ventral mesothoracic keels (exception, Gelastocoridae). There were also no anterior mesothoracic phragma medial keel, ventral apodeme, anterior mesothoracic shelf, pores, pits, integument cavities, anterior mesothoracic ventral bridge, or large posterior mesothoracic phragma with
lateral arch; there were some palisades, $30 \%$ coxae invagination, dorsoventral rectangular prothorax, and spiracle 1 in segma coria.

Pleidae had numerous nepomorphan characters, yet there were at least 20 features that made Pleidae Gerromopha-like. Table 4 illustrates this by comparing Pleidae with Notonectidae.

Macroveliidae and Mesoveliidae were positioned between notonectids and pleids (Fig. 50). This arrangement is problematic and needs further inquiry. There were possibly two reasons for this: macroptery of the mesoveliid and macroveliid and small sample size with one species representation.

Notonectidae (Nepomorpha) had more complex endoskeletons than gerromorphs and enicocephalomorphs (Appendix 4). In Nepomorpha each character state was retained across a greater number of families, whereas in Gerromorpha and Enicocephalomorpha this kind of continuity was often lacking. Two groups in Nepomorphs were determined by similar analysis. They were Gelastocoridae/Naucoridae with Notonectidae; and Nepidae/Gelastocoridae including Saldidae (Leptopodomorpha).

Corixidae, Naucoridae, and Gelastocoridae (but not Notonectidae) had coxal III hoods with almost $100 \%$ invagination, and steep anterior tilt, making wine-barrel-shaped structures with collars; metathoracic ventral bridge apodemes, very large (including Notonectidae).
Table 5: Characters which distinguish Pleidae from Notonectidae

| Pleidae | Notonectidae |
| :--- | :--- |
|  |  |
|  |  |
| Anterior mesothoracic phragma lateral keel-large | Anterior mesothoracic phragma lateral keel- absent |
| Anterior mesothoracic ventral bridge apodeme-large | Anterior mesothoracic ventral bridge apodeme-small |
| Apodeme alpha-large | Apodeme alpha-small |
| Apodeme beta-present | Apodeme beta-absent |
| Metathoracic ventral bridge-large | Metathoracic ventral bridge-absent |
| Metathoracic ventral bridge apodeme-large | Metathoracic ventral bridge apodeme-absent |
| Metathoracic ventral bridge extension-large | Metathoracic ventral bridge extension-absent |
| Posterior mesothoracic phragma crown-wide | Posterior mesothoracic phragma crown-narrow |
| Posterior mesothoracic phragma-touching ventrad | Posterior mesothoracic phragma- fusing with ventrad |
| Ridge 1-large | Ridge 1-small |
| Ridge 3-large | Ridge 3-small |
| Spiracle 1-small | Spiracle 1-moderately small |
| Spiracle 2-small | Spiracle 2-large |
| Thoracic floor-smooth | Thoracic floor-rough |
| Thoracic wall-smooth | Thoracic wall-rough |
| Wing muscle opening-small | Wing muscle opening-large |
| Thoracic contour-oval | Thoracic contour-filiform |
| Spiracle 2-vertical | Spiracle 2-horizontal |
| Coxae angles $30^{\circ}-60^{\circ}$ | Coxae angles vertical - $60^{\circ}$ |
| Coxae II+III close together, I separate | Coxae I+II close together, III separate |

Characters common to Naucoridae/Gelastocoridae were: large grappling front legs with boxshaped prothoraces; thoraces pyriform; anterior mesothoracic ventral bridge apodemes large, flat; anterior mesothoracic phragma large; posterior mesothoracic phragma tubelike with wide crown; apodeme beta large, flat. With external pressure, the phragma presses into apodeme beta, preventing crushing (personal observation). As creeping predators, their pyriform thoracic contours may assist in lifting the prothorax off the ground, allowing the front legs greater movement (Figs. 12, 13) (see comments on Cimicidae, in discussion).

Between Corixidae and Nepidae were two cimicids paired with Retrocorixa semistriata (Corixidae). Characters common to Cimex lectularius, and Oeciacus vicarious (Cimicidae), and R. semistriata (Corixidae), were: anterior mesothoracic phragma smooth without ventral lobes, with apodemes and keels; no anterior mesothoracic ventral bridge; and no anterior mesothoracic shelf. Nepidae, Belostomatidae, Corixidae, and Saldidae (Leptopodomorpha) were linked by several endoskeletal character states (Fig. 50).

Common characters of Nepidae/Belostomatidae with Saldidae were: thin anterior mesothoracic phragma, no ventral lobes; anterior mesothoracic ventral bridge small; apodeme beta large with wide base and triangular head (Ranatra fusca [Nepidae] differed, having small apodeme beta with triangular base, no head); large shortened posterior mesothoracic phragma, with wide crown, lateral arch, humanlike foot (saldids had a smaller version of this); ridges 1,2 , 3 curved; and very large coxa III.

Common characters of Nepidae/Belostomatidae were: no spiracles; dorsal wing muscle openings; anterior mesothoracic ventral bridge apodemes large with long posterior arms; ventral thoracic floor keels, and coxae $30-60 \%$ invaginated with ridges and apodemes. Coxae I is least
invaginated and coxae III the most. Nepids had a $90^{\circ}$ bend in anterior mesothoracic phragma, but belostomatids do not.

Common characters of belostomatids with saldids were: filform thoraces (nepid's were oval); very large coxa III tilted at $80^{\circ}$ with large anterior apodemes; apodeme beta base stemlike fused to dorsal ridges of posterior mesothoracic ventral bridge. Differences were: coxae of Saldidae invaginated 60-80\% and those of Belostomatidae were not; belostomatids had an occipital condyle and saldid's do not.

Unique family characters found in Nepomorpha were: Nepidae with unusually long goose-neck-like prothoraces ribbed for strength (Rhyparachromidae [Pentatomomorpha] had a similar elongation as a posterior extension of head); Nepa apiculata (Nepidae) with linear ribbed region dorsal to posterior mesothoracic phragma; Ranatra fusca (Nepidae) anterior mesothoracic phragma with single medioventral cupshaped hooked apodeme; and anterior mesothoracic ventral bridge with double rings of cuticle. Belostomatidae with large bird-headshaped apodeme alpha (Fig. 17), metathoracic ventral bridge apodeme extremely large, C-shaped (Fig. 17a), large fold of cuticle fusing metathorax with abdomen. Corixidae had balloonlike spiracle 2 ; apodeme alpha moved to anteroventral mesothoracic wall; metathorax with third spiracle. Saldidae (Leptopodomorpha) (Figs. 18,50) with arched apodeme alpha base; large coxa I apodeme with large coneshaped head.

Cimicomomorpha (Appendix 4, Figs. 19-26)
Cimicomorphan characters were: prothorax moderately large, usually rectangular; integument thick usually with external ornamentation; apodeme beta usually coneshaped; apodeme alpha variable; posterior mesothoracic phragma usually triangular, small. Generally
endoskeletal structures were blunt in shape and somewhat thick.
The groupings of families in Cimicomorpha (Fig. 50) were Anthocoridae/Tingidae; two reduviid species Acholla multispinosa, Arilus cistatus with Aradidae (Pentatomomorpha), and Nabidae; and Miridae/Reduviidae.

Common characters of anthocorids and tingids were: cunate thoracic contours; small anterior mesothoracic ventral bridge; large apodeme alpha with deeply scoopshaped head; apodeme beta with triangular base, stem, and coneshaped head; posterior mesothoracic phragma triangular with wide crown; ridges $1,2,3$ small; spiracles small with spiraclel fused in segma coria spiracle 2 oval, vertical; thoracic wall smooth; dorsal wing muscle opening small; prothorax dorsoventrally rectangular.

Anthocoridae had a unique character: a region of glands between ridges 1 and 2 (Figs. $20 \mathrm{~b}-\mathrm{g}$ ). Each gland has a dark porelike base, stalk, and bulbous head bent $90^{\circ}$ to the stalk. The head was dark and the stalk, white. There were also large lateral thoracic wall lobes on mesothorax, not observed in the other cimicomorphs in study, and similar to those in some pentatomomorph families (Figs. 29, 30, 36, 39).

The two reduviids, Acholla multispinosa and Arilus cristatus, both harpactocorines, were similar in several characters to Aradidae, and therefore problematic. They illustrate a lack of phenotypic resolution in Reduviidae (Tables 6, 7).
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Table 6: Characters which distinguish Aradidae from Cydnidae/Coreidae

1. Anterior mesothoracic phragma: small, round with thick Anterior mesothoracic phragma: large, domed, thin cuticle, with
lateral and medial keels
Anterior mesothoracic ventral bridge apodeme: anvil-shaped
Anterior mesothoracic shelf: large
Apodeme beta base: anvil-shaped
Posterior mesothoracic phragma: touching ventrad
Posterior mesothoracic phragma: crown narrow, scooped foot
Posterior mesothoracic phragma medial ridge: large, finlike
Metathoracic ventral bridge: arched
Metathoracic ventralbridge extension: large, curving
Ridges 1, 2, and 3: small and linear
Spiracle 1: moderately small, oval
Spiracle 2: moderately large, semihorizontal
Thoracic floor/wall: smooth mixed pores and pits
Coxae angles: $60^{\circ}$ to $90^{\circ}$
Integument: moderately thick to thin 1. Anterior mesothoracic phragma: smal, round with thick
cuticle, medial and lateral keels missing
2. Anterior mesothoracic ventral bridge apodeme: spinelike
3. Anterior mesothoracic shelf: missing
4. Apodeme beta base: triangular
5. Posterior mesothoracic phragma: not touching ventrad
6. Posterior mesothoracic phragma: crown wide; foot variable
7. Posterior mesothoracic phragma medial ridge: missing
8. Metathoracic ventralbridge extension: missing or small
9. Metathoracic ventralbridge extension: missing or small
10. Ridges 1,2 , and 3 : large and linear
11. Spiracle 1: usually extremely large, round
Spiracle 2: moderately small, vertical
12. Metathoracic ventral bridge: domed
Ardidae
Ardidae Cydnidae/Coreidae
13. Metathoracic ventralbridge extensio
14. Thoracic floor/wall: rough with pores and pits 13. Coxae angles: nearly vertical
15. Integument: thick
§
Table 7: Some character states which distinguish or were common between Aradidae (Aradimorpha) and Cydnidae/Coreidae
(Pentatomomorpha), Acholla multispinosa \& Arilus cristatus (Reduviidae: Cimicomorpha), and character states for all three
infraorders.
Distinguishing character states for Aradidae spp. (Aradimorpha) from Cydnidae/Coreidae (Pentatomomorpha)
Common character states for Aradidae spp. (Aradimorpha) and Cydnidae/Coreidae (Pentatomomorpha)
Distinguishing character states for Aradidae spp. (Aradimorpha) from Anasa tristis (Coreidae: Pentatomomorpha)
Common character state for Aradidae spp. (Aradimorpha) and Anasa tristis (Coreidae: Pentatomomorpha)
$\star \quad$ Distinguishing character states for Aradidae spp. (Aradimorpha) from Acholla multispinosa \& Arilus cristatus (Reduviidae:

## Cimicomorpha)

Cimicomorpha)
Distinguishing character states for Aradimorpha, Cimicomorpha, and Pentatomomorpha
Common character states for Aradimorpha, Pentatomomorpha, and Cimicomorpha

| Characters | Aradidae (Aradimorpha) |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| anterior mesothoracic phragma | - | - 0 | $\star \star$ | $\star$ | $\diamond$ |
| anterior mesothoracic phragma lateral keel | $\square$ | - $\bigcirc$ | * | $\pm$ | $\bullet \diamond$ |
| anterior mesothoracic phragma medial keel | $\square \square$ | $\bigcirc$ | $\star$ | $\star$ | $\bullet \diamond$ |
| anterior mesothoracic phragma ventral apodeme | $\square$ | - | * | * | $\bullet \diamond$ |
| anterior mesothoracic ventral bridge | $\square$ | - 0 | $\star$ * | $\star$ | $\bullet \diamond$ |
| anterior mesothoracic ventral bridge apodeme | ■ | - | $\star$ | * | $\bullet \diamond$ |
| anterior mesothoracic shelf | $\square$ | $\bigcirc$ | $\cdots$ | * | $\bullet$ |
| apodeme alpha | - | $\bigcirc$ | ts | * | $\diamond$ |
| apodeme beta | $\square$ | - $\bigcirc$ | $\star$ * | * | $\diamond$ |
| metathoracic ventral bridge | $\square$ | - 0 | $\star$ * | $\star$ | $\bullet \diamond$ |
| metathoracic ventral bridge apodeme | $\square$ | $\bigcirc$ | $\star$ * | $\star$ | - |
| metathoracic ventral bridge extension | ■ | - | $\star$ 家 | S | - $\diamond$ |
| posterior mesothoracic phragma | $\square$ | - 0 | $\star$ * | $\star$ * | $\diamond$ |
| posterior mesothoracic phragma medial ridge | $\square$ | - | * | $\star$ * | - $\diamond$ |
| ridge 1 | - | - $\bigcirc$ | $\star$ * | $\star$ | $\bullet \diamond$ |
| ridge 2 | $\square \square$ | - $\bigcirc$ | $\star$ | $\star$ | - $\diamond$ |


| ridge 3 | $\square$ | - 0 | $\star$ | $\star$ | - $\diamond$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| spiracle 1 | - | - 0 | * 动 | $\star$ 动 | $\diamond$ |
| spiracle 2 | ■ | - 0 | $\pm$ | $\star$ * | $\diamond$ |
| thoracic floor | - | - 0 | * | * | $\bullet \diamond$ |
| thoracic wall | ■ | - 0 | $\star$ * | $\star$ * | - $\diamond$ |
| thoracic contour | ■ | - 0 | $\star$ | $\star$ | $\bullet \diamond$ |
| Integument thickness | $\square$ | - | * | is | - $\diamond$ |
|  | Cydnidae spp. | Anasa tristis (Coreidae) | Acholla <br> multispinosa <br> (Reduviidae) | Arilus cristatus (Reduviidae) | infraorder <br> character states |

Details found in Appendix 4
Table 8：Character states common or distinguished in Acholla multispinosa \＆Arilus cristatus with other Reduviidae in study．

## Distinguishing character states in Acholla multispinosa \＆Arilus cristatus with other Reduviidae in study（Cimicomorpha） <br> Common character states in Acholla multispinosa \＆Arilus cristatus with other Reduviidae in study（Cimicomorpha） <br> Mixed character states in Acholla multispinosa \＆Arilus cristatus with other Reduviidae in study（Cimicomorpha） <br> 回

| Characters／2 Reduviidae species | Acholla multispinosa |  |  |  |  |  |  |  | Arilus cristatus |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| anterior mesothoracic phragma | 回 | 回 | 回 | 回 | 回 | 回 | 回 | $\square$ | E | 1 | 的 | － | 帾 | － | － | － |
| anterior mesothoracic phragma lateral keel | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| anterior mesothoracic phragma medial keel | $\square$ | $\square$ | $\square$ | $\square$ | ■ | $\square$ | $\square$ | $\square$ | － | 2 | － | － | － | 教 | E | － |
| anterior mesothoracic phragma ventral apodeme | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| anterior mesothoracic ventral bridge | 回 | 回 | 回 | 回 | 回 | 回 | 回 | 回 | $\square$ | $\square$ | － | － | － | E | － | \％ |
| anterior mesothoracic ventral bridge apodeme | 回 | 回 | 回 | 回 | 回 | 回 | 回 | 回 | $\square$ | $\square$ | E | E | nㅐㄹ | E | 析 | 筑 |
| anterior mesothoracic shelf | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| apodeme alpha | $\square$ | 回 | 回 | 回 | 回 | $\square$ | $\square$ | 回 | ［］ | 國 | $\square$ | ［ $\square$ | ［］ | ［］ | ［ | －${ }^{\text {c }}$ |
| apodeme beta | 回 | $\square$ | 回 | 回 | 回 | 回 | $\square$ | 回 | ［ | © | 果 | ［區 | ［ | 兆 | ［ | ［匀 |
| metathoracic ventral bridge | $\square$ | $\square$ | E | $\square$ | $\square$ | $\square$ | ■ | $\square$ | $\square$ | ＊ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| metathoracic ventral bridge apodeme | $\square$ | E | $\square$ | $\square$ | $\square$ | $\square$ | ■ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| metathoracic ventral bridge extension | $\square$ | E | $\square$ | $\square$ | $\square$ | $\square$ | E | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | D | $\square$ | $\square$ | $\square$ |
| posterior mesothoracic phragma | 回 | 回 | 回 | $\square$ | 回 | 回 | 回 | 回 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| posterior mesothoracic phragma medial ridge | $\square$ | ■ | $\square$ | $\square$ | $\square$ | ■ | $\square$ | ■ | $\square$ | U | － | $\square$ | 0 | 数 | － | 輏 |

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| ${ }^{\text {b }}$ | － | 㽞 | $\square$ | 回 | ［0］ | ［或 | 0 | 0 | Triatona dimiduta |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m | － | － | $\square$ | ［ | ［0］ | 回 | $\square$ | $\square$ | Stenopodainae sp． |
| － | － | － | $\square$ | 國 | ［1］ | ［ | － | $\square$ | Zolus exsonguis |
| － | E | ［ | $\square$ | 回 | ［ | ［0］ | $\square$ | $\square$ | Smea dialema |
| － |  | E | $\square$ | 回 | 回 | 圆 | $\square$ | $\square$ | Rhodnius prolixus |
| 回 | 響 | 気 | $\square$ | E | ［1］ | 國 | $\square$ | $\square$ | Redsoius personotus |
| － | 䉕 | 戓 | $\square$ | E | 回 | ［ | $\square$ | $\square$ | Psellopus cincuas |
| － | － |  | $\square$ | 回 | ［ | ［1］ | $\square$ | $\square$ | Melamolestes picipes |
| 回 | $\square$ | $\square$ | $\square$ | 回 | 回 | 回 | $\square$ | $\square$ | Triatoma dimidiata |
| 回 | $\square$ | $\square$ | $\square$ | 回 | 回 | 回 | $\square$ | $\square$ | Stenopodainae sp． |
| $\square$ | $\square$ | $\square$ | $\square$ | 回 | 回 | 回 | － | $\square$ | Zelus exsanguis |
| － | $\square$ | $\square$ | $\square$ | 回 | 回 | 回 | $\square$ | $\square$ | Sinea diadema |
| 回 | $\square$ | $\square$ | $\square$ | 回 | 回 | － | $\square$ | $\square$ | Rhodnius prolixus |
| － | $\square$ | $\square$ | $\square$ | ■ | 回 | 回 | $\square$ | $\square$ | Reduvius personatus |
| － | $\square$ | $\square$ | $\square$ | 回 | 回 | 回 | $\square$ | $\square$ | Pselliopus cinctus |
| 回 | $\square$ | $\square$ | $\square$ | 回 | 回 | 回 | $\square$ | $\square$ | Melanolestes picipes |
| $\begin{aligned} & \overline{0_{0}} \\ & \text { 品 } \end{aligned}$ |  | $\begin{aligned} & \text { n } \\ & \text { go } \\ & \text { an } \end{aligned}$ | $\begin{aligned} & \stackrel{\rightharpoonup}{0} \\ & \stackrel{y}{\ddot{2}} \\ & \stackrel{\rightharpoonup}{n} \end{aligned}$ | $\begin{aligned} & \text { N } \\ & \frac{0}{g} \\ & \text { \#\# } \\ & \hline \end{aligned}$ |  |  |  |  |  |

Ten species of Reduviidae were examined. The similarities of 8 place them together (Table 8), but A. multispinosa and A. cristatus grouped with the Aradidae (Fig. 50, Table 8). Common characters of the eight reduviids were: anterior mesothoracic phragma large, round, smooth, thin with medial finlike keel and no ventral lobes; anterior mesothorcic ventral bridge large and squwere (eight species including A. multispinosa; absent in Melanolestes picipes); anterior mesothorcic ventral bridge apodeme large with filament (eight species including $A$. multispinosa; absent in A. cristatus and Pselliopus cinctus); apodeme alpha large with various lobes, small base, stem, discshaped head (including A. multispinosa); apodeme beta base anvilshaped, stem with coneshaped head; posterior mesothoracic phragma large, triangular with wide crown, no arch, not touching ventral surface (including A. cristatus and A. multispinosa), phragma foot either scoopshaped ( 5 species) or pointed (3 species), medial ridge linear, either small ( 6 species including $A$ cristatus) or large ( 3 species); ridges 1, 2,3 small, fused (including A. multispinosa); spiracle 1 small, oval, fused in segma coria (including A. cristatus); spiracle 2 large, oval, either in ventral lateral position on mesothoracic wall (seven species) or dorsal (three species, including $A$. cristatus and $A$. multispinosa) and tilted semi-horizontally (not including $A$. cristatus, A. multispinosa); thoracic floor smooth with pits ( 5 species); thoracic wall smooth (6 species), rough ( 4 species including A. cristatus, A. multispinosa) with pits ( 6 species, including A. cristatus, $A$. multispinosa); wing muscle opening small, round (including A. cristatus, $A$. multispinosa); coxae II, III closer together than I, with $30 \%$ invagination (including A. cristatus, A. multispinosa); integument moderately thin; rectangular prothorax $1 / 3$ size of mesothorax; thoracic contour pyriform with flat dorsum and occipital condyle present (8 specimens including A. cristatus) (Tables 7, 8 and 11-46)

Unlike Reduviidae, Miridae species had many common character states (Tables 10-46). The phenogram groups Miridae with Reduviidae and Nabidae (Fig. 50). The phenogram indicates a close or high level of similarity between Tingidae and the group formed of Anthocoridae and Aradidae. This suggests that Cimicomorpha with elevated levels of variability (Appendix 4) were unresolved in endoskeletal morphology and need more study.

Common characters for Miridae/Reduviidae and Nabidae (Fig. 50) were: pyriform thoraces; anterior mesothoracic phragma large, smooth, domed; cuticle thin with large medial keels; apodeme alpha large with discshaped head; posterior mesothoracic phragma large, triangular with wide crown, lateral arch, touching ventral surfaces; posterior mesothoracic phragma foot alternating between scoop or boatshapes; ridges $1,2,3$ small; thoracic floor, wall smooth; coxae II and III closer than I; prothorax squwere, half the size of mesothorax; and spiracle 2 oval, almost horizontal.

Miridae had 3 unique characters: extra keel on anterior mesothoracic phragma; two posterior mesothoracic phragma openings (windows); and a starlike 5 ridge configuration on mesothoracic dorsum. The phragma openings may be to reduce weight, while maintaining strength (Fig. 22). Nabidae also had a phragma opening, but a single one (Fig. 21). Nabidae were interesting, being the only family with filiform thoraces in a group of families which had cunate thoraces.

| Characters／Species |  |  |  |  | $\begin{aligned} & \text { n } \\ & \text { 令 } \\ & 0 \end{aligned}$ |  |  |  |  | $\begin{aligned} & \text { 急 } \\ & \text { s. } \\ & \text { B } \end{aligned}$ | $\begin{aligned} & \text { N} \\ & \vdots \\ & 0 \end{aligned}$ | $\begin{aligned} & \text { ? } \\ & \text { है } \\ & \text { Uै } \\ & \text { है } \\ & \text { है } \end{aligned}$ | $\begin{aligned} & \tilde{\text { ® }} \\ & \text { स } \end{aligned}$ | $\frac{\tilde{S}_{3}^{2}}{2}$ | 第 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| anterior mesothoracic phragma | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | 口 |
| anterior mesothoracic phragma lateral keel | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | － | $\square$ |
| anterior mesothoracic phragma medial keel | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| anterior mesothoracic phragma ventral apodeme | $\square$ | － | $\square$ | － | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | － | 口 |
| anterior mesothoracic ventral bridge | $\square$ | $\square$ | － | $\square$ | $\square$ | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| anterior mesothoracic ventral bridge apodeme | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ |
| anterior mesothoracic shelf | － | $\square$ | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | 口 | $\square$ |
| apodeme alpha | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | 口 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| apodeme beta | $\square$ | $\square$ | 回 | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| metathoracic ventral bridge | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | － | $\square$ | $\square$ |

s0Z

| metathoracic ventral bridge apodeme | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| metathoracic ventral bridge extension | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| posterior mesothoracic phragma | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| posterior mesothoracic phragma medial ridge | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| ridge 1 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| ridge 2 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| ridge 3 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| spiracle 1 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| spiracle 2 | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| thoracic floor | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| thoracic wall | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| thoracic contour | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |
| Integument thickness | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ | $\square$ |

Details found in Appendix 4

Characters linking Phymatidae with Pentatomomorpha were: prothorax with palisades; ridges $1,2,3$ with "proto" three ridge " N " configuration, meaning 3 ridges were beginning to orient into the " N " configuration commonly found in Pentatomomorpha; ridges 1, 2 broad, ridge 2 dorsally inserted between ridge 1 and thoracic wall, ridge 3 narrow, linear, fused dorsally with apodeme alpha; apodeme beta base broad, somewhat anvilshaped (Pentatomomorpha had anvilshaped apodeme beta bases) with two anterior arms and one posterior arm, posterior arm fingerlike, primary anterior arm filamentous progressing to small discshaped head, secondary anterior arm filamentous with frayed featherlike head; posterior mesothoracic phragma triangular, crown broad narrowing to scoopshaped foot, resting on apodeme beta (Fig. 25, 25a). Characters linking Phymatidae with Cimicomomorpha were: prothorax moderately large, rectangular; apodeme alpha head flat, clublike with ventral surface rugose; mesothorax dorsal surface with lobes; and integument thick with external lobes. Characters unique to Phymatidae were: anterior mesothoracic phragma medial keel triangular with dorsal trough; anterior mesothoracic phragma dorsolateral with rectangular cavity; apodeme beta with second anterior arm.

Pentatomomorpha (Appendix 4, Figs. 27-42)
Pentatomomorpha characters were: large cunate thoraces; small prothorax; usually large triangular posterior mesothoracic phragma touching ventral surface, with a lateral arch; apodeme beta with anvilshaped base, thin stem, coneshaped head; thin integument.

Although Aradidae held many endoskeletal character states in common with Pentatomomorpha, they had many other characters unlike those of pentatomomorpha. This was suggestive of an Aradimorpha group. Cydnidae and Coreidae were chosen from

Pentatomomorpha for comparison (Tables 6, 7).
Characters common to Aradidae, Cydnidae, and Coreidae were: cunate thoracic contours, slightly broadening posteriorly; anterior mesothoracic phragma smooth with no ventral apodeme and lobes; anterior mesothoracic ventral bridge small, round, with small apodeme; apodeme alpha large with discshaped head; apodeme beta with discshaped head, filamentous stem; spiracle 1 fused in segma coria; spiracle 2 oval in ventral lateral position on thoracic wall; wing muscle opening small, round; coxae II, III closer together than coxa I, invaginations from 0 to $30 \%$; mesothorax twice size of prothorax. Some Cimicomorpha characters were: small anterior mesothoracic phragma; anterior mesothorcic shelf absent; apodeme beta base usually triangular; posterior mesothoracic medial ridge absent; thoracic floor, wall rough; integument thick.

Families throughout Pentatomomorpha had similar character states, unlike the more variable character states of Enicocephalomorpha, Nepomorpha, Leptopodomorpha, and Cimicomomorpha. This phenetic division was more shallow than that in Nepomorpha (Fig. 50). Pentatomidae group (Appendix 4, Figs. 27-33, 50)

Families were grouped as: Pentatomidae/Scutelleridae with Cydnidae; Acanthosomatidae/Parastrachiidae with Thyrecoridae and Tessaratomidae. Cydnidae were somewhat like other pentatomomorphs, with large anterior mesothoracic phragma; anterior mesothoracic shelf; posterior mesothoracic phragma large with crown, scoopshaped foot; apodeme beta base anvilshaped; apodeme alpha discshaped; but they had some Cimicomomorpha characters: large prothorax; thick integument; straight ridges 1, -3 all lacking Pentatomomorpha 3-ridge " N " configuration. Common characters of Pentatomidae/Scutelleridae with Cydnidae were: anterior mesothoracic phragma large, smooth; anterior mesothoracic shelf
large; apodeme alpha large with discshaped head, stemlike base; apodeme beta with anvilshaped base, stem, discshaped head; metathoracic ventral bridges fused in segma coria between metathorax and first abdominal segment; posterior mesothoracic phragma large, triangular with lateral arch, narrow crown, touching apodeme beta; spiracle 1 oval; spiracle 2 oval on lateral mesothoracic wall; integument moderately thick with no cavities. Common characters of Pentatomidae and Cydnidae were: anterior mesothoracic phragma with scimitar-shaped lateral keel, no ventral apodemes (Scutelleridae with hooked ventral apodemes); metathoracic ventral bridge apodeme fingerlike; metathoracic ventral bridge extension large (Scutelleridae: small); and posterior mesothoracic phragma medial ridge large, linear (Scutelleridae: finlike). Common characters of Pentatomidae and Scutelleridae were: anterior mesothoracic phragma with small scimitar-shaped medial keel; metathoracic ventral bridge small; posterior mesothoracic phragma foot boatshaped (Cydnidae: foot scoop-shaped); spiracle 1 moderately large; spiracle 2 vertical with palisades (Cydnidae: with no palisades); wing muscle opening large, oval, dorsal (Cydnidae: small, round); coxae evenly spaced (Cydnidae: coxae II, III closer together, I separate); oval thoracic contour with widest point fused to abdomen (Cydnidae: thoracic contour cunate). Common characters of Acanthosomatidae/Parastrachiidae with Thyreocoridae were: anterior mesothoracic phragma with fingerlike ventral apodemes; posterior mesothoracic phragma large, triangular, touching ventral surfaces, with narrow crown, arch, dorsal ridge; apodeme beta with anvilshaped base, stem, coneshaped head; apodeme alpha with discshaped head, stemlike base; palisades, anterior mesothoracic ventral shelf, present. Tessaratomidae and Thyreocoridae were phenotypically allied through characters: anterior mesothoracic phragma with fingerlike ventral apodemes; anterior mesothoracic ventral bridge with large apodeme; apodeme alpha large with
discshaped head, stemlike base; apodeme beta with stem, coneshaped head, bases variable; posterior mesothoracic phragma triangular, touching ventral surfaces.

Unique characters of Thyreocoridae were: anvilshaped apodeme beta base fused with metathoracic ventral bridge apodeme; posterior mesothoracic phragma large with large finlike medial ridge. Other families had unique characters (Table 4).

Coreidae group (Appendix 4, Figs. 34-42, 50)
Included were Coreidae/Alydidae with Rhopalidae; Pyrrhocoridae/Largidae with Lygaeidae (sensu stricto); and Berytidae/Rhyparochromidae with Blissidae. The Coreidae group with few exceptions has many similar characters, including: cunate thoraces; three-ridge " N " configuration and palisades around numerous structures including coxae, spiracles, and intersegmental regions; posterior mesothoracic phragma large, wide, triangular, touching ventral surfaces; apodeme beta base triangular; thoracic walls, floors with pits, pores, or lobes; spiracles 1, 2 very large; apodeme beta with thin stem and coneshaped head; coxae angles nearly vertical; integument thin. Common characters of Pyrrhocoridae/Largidae with Lygaeidae (sensu stricto) were: posterior mesothoracic phragma moderately narrow, fused to apodeme beta; palisades very large; and mesothoracic dorsum with variable secondary structures.

One character of interest, common to Berytidae/Rhyparochromidae with Blissidae,were large thoracic lobes. Blissidae also had large triangular posterior mesothoracic phragmata fused to ventral surface as a column; in the other two families it was not fused. Internal pubescence was not found in Heteroptera. However, exceptions were seen in Berytidae with the head of apodeme beta and lateral thoracic wall patches in Naucoridae (Figs. 39b-e).

Among the nine families of the Coreidae group, Rhopalidae, Blissidae,

Rhyparochromidae, and Berytidae all had large endothoracic lobes; whereas in Coreidae, Alydidae, Lygaeidae, Largidae, and Pyrrhocoridae the endothorax has no lobes and was smooth with pits and pores. In Largidae, Lygaeidae, Pyrrhocoridae, and Blissidae the posterior mesothoracic phragma was dorsoventrally fused..

In Alydidae and Rhyparochromidae apodeme alpha has a large ventral spine inserted into the coneshaped head of apodeme beta. Both Myodocha serripes (Rhyparochromidae) and Alydidae species had highly arched thoracic dorsi (Figs. 35, 41). Alydus eurinus (Alydidae) showed possible injury where the apodeme alpha ventral spine rubbed against the inner wall of the apodeme beta head (Figs. 35b,c)

Each infraorder shows certain overarching traits among families. Following are summaries of some infraordinal heteropteran characters.

## Summary of examined infraordinal heteropteran characters

Enicocephalomorpha (Stichel 1955-56): Simple endoskeletons, lacking many structures. No occipital condyle. Keels large; apodemes alpha, beta small, filamentous; posterior mesothoracic phragma lobed sheet; cunate thoracic contour with thin smooth cuticle. Little interspecific variability among species (Figs. 2, a).

Gerromorpha (Popov 1971a): Simple endoskeletons, most structures small; occipital condyle common; keels absent; many species with fused posterior mesothoracic phragmata; thoracic contour filiform with pitted thin cuticle. Ptergyopolymorphism common (Møller Andersen 1982). Little interspecific variability among species (Figs. 3-9).

Nepomorpha (Štys and Jansson 1988): More complex endoskeletons than Enicocephalopmorpha and Gerromorpha. No occipital condyle. Keels variable or absent. Large anterior mesothoracic ventral bridge apodemes; posterior mesothoracic phragmata generally tubelike with lateral arch, usually touching apodeme beta; thoracic contour variable, e.g., ovate, cunate, filiform, with smooth thin cuticle. Considerable interspecific variability among species (Figs. 10-17).

Leptopodomorpha (Popov 1971b): Complex endothoraces somewhat intermediate between Nepomorpha and Enicocephalomorpha-Gerromorpha (speculative because of few specimens); occipital condyle and keels absent; posterior mesothoracic phragmata triangular; coxae openings large; spiracle 2 large; thoracic contour filiform with smooth thin cuticle (Fig. 18).

Cimicomorpha (Leston et al. 1954): Complex endoskeletons with highest interspecific variability of suborder; occipital condyle absent; keels uncommon, large when present; prothorax moderately large, rectangular or round; apodeme alpha head clublike, usually fused with ridge 3 ; apodeme beta usually with stem and coneshaped head, base variable; posterior mesothoracic phragmata short, triangular; thoracic contour variable, e.g., cunate, filform, or pyriform with moderately thick cuticle (Figs. 19-25.)

Pentatomomorpha (Leston et al. 1954): Complex endoskeletons less variabile than Cimicomorpha but more than Enicocephalomorpha, Gerromorpha, Nepomorpha and Leptopodomorpha; posterior mesothoracic phragmata large, triangular, large foot touching apodeme beta, with crown and lateral arch; apodeme alpha usually discshaped head and stem; apodeme beta usually anvilshaped with stem and discshaped head; palisades and large thoracic wall lobes common; ridges $1,2,3$ usually in " N " configuration; spiracles large; thoracic contour cunate, cuticle thin (Figs. 26-42).
Fig. 50. Phenogram neighbor-joining analysis for 39 heteropteran and 3 Auchenorrhynchan families.



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## Discussion

There is no all-inclusive study of the heteropteran endoskeleton. Even the most detailed thoracic studies usually overlooked the endoskeleton as a morphological region of interest (Guthrie and Tindal 1968, Takadi 1938, Weber 1930, Fig. 54). When names were given they were often generalized, and over-used, because early morphologists in their most influential studies had worked with primitive insects with simpler endothoraces, e.g., Snodgrass (1935, 1947) on Blattoidea, and Comstock (1924) on Orthoptera and Thysanura. Morphologists had underestimated the taxonomic value of the endoskeleton and by examining only a few specimens had applied names to structures in other insects with the tacit assumption that all insects were similar (Chapman 1982, 2006, Duporte 1959, Lawrence et al. 1991, Snodgrass 1935).

Four endoskeletal structures were presented by Snodgrass (1935, Fig. 103a): median apodemal process of the spinasternum, pleural apophysis, sternal apophysis, and phragmata. "Phragmata" was a generalization, used more as place holder than useful identifier. This tendency for nomenclature generalization has been repeated by such authors as Chapman (2006; his Fig. 7.6 is Snodgrass's [1935] Fig. 103a), Comstock (1924), Naumann et al. (1991), and Borror et al. (1989). Moreover, names given to endoskeletal structures were often too inconsistent to be of great value, a fact exemplified by the structure apodeme beta. Names for this structure included "mesothoracic furca" (Parsons [1960] and Goel [1966], who closely followed Parsons), "pleural apophysis" (Snodgrass 1935), "pleural arm" (Snodgrass 1937), and "pleural process" (Bitsch 2002).

The main problem with endoskeletal nomenclature was that nearly all important studies were focused on musculature or other soft tissues. Even in Heteroptera, Parsons (1960, 1963) and Goel (1966), who wrote good descriptions of the heteropteran endothorax, did not give full accounts of the endoskeletal structures because they were interested in the musculature. Each examined only a single species (Gelastocoris oculatus (Fabricius), Gelastocoridae: Parsons [1960]; and Coridius janus (Fabricus) Dinidoridae: Goel [1966]), a continuation of the approach of early morphologists.

Up to now no one has surveyed a group of related species to determine whether endothoracic structures that occur in one species also occur in others. This study of over 180 heteropteran, auchenorrhynchan, dipteran, and hymenopteran species shows that indeed these structures are present in nearly all the species and that they differ among taxa.

Previous studies often presented overly stylized illustrations. Parsons for example in her 1960 paper shows the ventral F II furca (Fig. 12 in her 1960 paper), here recognized as apodeme beta, as tilted such that a triangle with 2 dorsal lobes is evident. New scanning electron micrographs from the lateral perspective show the apodeme to be a square post with a flat dorsum on which the two lobes in Parson's illustration are in fact small overhangs of the apodeme's dorsum (Figs. 13, 13a). In addition, some published drawings show lines that became dashes to indicate they were behind a structure (Savinov 1983, 1990); this can be confusing.

A preliminary study of 80 male and female coreids showed the heteropteran endoskeleton to be bilateral, with no sexual dimorphism, and that a single specimen from each family could represent most of these families in Heteroptera (exceptions Reduviidae, Aradidae,
and ptergopolymorphic species in Mesoveliidae). Species from Gerridae, Miridae and Corixidae were also examined for variability and results were the same as the coreids. Once these issues were addressed, the integument (which defines body shape, size and color of the insect [Gordh 2001]) was closely examined. On most occasions, both the inner (endoskeleton) and outer surfaces of the integument contributed information for special identification, but sometimes they were different. An example of this was in the family Rhopalidae. Separated populations of Liorhyssus hyalinus (Rhopalidae) (Korea and Arizona, USA) (Figs. 36a,b) showed the outer surface identical, but the endoskeleton had differences. By contrast, two very close Connecticut (USA) populations of Anasa tristis (Coreidae) showed no intraspecific variability (Figs 33a-c). Further studies should be made comparing geographically separate and contiguous populations of species within a single family to test the likelihood that different selective pressures might influence the outer and inner integument surfaces independently.

## The structures

Three regions of the thorax are highly variable, the thoracic contour (profile of the integument), internal flight structures, and prothorax (Figs. 1, 1a). There are primarily three thoracic contour shapes in Heteroptera: filiform (Fig. 3), cunate (Fig. 27), and pyriform (Figs. 22, 22a). The filiform thoracic contour is common in Gerromorpha and Nepomorpha (Figs. 3, $4,5,6,10,17$ ). In Leptopodomorpha, Cimicomorpha, and Pentatomomorpha, the filiform contour is not observed except in one cimicomorphan, Nabidae (Fig 21). The cunate thoracic form is found in many families throughout Heteroptera. (Figs. 25, 27, 37, 39, 40). It is uncommon in Gerromorpha, Nepomorpha, and Enicocephalomorpha, more common in Leptopodomorpha and Cimicomorpha, and very common in Pentatomomorpha. Pyriform
thoraces are found in Nepomorpha and Cimicomorpha (Figs. 12, 13, 22, 24, 25). Insects with pyriform thoraces have flat dorsums, and deeply concave ventral mesothoraces. The filiform shape may enhance protection against crushing; the cunate shape may increase surface area for muscle and organ attachment; and the pyriform shape may help elevate front legs for hunting and/or improve feeding efficiency.

The prothorax and its size and shape variability may be an evolutionary response to diet. In predators, size and condition of prey may dictate prothoracic size, related to foreleg size and strength for grappling (Figs. 15-17). For example, notonectid prothoraces generally are small; they feed on small prey (Cronin \& Travis 1986; Chesson 1984) and perhaps do not need to be heavily reinforced (Fig. 11). In contrast belostomatids capture large more active prey (Toledo 2003; Hinshaw \& Sullivan 1990) and have large prothoraces with large anterior mesothoracic ventral bridge apodemes to support large strong foreleg muscles that exert much more force in their points of attachment (Figs. 17, 17a). Belostomatids are also much bigger insects than notonectids and so scaling effects may also play a role in prothorax form.

Hematophagus cimicids (Fig. 19), and triatomines (Fig. 24c) have large round prothoraces with a segma coria constriction between the pro-and mesothoraces, perhaps to facilitate blood ingestion. I suggest that the round prothorax of cimicids may reduce fluxes in blood pressure, while a small segma coria cervical necklike constriction between the pro-and mesothoraces might control blood flow. Once through this cervical constriction, blood enters a large mesothorax, perhaps a low pressure region which enhances a flooding effect by providing more space for blood to flow into. This may be a passive mechanism to draw blood from the prothorax, enhancing feeding efficacy and speed feeding time. Triatomines have a similar
construction (Fig. 24c).
Triatominae do not have the laterally flattened mesothoraces of Cimicidae; instead, like other reduviids, they have dorsoventrally round mesothoraces while retaining the round prothoraces of cimicids. The relative size and volume of the mesothoraces of cimicids and triatomines are similar; triatomines are simply shaped differently, possibly reflecting a different ancestry. The function of the round prothorax, cervical constriction, and large mesothorax in both, seems to be the same. The round mesothorax of triatomines, is also present in other reduviids which are not hematophagous but feed on the fluids of other arthropods (Figs. 24, 24ah).

The round mesothorax in Reduviidae I speculate may be related to expediting fluid absorption. Most reduviids feed on live arthropods and in the early stages of feeding may rapidly remove some hemolymph to quickly incapacitate the prey, reducing their chance of injury (Cohen 2000). They then feed on the tissues of the prey by reducing solid tissues to a liquid state. Cohen (2000) describes how the stylets are used inside the prey to cut, tear, and rasp tissues, thus both chemical and mechanical mechanisms are employed together to effectively process prey tissue. Edwards (1961) and Cohen (1996) discuss the use of venom (digestive enzymes) by many predaceous Heteroptera in the subduing and subsequent feeding processes.

Prothoraces were generally small in phytophagous families (Figs. 22, 36). Forelegs were usually thin and used for finding footholds and grooming (personal observation). Foreleg muscles are reduced because there is no requirement to hold a struggling prey.

The posterior mesothoracic phragmata can either touch or fuse with ventral surfaces
(Figs. 10, 20). Fused phragmata are common in two heteropteran infraorders, Gerromorpha and Pentatomomorpha (Figs. 5, 9, 40, 42). This character is absent in Nepomorpha, Cimicomorpha, and possibly Leptopodomorpha and Enicocephalomorpha (only one species was studied in each of these last two infraorders). In aquatic and semi-aquatic families, such as Hebridae, Pleidae, and Gerridae, the columnlike fused phragmata may resist external pressures (Figs. 3, 9, 10).

Some Gerromorpha and Pentatomomorpha species had dorsoventrally fused posterior mesothoracic phragmata (Figs. 3, 5, 7, 9, 10, 37, 38, 40, 42); and gerromorphs seem to have a single structure while pentatomomorphs have two fused structures, e.g., the phragma fused to apodeme beta. Why Gerromorpha have an apparent single structure while Pentatomomorpha have two, is uncertain. The Gerromorpha fused phragma may possibly be because this group frequents viscous environments and may need a pillarlike internal structure to prevent thoracic collapse (Figs. 3, 9, 10). Possibly the fused pentatomomorphan phragmata may have formed in only a few families (Figs. 37, 38, 40, 42) from repeated compressions caused by activity of flight on a narrow posterior thoracic region, eventually causing apodeme beta and the phragma to fuse.

Fused phragmata may occur only in adult Heteroptera. Nymphs were not examined. Nymphs should be examined to see if phragmata in gerromorphs and pentatomomorphs are fused during heteropteran development. I suggest dorsoventrally fused phragmata may not be expressed in nymphs because of molting, and is only expressed in adults. Why fused phragmata are seen in some but not all pentatomomorphan families cannot now be explained. More distantly related groups such as Hymenoptera and Diptera (endurance fliers) show variability of this trait; in Vespidae (Hymenoptera) the posterior mesothoracic phragma is detached whereas
in Tabanidae (Diptera) it is fused.
A variant of the fused phragmata is the shortened tubelike phragma with flat foot seen in Naucoridae, Gelastocoridae, and some aradids (Figs. 12, 13, 26). When external pressure is exerted, the phragma presses pistonlike into the apodeme (personal observation). Once pressure is released, the natural spring in the cuticle restores the thorax to its original shape. This again may be a mechanism for physical protection against crushing.

In numerous pentatomomorphs (Figs. 28, 30, 32, 34), some cimicomorphs (Figs. 21, 22, 25), and a few nepomorphs (Figs. 14, 15), phragmata are triangular and sheetlike. The triangular phragmata, which touch ventral surfaces, are springlike, possibly cushioning against external pressure and allowing greater thoracic flexibility. They may also provide more surface area for flight muscles. Some cimicomorphs have triangular phragmata, which do not touch the ventral surfaces (Figs. 19, 21, 23). This may be a trade-off between integument thickness and phragma size. Cimicomorphans usually have thicker integuments. Protection from crushing may be switched to the integument, leaving phragmata reduced.

Other structures associated with the endoskeleton were seen, e.g., glands, pubescence, lobes, features of the spiracles, palisades, and degrees of coxal spacing. Anthocoridae have a cluster of unique anterodorsal thoracic gland ducts between ridges 1 and 2. The Israeli specimen has hyphaelike ducts (Figs. 20, 20a-e), while the Nevada (USA) specimen has short conelike ducts (Fig. 20g). This feature does not occur in any other heteropteran family. It is not uncommon to find dorsal abdominal glands in taxa of Enicocephalomorpha, Cimicomorpha, and Pentatomomorpha persisting from nymphs into adults (Weirauch 2005); but it is unusual to observe glands in the thoracic dorsum.

Scent glands in heteropteran families are located in the ventral metathorax, posterior to the posterior mesothoracic ventral bridge, a defining apomorphy of Heteroptera (Staddon et al. 1987, Janaiah 1988, Schuh 1995, Weirauch 2005). In some families these glands may effect the shape of the posterior mesothoracic ventral bridge apodeme. For example, in Acanthosomatidae, Coreidae, and Rhyparochromidae the apodeme is ringshaped (Figs. 30, 34, 41), providing possible support for a duct; in Pentatomidae and some cimicomorphan families (Figs. 20, 21, 27, 37, 38, 42), the apodeme is hookshaped. The apodeme in other heteropteran groups is often knobshaped (Figs. 22, 35) and very large, for possible muscle support (Figs. 12, 13,17 ).

Naucoridae have patches of pubescence between ridges 1 and 2 (Figs. 12, 12a, b) and Blissidae have ladyfinger-shaped pubescence along the prothorax wall (Fig. 42). This may be a form of heat regulation. No other Heteroptera have this pubescence. Diptera (Fig. 48), and in particular Hymenoptera (Figs. 47, 47a-d), have extensive thoracic pubescence. These insects are endurance flyers, with a by-product of muscle heat. Rows of ladyfinger-shapes and irregular patches of pubescence along the thoracic wall (Figs. 47, 47a-d) may be a mechanism for shedding heat. Heat may be transferred through the pubescence and integument to the environment by radiation or convection (Church 1959). Large thoracic lobes may act also to regulate heat. Seen in many Heteroptera (Figs. 39, 39a), they may increase the surface area of the thoracic wall.

In the morning many insects including Hymenoptera raise their body temperatures for flight by sun basking. These pubescent patches may function to speed up heat absorption (Chapman 1982). The pubescent patches are located in the dark most heavily sclerotized
regions of the thorax and not in light-colored regions (Fig. 47) (Figure 47a shows the white coloration as a region of rough cuticle), that is, in regions which absorb, not reflect, heat.

Berytidae have pubescence on the dorsal surface of apodeme beta base in the posterior mesothorax (Figs. 38, 38b-d). The apodeme is sloped and the pubescence may prevent the posterior mesothoracic phragma from slipping when it touches the apodeme.

In Heteroptera, the first thoracic spiracle is herein renamed spiracle 1, because it may be found in three different locations. Occasionally it occurs on the posterior prothorax (Figs. 3, 4, 39) (Berytidae, Gerridae, Veliidae), the segma coria between the pro-and mesothoraces (Figs. 5, 38, 40, 42) (Tingidae, Largidae, Rhopalidae, Macroveliidae, Pleidae, Habridae, macropterous Mesoveliidae, Alydidae), or the anterior mesothorax (Figs. 6, 26) (Nepidae, Thyreocoridae, Hydrometridae, apterous Mesoveliidae). Reasons for these different positions are uncertain.

Snodgrass (1935), called this spiracle the "first thoracic spiracle," and wrote "the spiracle of the mesothorax, often displaced into the posterior part of the prothorax" $(1935, p$ 191); and, further, that "during development, the meta and mesothoracic spiracles migrate forward and come, thus, to have a definitive position in the secondary intersegmental membranes or in the posterior part of the segment preceding" (1935, p 427). He goes on to write, the mesothoracic spiracles "particularly were subject to this anterior migration and hence often occur in larval or adult insects on the side of the prothorax, for which reason they were frequently called the 'prothoracic' spiracles." By "frequently" he indicated that the spiracle had more than one name. I chose "spiracle 1 " in part to avoid the assignment of a specific segment to the spiracle. Spiracle 2 also may shift position, up and down the posterior mesothorax, but not between segments. I named it spiracle 2 for consistency (Figs. 10, 14, 22, 35).

In Cimicidae, spiracle 1 is a flattened oval tube with its posterior wall fused into the mesothorax while the anterior wall is embedded in the segma coria (Fig. 19). It may be an adaptation for blood feeding by protecting the spiracular opening from variable fluid pressures within thorax.

The spiracles are vestigial in the Nepidae and Belostoma flumineum (Belostomatidae). The dorsal ring of Renatra fusca's (Nepomorpha) anterior mesothoracic ventral bridge's double rings may be a vestigial spiracle 1 (Fig. 15); Nepa apiculata also has what may be a vestigial spiracle -- an oval spiracle 2-like structure ventral to the anterior mesothoracic phragma (Fig. 16). This may also be the true in belostomatids; the posterior mesothoracic ventral bridge extension has a " Y " fork around what may had been spiracle 2 (Fig. 17).

Palisades are located around integument openings (Fig. 40). In pentatomomorphs, palisades are around spiracle 2 (Figs. 29, 38) coxal openings (Fig. 34), and at intersegmental margins (Fig. 40). Palisades are absent in enicocephalomorphs, gerromorphs (except apterous Mesoveliidae), and nepomorphs, and are occasionally seen in cimicomorphs (Fig. 23). Palisades may reduce cuticular weight around integument openings. The Arizona pyrrhocorid has unusual palisades because they are filamentous with one end detached (Figs. 37c-f); they ring spiracle 2 and point into the atrium valve. Perhaps the needle-like palisades with round tips may prevent the atrium valve from touching the endothoracic wall.

The wing muscle opening is the exception. Palisades do not occur around this muscle opening. Stresses in the integument may be high in this region because of flight, so rigidity is a benefit over the flexibility and weight conservation, that palisades may provide.

Coxal openings into the thorax in Heteroptera are variably spaced, a fact apparently not
mentioned elsewhere. Schaefer \& Ahmad (2007) did observe width variability between hind and mid coxae in Alydidae (Burtinus spp.), but spacing between the three coxae was not discussed. Gerridae, for example, are active on water and their coxae II and III are close together, whereas I is separate (Fig 3). This may help with movement on water. Hebridae live in semi-aquatic environments and their coxae I and II are close, but III is separate (Fig. 9). This may provide extra anterior strength for pulling through and clearing away moist detritus at water margins. This doubling of leg pairs may be a mechanism to enhance strength for movement on, in, and around viscous environments. Additionally, Hebridae have $30 \%$ coxal invagination with $30-60^{\circ}$ angle tilt, which may be helpful for pushing (Figs 9-9b). In Nepidae, as in Gerridae, coxae II and III are close, whereas I is considerably separate. This may be an example of adaptation for predation allowing anterior legs greater freedom for snatching pray, while the hind coxae are used for stabilization and securing footholds.

In some phytophagous heteropterans such as Coreidae and Largidae, the three coxae are more evenly spaced, yet the hind two coxae are still slightly closer together than the front coxa which is more separate. Instead of using the forelegs for hunting these insects use them to seek good footholds, and the other coxae are used to secure those footholds (personal observations).

## The Heteropteran Groups

Using 403 states (Appendix 3 ), from the 32 characters (Table 2) a neighbor-joining test of similarity phenogram and bootstrap analysis trees were generated (Figs. $50 \& 51$ ). The neighbor-joining analysis was used because it could analyze large data sets. Other considered programs could not do this easily and were not selected. These were the maximum likelihood and maximum parsimony tests. The fourth program of choice was a basian analysis which was
not available.
The neighbor-joining test of similarity is a visual representation of per cent pairwise differences among all taxa. Each horizontal line represents the degree of change between taxa. On the bottom left of the phenogram (Fig. 50) is a horizontal line followed by " 5 changes." The length of this line representations 5 morphological changes giving a 0.05 pairwise distance between taxa. The 0.05 pairwise distances are cumulative, for example in Nepomorpha a pairing of Nepa apiculata and Ranatra fusca is approximately a 30\% pairwise distance, $20(4 \times$ $0.05)$ for $R$. fusca and $10(2 \times 0.05)$ for $N$. apiculata. These two nepomorphs are in turn approximately a $28 \%$ pairwise distant from Belostoma flumineun and Lethocerus americanus. N. apiculata with the shorter line has less per cent change than $R$. fusca relative to the Belostoma group. What does this mean? B. flumineum and L. americanus have no per cent pairwise distance between them suggesting they are morphologically very similar. N. apiculata has approximately a $30 \%$ pairwise distance while $R$. fusca is closer to a $50 \%$. This suggests $N$. apiculata is morphologically more similar to the belostomatid group than R. fusca. The bootstrap analysis supports a strong relationship in the belostomatid group with a reading of 100; N. apiculata and R. fusca are 70 and between the two groups the reading is 54 . The higher the bootstrap number the stronger the relationship between taxa with 100 as the most significant number. What does this show? A comparison of this result with the cladistic work of Hebsgaard et al. (2004) at the generic level only (because the species he uses are different from those in this study), indicates that the endoskeletal characters have phenotypic and possible cladistic usefulness. Results of his study and this one are almost identical regarding taxonomic relationships. If this is true, then the heteropteran endoskeletal characters may be trusted to
yield good results (Fig. 50). This result also validates species selection for the study, because results of the two studies are compatible.

The phenogram clearly shows species in most families with numerous interspecific similarities. Exceptions are ptergyopolymorphism in Mesoveliidae and high interspecific variability in Reduviidae. Pterygopolymorphism (common in Gerromorpha) dramatically affects the thoracic endoskeleton (Figs. 13, 14). It can confound phenotype analyses, because a single species may contain apterous, brachypterous, and/or macropterous individuals (Schuh \& Slater 1995) which correspondingly affects endoskeletal flight structures. Primary structures affected are the anterior mesothoracic phragma, apodeme alpha, posterior mesothoracic phragma, and apodeme beta (Tables $10-12,16,17,21-23$ ).

Mesovelia mulsanti (Mesoveliidae) was chosen to examine this phenomenon (Figs 13, 14). The posterior and anterior mesothoracic phragma is missing or vestigial in apterous species, but large in macropterous specimens (Figs. 7, 8). The posterior mesothoracic phragma is fused to apodeme beta as a single structure in the macropterous taxa (Figs. 8, 8a). The absence or presence of the phragma seems to relate to flight. In macropterous specimens, it supports musculi mesonoti primus and m. mesonoti secundus. Apodeme alpha is also affected. When the posterior mesothoracic phragma is missing or reduced, the apodeme is vestigial and when the phragma is large, the apodeme is large. Apodeme beta is affected at a more complex level, because of multiple functions. In Heteroptera it opposes, supports, or fuses with the posterior mesothoracic phragma, provides support for ventral thoracic muscles, and is an attachment for apodeme alpha's m. furca-pleuralis.

In pterygomorphic species, these four structures seem to be relatively simple. This may
be because of morphological cycling between apterousness and macropterousness for whatever reason in M. mulsant populations. Galbreath (1975) recognized three thoracic morphs resulting from wing polymorphism in M. mulsanti. What causes these changes is not clear, but Galbreath suggests environmental factors may play a role.

Reduviidae do not have many characters in common. Indeed, Acholla multispinosa and Arilus cristatus (Harpactorinae) more closely resemble Aradidae (Fig. 50). The remaining eight reduviid species in the study group together, but with much interspecific variability (Appendix 4). This variability within the family lends support to suggestions that Reduviidae may not be monophyletic (discussed in Schaefer 2003, 2005). By contrast, the thoracic endoskeleton of all mirids have negligible intraspecific variability, suggesting the family is indeed monophyletic ( Table 8; Carvalho 1957, 1958a,b, 1959, 1960; Henry and Wheeler 1988; Kerzhner and Josifov 1999). Because there are very high levels of similarity among mirid species (Table 8), the neighbor-joining analysis failed by continuously generating trees ad infinitum. Single species were randomly removed, and after 3 were deleted from the data base, the program worked. The removed species were Lygocoris quercalbae, Microphylellus flavipes (Mirinae), and Trigonotylus ruficornis (Orthotylinae).

Cimicomorpha have the highest interspecific variability, followed by Pentatomomorpha, Nepomorpha, Gerromorpha, and Enicocephalomorpha. Leptopodomorpha, although variable, were inconclusive, because they are similar to Nepomorpha, as suggested by Schuh (1979). For a summary account of infraorder traits see "Summary of infraorder traits," under "Results, and some discussion, by taxon."

Many structures in Enicocephalomorpha and Gerromorpha were either small or absent
(Figs. 2-9). Dipsocoromorpha (Miyamoto 1961a; Stys and Kerzhner 1975) and Coleorrhyncha (Schlee 1969; Schuh 1979) were not included in the study because of a lack of specimens. Their inclusion may be important to clarify the situation in the heteropteran infraorders with simple endothoraces, where information from small and reduced structures is poor.

Gerromorpha families fall into two groups: the Veliidae/apterous Mesoveliidae with Gerridae; and Hydrometridae/Hebridae with Pleidae, Macroveliidae, and macropterous mesoveliids (Figs. 50,51). Damgaard et al. (2005) in their molecular studies of Gerromorpha suggest Gerridae and Veliidae have common characters, a fact corroborated here by the endoskeleton. However, although placed together here, Hebridae and Hydrometridae are separated in the molecular studies of Damgaard et al. (2005).

Nepomorpha also fall into two groups, Corixidae and Nepidae/Belostomatidae, and Notonectidae and Naucoridae/Gelastocoridae (Figs. 50, 51). Corixidae are problematic (Rieger 1976; Mahner 1993). Corixids, as bottom feeders, consume primarily algae, with some predation, ans so differ from most nepomorphans (Merritt \& Cummins 1978; Hungerford 1948). The corixid endoskeleton (Fig. 14) differs from that of other nepomorphans (Figs. 10-13 \& 1517). It has a large posterior mesothoracic phragma touching the ventral surface, large anterior mesothroacic phragma, palisades, and a round mushroomlike apodeme alpha resembling the disc/coneshaped heads seen in Pentatomomorpha (Figs. 28, 29, 41). Noncorixid nepomorphans have shortened posterior mesothoracic phragmata, small anterior mesothoracic phragmata (except Nepidae [Figs. 15, 16]), no palisades, and variably shaped apodeme alpha heads (Figs. 12, 13). Also, corixids have many unique endoskeletal characters (Fig. 14, 14a-c. Table 3). Despite these differences, the neighbor-joining phenogram shows many similarities with

Nepidae and Belostomatidae, e.g., ventral keels, large anterior mesothoracic ventral bridge apodemes, etc. (Tables 14, 30). This corroborates Mahner (1993), who places Nepidae, Belostomatidae, and Corixidae phylogenetically close. Rieger (1976), on the other hand, indicates Corixidae is similar to Gelastocoridae and Naucoridae.

Pleidae have been considered the sister taxon to Notonectidae (Hebsgaard et al. 2004). Although similar in form (but smaller), pleids do not posses the oarlike hind legs of notonectids which was one reason they were elevated from subfamily to family level by Esaki and China (1928). Table 4 shows 20 character-state differences between Pleidae and Notonectidae. Many structures are either reduced in size or absent in Pleidae but present and large in Notonectidae. Pleids also have a fused posterior mesothoracic phragma, and in this character they resemble gerromorphs more than they do nepomorphs. Appendix 4 clearly show this, as the transect dots identifying character states change pattern between Pleidae and Notonectidae. Although there are external-morphological (Usinger 1956) and behavioral similarities between Notonectidae and Pleidae (Schuh and Slater 1995) (e.g., inverted swimming positions, rowing, and air sequestration [Gittelman 1974, 1975]), the endoskeleton indicates deep differences between the two families (Appendix 4). Additional complexity in Nepomorpha with the split in the infraorder and a close resemblance of Nepidae and Belostomatidae with Leptopodomorpha, clearly indicates need for further study.

Cimicomorpha are the best represented infraorder in the study. They are morphologically complex with high interspecific variability. Although evidence is weak and not tested, it has been suggested that Reduviidae are not monophyletic (discussed by Schaefer 2003, 2005), and the endoskeletal evidence supports this. Conversely, the species of Miridae are strongly similar
(Fig. 22, $22 \mathrm{a}-\mathrm{d}$ ), numerous species being nearly identical (Table 8)
The phenogram groups Miridae with Reduviidae and Nabidae (Fig. 50). This conflicts with current literature which group Tingidae with Miridae (Schuh \& Stys 1991, Nelson 1973).

An interesting anomaly is the close resemblance of Aradidae (Pentatomomorpha) to the Anthocoridae-Tingidae-Nabidae group. This possibly may be convergence. The infraordinal grouping and status of Aradidae has been much discussed.

Henry (1997) and most earlier authors placed Aradidae in Pentatomomorpha, because of pulvillus structure, tubular salivary glands, egg morphology, and trichophoran-type spermatheca. Henry's cladistic analysis of other Pentatomomorpha (1997) used Aradidae (Aradoidea) as the principal outgroup. Schaefer $(1981,1993)$ suggested Aradoidae might be worthy of infraordinal rank, and placed it as sister-taxon to Cimicomorpha + Pentatomomorpha, based on labrum morphology and behavior. Arguing against Schaefer, Schuh (1996) stated they were pentatomomorphs. Wheeler et al. $(1993)$ concurred with Schaefer. Sweet $(1996,2006)$ provided considerable evidence of the group's infraordinal status. Tables 5 and 6 illustrates this, showing 14 differing character states between Aradidae and Cydnidae/Coreidae, strongly suggesting Aradidae are not pentatomomorphans. Cydnidae were chosen for comparison for two reasons. They are pentatomomorphan pentatomoids, possessing many characters of the group, such as large domed anterior mesothoracic phragma, anterior mesothoracic shelf, posterior mesothoracic phragma touching ventral surfaces, apodeme beta anvilshaped, and thoracic wall and floor smooth. Aradidae have none of these features. Cydnidae are also the pentatomomorphan family most similar to Aradidae (Appendix 2) in this study. Although Cydnidae are pentatomoids, endoskeletal features such as coxal angles from $60^{\circ}$ to $90^{\circ}$ and a moderately thick integument are
not typically found in Pentatomomorpha and so the family occurs between cimicomorphs and the pentatomomorphs in the phenogram (Fig. 50). Coreidae were chosen because they are pentatomomorphans with typical characters of the infraorder, e.g., anvil-shaped apodeme beta base, disc-shaped apodeme alpha, 3-ridge " N " configuration, and triangular posterior mesothoracic phragma.

Phymatidae and Cydnidae show features of both Cimicomorpha and Pentatomomorpha. For example, they both have Pentatomomorpha-like apodemes beta with a large posterior mesthoracic phragma, but the variability of the three ridges and of apodeme alpha, a thick integument, and a large prothorax is Cimicomorpha-like. Of the two, Cydnidae is more a pentatomomorph, whereas Phymatidae is closer to the cimicomorphs (Figs. 25, 25a, 27, 27a).

The Pentatomomorpha families have many common characters, with the least interfamilial variability of any infraorder. States are common to numerous families: anvilshape of apodeme beta base (Fig. 31), discshape apodeme alpha (Fig. 28), the 3-ridge " N " configuration (Fig. 38), triangular posterior mesothoracic phragma (Fig. 41), are typical. More common in pentatomomorphs than in other infraorders are palisades (Fig. 37) and large thoracic wall lobes (Figs. 39, 41). Pentatomomorphs may need cuticular lightness, and a thin integument and palisades to facilitate this.

The phenotypic family groupings of pentatomomorphs in Figure 50 mostly agree with current literature (Schuh 1986, Henry 1997). Figure 50 divides the infraorder into two groups, the Pentatomidae ( 6 families) and Coreidae ( 9 families) groups.
Table 10: Some thoracic endoskeletal characteristics of heteropteran infraorders
Abbreviations: a ms ph - anterior mesothoracic phragma: p ms ph - posterior mesothoracic phragma; a ms vb-anterior mesothoracic

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| Enicocephalomorpha | absent | large | large <br> with <br> keels | small <br> bi-lobed | small <br> filament | small <br> filament | large lobed ap. | small | small | II \& III close; I separate | small | smooth | cunate |
| Gerromorpha | present | absent | small | fused <br> column | small <br> fingerlike | small <br> fingerlike | small lobed ap. | small <br> lobed ap | small <br> round/ova <br> 1 | variable | small | smooth | filiform |
| Nepomorpha | absent | medium to <br> large | large | tubular | variable | variable | variable | small | variable | tilted, up to $90^{\circ}$ | medium to large | smooth | variable |
| Leptopodomorpha | absent | absent | large | triangle | large | filament | small | small | large oval | tilted, up to $90^{\circ}$ | large | smooth | filform |
| Cimicomorpha | absent | variable | variable | triangle | variable | variable disc <br> head, stem, <br> base | variable | variable | variable | II \& III close; I separate | large <br> round | rough <br> lobed | variable |


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| Pentatomomorpha | absent | absent | large | large <br> triangle | disc <br> shaped | disc head, <br> stem, variable base | small | small | large oval | II \& III <br> close $;$ I <br> separate | small | smooth <br> lobed | cunate |

Heteroptera characters shared by other insect groups

Auchenorrhyncha (Figs. 43-46), Diptera (Figs. 48-49), and Hymenoptera (Fig. 47). Auchenorrhyncha, like Heteroptera, vary in
endothoracic complexity, Cicadidae (Fig. 44) being the most complex and Membracidae (Fig. 46) the most simple. Cicadas possess nearly
all heteropteran endoskeletal structures at a level of complexity exceeding that of most heteropterans. There are more structures in the
prothorax than in Heteroptera and the region around spiracle 2 has additional lobes and ridges. Cercopidae (Fig. 43, Table 47) also have
many heteropteran endoskeletal structures, and seem closer in character organization to Heteroptera than do cicadids. For example,

[Fig. 46]). The cercopid apodeme is more dorsal, deeply cupped, and separated from apodeme beta (Fig. 43). The two families least like
Heteroptera are Cicadellidae and Membracidae, although they share many structures with Heteroptera, such as the posterior and anterior
mesothoracic phragmata, ridges 1, 2, and 3, and apodemes alpha and beta. These structures are also found in Hymenoptera and Diptera,
which suggest they occur in many insect orders and are a fundamental ground plan for insects that fly.

Data found in this study indicate that the Auchenorrhyncha do not clearly differ from Heteroptera. This supports the view that the two groups, once considered suborders, are more closely intertwined phylogenetically (Schaefer 1996). Further study and analysis of the auchenorrhynch thoracic endoskeleton is needed, to determine relationships within the Auchenorrhyncha and between its groups and other hemipterans (Fig. 50).

Apodeme alpha seems differently shaped in long-distance flying insects, Diptera and Hymenoptera; it is feathery and either coneshaped in Diptera (Fig. 48) or bladelike in Hymenoptera (Fig. 47). In the Auchenorrhyncha and Heteroptera it tends to be cupped or discshaped with no feathering (Figs. 20, 29, 43, 44).

Apodeme beta also has feathery features in Diptera (Fig. 48) and Hymenoptera (Fig. 47), but in Heteroptera and Auchenorrhyncha it tends to be anvilshaped (Figs. 31, 46) (common in Pentatomomorpha) with various appendages (Figs. 32, 37,44, 46).

The anterior mesothoracic phragma in Diptera (Fig. 48, Table 48) and Hymenoptera (Fig. 47, Table 48) is domed and very similar to that found in Heteroptera and Auchenorrhyncha, as is the posterior mesothoracic phragma, which is either fused to the ventral surface in Diptera or is a broad sheet of cuticle in Hymenoptera. The dipteran (Tabanidae) endothorax is the most complex of all the specimens examined in this study, with many additional lobes, plumose filaments, and an apodeme beta rich with features. The vespid endothorax on the other hand, is relatively simple, but differs in that the prothorax is inserted into the mesothorax as a wedge.

The Tabanidae endothorax is similar to that of Heteroptera, but ornamented with featherlike tufts (also seen in Vespidae) attached to apodeme alpha, ridge 2, and other structures. The thoracic dorsal wall in Diptera and Hymenoptera have ladyfinger shaped rows and patches of pubescence for
possible thermoregulation in flight. The tabanid posterior mesothoracic phragma and apodeme beta are different. The phragma is fused to the mouth of a large cornucopia-shaped apodeme beta. The mouth faces posteriorly whereas the rest of the apodeme lies along the thoracic floor narrowing anteriorly to a point. Tabanidae also have a mesothoracic ventral keel with a large dorsal apodeme.

What is highly significant is finding that more distantly related groups, e.g., Diptera and Hymenoptera, share characters found in Heteroptera; that the basic structures for flight, the anterior and posterior mesothoracic phragmata and apodemes alpha and beta, may have evolved relatively early in flying insects. The study of ptergopolymorphic species may increase an understanding of the apterous and macropterous processes, which may be helpful in studies of flightless insects. Although speculative, because flightless insects were not examined in this study, and only 3 species from Gerridae and Mesoveliidae with ptergoploymorpgism were examined, it is certainly an observation worthy of further study.

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| oun |  | $m$ |  | $m$ | $\cdots$ | c． | $\cdots$. | 6. | $\cdots$ |
| M1 |  | $\nabla$ |  | $\nabla$ | ナ | ナ | $\nabla$ | $\nabla$ | $\checkmark$ |
| $\ddagger$ |  | $\nabla$ |  | $n$ | $\checkmark$ | $\checkmark$ | $\checkmark$ | $\nabla$ | $\checkmark$ |
| ds |  | $n$ |  | $n$ | $n$ | $n$ | $n$ | $n$ | $n$ |
| $\mathcal{E}$ J |  | N |  | N | N | N | N | N | N |
| Z．I |  | N |  | N | N | N | N | N | N |
| ［．I． |  | N |  | N | $N$ | N | N | N | N |
| q $\wedge$ suod |  | － |  | － | $\cdots$ | $\square$ | $\square$ | － | $\square$ |
| ju पd su d |  |  |  |  |  |  |  |  |  |
| yd suld |  | N |  | N | － | N | N | 6 | $\bigcirc$ |
| －q＾ұ $\downarrow$ |  | N |  |  | N | m | m |  |  |
| de q＾$\downarrow$ ¢ |  | N |  | N |  |  |  |  |  |
| qı $\ddagger$ U |  | N |  | N | N | N | N | N | N |
| qde |  | in |  | $\nabla$ | $\nabla$ | ナ | $\nabla$ | $\nabla$ | $\nabla$ |
| ede |  | $\checkmark$ |  | $\nabla$ | $\nabla$ | ナ | $\nabla$ | － | $\nabla$ |
| ys suie |  | － |  | $\square$ | － |  |  |  |  |
| dequ sume |  |  |  | N | N |  |  | N | N |
| qı suie |  | N |  | N | N | N | N | N | N |
| de $\wedge$ yd sume |  |  |  |  |  |  |  |  |  |
| yur yd sur e |  |  |  |  |  |  |  |  |  |
| YI Yd sure |  | m |  | m |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  | Tibicen canicularis（Cicadidae） |  |  |  |  |

LEZ
Table 12: Heteropteran characters shared by Tabanus sulcifrons (Tabanidae: Diptera) and Vespula maculifrons (Vespidae: Hymenoptera)
as shown by transect dots.


## Conclusion

This preliminary study had two goals: To determine if the structures of the heteropteran thoracic endoskeleton might be useful in systematic work (and at what systematic levels), and to standardize nomenclature of those structures. Both goals were reached: These structures were systematically useful at several taxonomic levels; and their nomenclature has been standardized, thus making comparative studies feasible.

Many questions were raised in the course of the study, primarily because this is the first one of its kind. In the past, the insect endoskeleton was mostly ignored because early morphologists worked in orders such as Blattària and Orthoptera with apparently simple endoskeletons. This may have led to the belief that endoskeletons had no systematic value. The purpose of the study was to determine if this is true for Heteroptera. It is not.

In the endoskeleton of the Heteroptera there is bilateral symmetry, no sexual dimorphism, and a single species often can represent a family. Exceptions were Reduviidae, Aradidae, and ptergopolymorphic families such as Mesoveliidae.

178 heteropteran species from 6 suborders and 39 families yielded 32 characters and 403 states, demonstrating that the thoracic endoskeleton, in particular that of the mesothorax, is a rich and morphologically diverse region. Additionally, five families from Auchenorrhyncha and two each from Hymenoptera and Diptera had numerous endoskeletal features like those of Heteroptera, suggesting these characters may have value in similar studies on other insect orders.

The neighbor-joining phenogram (Fig. 50) of course is not a phylogenetic sequence, yet it clearly supports the order of infraorders and many family groupings generated cladistically by others.

This agreement (and occasional disagreement, e.g., in Reduviidae, Aradidae, Mesoveliidae, and Pleidae) indicates the characters presented here can be useful in cladistic studies.

The positions of some families in the phenogram diverged from current literature. Two infraorders showed division (Nepomorpha and Pentatomomorpha) and some families had unusual morphologies, warranting further investigation. Aradidae more closely resembled Cimicomorpha than Pentatomomorpha, with enough variability to strongly suggest it be a separate infraorder, supporting Sweet's $(1996,2006)$ position. Pleidae were more like Gerromorpha than Nepomorpha (Figs. 10, 11). Corixidae, although nepomorphan, showed enough morphological difference to warrant further investigation (Fig. 14); Phymatidae and Cydnidae showed features of both Cimicomorpha and Pentatomomorpha (Figs. 25, 27); and Reduviidae were unresolved.

This study of heteropteran endoskeleton has shown some heretofore unknown features of interest: different body cavity sizes presumably to assist blood feeding in Cimicidae and triatomines (Reduviidae) (Figs. 19, 24c); specific glandular structures in Anthocoridae (Fig. 20); palisades for weight reduction while maintaining strength (Figs. 29, 30, 37) and keels to enhance strength (Figs. 14, 22); pubescence in Naucoridae and Blissidae (Figs. 12, 42), Hymenoptera (Fig. 47) and Diptera (Fig. 48), perhaps for heat regulation; and the variable locations of spiracle 1 (Figs. 3, 6, 22). These and other features help define a region of high dynamic complexity that has long been understudied.

## Glossary

| Anvil-shaped | The shape of a blacksmith's anvil; base (manubrium) broad with dorsal |
| :--- | :--- |
| anterior and posterior extensions (arms) in "T" configuration. Seen |  |
| with apodeme beta and anterior mesothoracic ventral bridge apodemes. |  |
| Apodeme | Any inner projection of cuticle used for muscle attachment that does not |
| proceed along the endoskeletal surface linearily. Structure usually |  |
| hollow. |  |
| Apophysis | In the endoskeleton, a projection of cuticle either tubular or spinelike |
| originating from another endoskeletal structure. Usually solid. |  |
| Arms | Fingerlike or filamentous dorsal anterior and posterior extensions of |
| anvilshaped apodeme beta. |  |
| Bridge | In Heteroptera a linear arched invagination of cuticle between two |
| points of articulation in the thorax, e.g., the coxae. It can also be a |  |
| Character state | thickening of the cuticle. Function to provide additional rigidity to |


| Contour | The silhouette of the thorax. |
| :--- | :--- |
| Coxal angle | The degree of angle from the vertical that a coxa is tilted anteriorly |
| relative to the thorax. |  |
| Crown | The dorsal and usually the widest third of the posterior mesothoracic |
| phragma that fuses with the dorsad of the thorax. |  |
| Cunate | Wedge-shaped, elongate-triangular shape. |
| Filiform | Long, slender, parallelsided, cylindrical shape. |
| Fur ventral tip of the posterior mesothoracic phragma which have many |  |
| different shapes, e.g., bulbous, scallop-shell shaped, pointed, hooked, |  |
| etc. |  |
| A forklike ventral inner projection of the integument, consisting of a |  |
| median base (manubrium) that divides dorsally into two opposing |  |


| Lobe | Domelike structure on thoracic wall and/or floor, e.g., Berytidae, |
| :---: | :---: |
|  | Blissidae. |
| Meander | Some ridges may wind, turn, or wander along a course, e.g., |
|  | Scutelleridae metathoracic ventral bridge extension. |
| Occipital condyle | Posterior extension of head capsule into prothorax as variously shaped |
|  | spine, e.g., Veliidae, Gerridae. |
| Phragma | Invagination of dorsal thoracic integument to accommodate flight |
|  | muscles. Variable in size and shape. |
| Pit | Depression in cuticle, e.g., Mesoveliidae. |
| Pore | Small raised domelike lobe with medial hole, on thoracic wall and/or |
|  | floor, e.g., Miridae. |
| Primary ridge | A ridge which is common and phenotypically informative. |
| Pyriform | Pear-shaped, globose-shaped. |
| Ridge | A linear inner projection or fold of integument, progressing along |
|  | endoskeletal surface. |
| Scimitarshaped | Resembling a saber with a curved blade. |
| Secondary ridge | A ridge which is usually a specific feature for one or two families and is |
|  | uncommon, e.g., Rhopalidae. |
| Segma coria | Thin membranous cuticle used for intersclerite expansion, contraction |
|  | and flexing. Spiracle 1 is commonly found in the segma coria between |
|  | the pro and mesothoracic segments in Heteroptera |
| Shaft | The medial third of the posterior mesothoracic phragma joining the |

Stem

Thoracic contour
Tongue of cuticle

## Window

crown with the foot.
Usually a thin rod of cuticle connecting the base with the head of apodeme beta.

In cross section, the profile or silhouette of the thorax.
Usually a rectangular flap of cuticle on either the thoracic wall or floor, e.g. Pleidae. Function undetermined.

A hole in a sheet or uniform area of cuticle to probably reduce weight while maintaining strength. Seen in posterior mesothoracic phragma lateral arch region, e.g., Nabidae and Miridae.

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## Appendix one

List of families and species, with collection locations. Unless otherwise stated, one specimen was examined from each species.

## HETEROPTERA

## Enicocephalomorpha

## Enicocephalidae

Sp . (undetermined)
Enicocephalinae
Hymenocoris formicinia Uhler
Tanzania
2 specimens
California
2 specimens
Gerromorpha

| Gerridae |  |  |
| :---: | :---: | :---: |
| Gerrinae |  |  |
| Gerrini |  |  |
| Gerris nyctalis Drake \& Hottes | Washington State | 2 specimens |
| Aquarius remigis (Say) | Minnesota, Wyoming, |  |
|  | Connecticut | 3 specimens apterous |
| Aquarius remigis (Say) | California | macropterous |
| Gerris insperatus Drake \& Hottes | Connecticut | macropterous |
| Limnoporus canaliculatus (Say) | Connecticut |  |
| Limnoporus notabilis (Drake \& Hottes) | Washington State | 2 specimens |
| Halobates robustus Barbe | Galapagos islands (Equador) | 2 specimens |
| Rhagodotarsinae |  |  |
| Rheumatobates palosi Blatchley | Minnesota |  |
| Veliidae |  |  |
| Microvelinae |  |  |
| Microveliini |  |  |
| Microvelia americana (Uhler) | Connecticut |  |
| Microvelia californiensis McKinstry | Oregon |  |
| Rhagoveliinae |  |  |
| Rhagovelia distincta Champion | Connecticut, Oregon | 2 specimens |
| Rhagovelia obesa Uhler | Connecticut |  |


| Macroveliidae <br> Macrovelia hornii Uhler <br> Hydrometridae <br> Hydrometrinae <br> Hydrometra martini Kirkaldy <br> Hydrometra stagnorum (Linnaeus) <br> Mesoveliidae <br> Mesoveliinae <br> Mesovelia furcata Mulsant \& Rey | Oregon | 2 specimens |
| :--- | :--- | :--- |
| Mesovelia mulsanti White | England |  |
| Mesovelia mulsanti White | Italy | 2 specimens |
| Hebridae | Connecticut,Oregon | 2 specimens |
| Hebrinae <br> Hebrus buenoi Drake \& Harris <br> Hebrus burmeisteri Lethierry \& Severin | Connecticut | macropterous |
| Connecticut | apterous |  |

Corixini
Callicorixa alaskensis Hungerford Inner Hebrides, Scotland
Callicorixa wollastoni (Douglas \& Scott) Inner Hebrides, Scotland
Hesperocorixa atopodonata (Hungerford) Connecticut
Hesperocorixa interrupta (Say) Connecticut
Hesperocorixa sp. Kirkaldy
Trichocorixa louisianae Jaczewski
Tropocorixa meridonalis Hutchinson
California
Florida
South Africa
Nepidae
Nepinae
Nepini
Nepa apiculata Uhler Minnesota
Ranatrinae
Ranatra fusca Palisot Minnesota

## Belostomatidae

Belostomatinae
Belostoma flumineum Say Connecticut
Lethocerinae
Lethocerus griseus (Say)
Connecticut
Lethocerus americanus (Leidy)
Connecticut

## Leptopodomorpha

## Saldidae

Chiloxanthinae
Pentacora hirta (Say) Connecticut 2 specimens
Pentacora sphacelata (Uhler)
Connecticut
Saldinae
Saldoidini
Saldula saltatoria (Linnaeus)
Connecticut

## Cimicomorpha

| Cimicidae |  |  |
| :--- | :--- | :--- |
| Cimicinae |  |  |
| Cimex lectularius Linnaeus |  |  |
| Oeciacus vicarious Horvath |  |  |$\quad$ Connecticut $\quad$ specimens

## Nabidae

Nabinae
Nabiini
Nabicula subcoleoptrata Kirby Connecticut
Nabis rufusculus Reuter Connecticut
2 specimens
Nabis americoferus Carayon
Canada
Miridae
Mirinae
Mirini
Adelphocoris lineolatus(Goeze) Connecticut
Capsus ater (Shilling)
Coccobaphes frontifer Walker
Connecticut
Lygidea mendax Reuter
Connecticut
2 specimens
Lygidea rosacea Reuter
Connecticut
2 specimens
Lygocoris pabulinus Linnaeus
Lygocoris quercalbae (Knight)
Minnesota
Connecticut
2 specimens
Connecticut
2 specimens
Lygus lineolaris (Palisot de Beauvois)
Poecilocapsus lineatus (Fabricius)
Tropidosteptes amoenus Reuter
Tropidosteptes cardinalis Uhler
Connecticut
Connecticut
2 specimens

Tropidosteptes palmeri (Reuter)
Resthenini
Prepops fraternus (Knight)
Prepops insitivus (Say)
Prepops nigricollis (Reuter)
Connecticut
Connecticut
2 specimens
Connecticut
4 specimens

Mirinae
Stenodemini
Collaria oculata (Reuter)
Leptopterna dolabrata (Linnaeus)
Trigonotylus ruficornis (Geoffroy)
Pennsylvania
Connecticut
Connecticut
2 specimens

Orthotylinae
Orthotylini
Inacora malina (Uhler)
Ceratocapsus modestus (Uhler)
Lopidea caesar (Reuter)
Lopidea media (Say)
Lopidea robiniae (Uhler)
Connecticut
2 specimens
Connecticut
Connecticut
2 specimens

Melanotrichus flavosparsus Carvalho \& Afonso Connecticut
Pseudoxenetus regalis (Uhler
Orthotylus cruciatus Van Duzee
Connecticut
Connecticut
2 specimens

Slaterocoris atritibialis (Knight)
Connecticut
Bryocorinae
Dicyphini

| Dicyphus rubi Knight | Massachusetts, Connecticut | 2 specimens |
| :---: | :---: | :---: |
| Bryocorini |  |  |
| Monalocoris americanus Wagner \& Slater | Connecticut | 2 specimens |
| Phylinae |  |  |
| Phylini |  |  |
| Atractotomus mali (Meyer-Dür) | Connecticut | 2 specimens |
| Lopus decolor (Fallén) | Connecticut | 2 specimens |
| Plagiognathus albatus (Van Duzee) | Connecticut | 2 specimens |
| Plagiognathus obscurus Uhler | Connecticut | 2 specimens |
| Plagiognathus politus Uhler | Connecticut | 2 specimens |
| Microphylellus flavipes Provancher | Connecticut |  |
| Hallodapini |  |  |
| Orectoderus obliquus Uhler | Connecticut |  |
| Pilophorini |  |  |
| Pilophorus laetus Heidemann | Connecticut | 2 specimens |
| Tingidae |  |  |
| Tinginae |  |  |
| Tingini |  |  |
| Corythucha caryae caryae Bailey | Massachusetts |  |
| Corythucha marmorata (Uhler) | Connecticut |  |
| Corythucha pergandei Heidemann | Massachusetts |  |
| Gargaphia angulata Heidemann | Massachusetts |  |
| Melanorhopala clavata (Stål) | Connecticut |  |
| Reduviidae |  |  |
| Harpactorinae |  |  |
| Acholla multispinosa (DeGeer) | Connecticut |  |
| Arilus cristatus (Linnaeus) | Connecticut |  |
| Pselliopus cinctus (Fabricius) | Connecticut |  |
| Sinea diadema (Fabricius) | Connecticut | 2 specimens |
| Zelus exsanguis Stål | Connecticut |  |
| Peiratinae |  |  |
| Melanolestes picipes (Herrich-Schaeffer) | Connecticut |  |
| Reduviinae |  |  |
| Reduvius personatus (Linnaeus) | North Carolina |  |
| Stenopodainae |  |  |
| Sp. (undetermined) Amyot \& Serville | Florida |  |
| Triatominae |  |  |
| Triatoma dimidiata Latreille | Guatemala |  |
| Rhodnius prolixus Stål | Guatemala | 2 specimens |
| Phymatidae |  |  |
| Sp . (undetermined) | Brazil |  |
| Sp. (undetermined) | Texas |  |
| Sp . (undetermined) | Massachusetts |  |

## Pentatomomorpha

## Aradidae

Aradinae
Aradus sp. Spinola
Aradus crenatus Say
Aradus quadrilineatus Say
Aradus robustus robustus Uhler
Aradus similis Say
Mezininae
Mezira sp. Amyot \& Serville
Cydnidae
Amnestus sp.
Sp . (undetermined
Sp. (undetermined)
Costa Rica
Indiana
Texas, Connecticut 2 specimens
Connecticut
Connecticut

Pentatomidae
Edessinae
Edessa sp. Fabricius
Brazil
Pentatominae
Halyini
Brochymena arborea (Say)
Connecticut
Pentatomini
Acrosternum hilare (Say)
Codophila sp. Mulsant \& Rey
Mormidea lugens (Fabricius)
Scutelleriday
Eurygastrinae
Eurygaster alternata (Say) Connecticut
Pachycorinae
Homaemus aeneifrons (Say)
Connecticut

## Acanthosomatidae

Acanthosomatinae
Elasmostethus cruciatus (Say)
Elasmucha lateralis (Say)
Tessaratomidae
Tessaratoma javanica (Thunberg)
Thyreocoridae
Galgupha aterrima Malloch
Galgupha atra Amyot \& Serville
Galgupha sp. (undetermined)
Galgupha sp. (undetermined)
Parastrachiidae
Parastrachia japonensis (Scott)
New Hampshire
Alaska

India

Connecticut
Connecticut
Florida
Colorado

Japan

## Coreidae

Coreinae
Acanthocephala terminalis (Dallas)
Ohio, Maryland
2 specimens
Anisoscelidini
Leptoglossus corculus (Say)
Leptoglossus occidentalis Heidemann
Leptoglossus phyllopus (Linnaeus)
Hygia opaca Uhler
Petillia calcar Dallas
North Carolina
2 specimens
Connecticut, North Carolina
4 specimens

Coreini
Anasa tristis (DeGeer)
Connecticut
Japan
Arizona

Nematopodini
Thasus gigas (Klug)
Connecticut
80 specimens

Thasus neocalifornicus Brailovsky \& Barrera California
Alydidae
Alydinae
Alydus eurinus (Say)
Connecticut
3 specimens
Alydus pilosulus Herrich-Schaeffer
Connecticut
2 specimens
Megalotomus quinquespinosus (Say)
Connecticut
Rhopalidae
Rhopalini
Liorhyssus hyalinus (Fabricius)
Korea
Liorhyssus hyalinus (Fabricius)
Arizona
Pyrrhocoridae
Odontopus nigricornis Stål
Dysdercus sp. Guérin-Méneville
India
Dysdercus sp. Guérin-Méneville
Arizona
Largidae
Larginae
Largus sp. Hahn
Largus. sp. Hahn
Largus sp. Hahn
Physopelta analis (Signoret)
California

Berytidae
Metacanthinae
Jalysus sp. Stål
Jalysus spinosus (Say)
Jalysus wickhami Van Duzee
Berytinus sp. Kirkaldy
Lygaeidae
Lygaeus kalmii Stål
Oncopeltus fasciatus (Dallas)
Rhyparochromidae

| Myodocha serripes Oliver | Connecticut | 2 specimens |
| :---: | :---: | :---: |
| Blissidae |  |  |
| Ischnodemus bosqui (Slater \& Wilcox) | Brazil |  |
| Auchenorrhyncha |  |  |
| Cercopidae |  |  |
| Philaenus spumaria (Linnaeus) | Connecticut |  |
| Cicadidae |  |  |
| Tibicen canicularis (Harris) | Connecticut | 2 specimens |
| Cicadellidae |  |  |
| Graphocephala coccinea (Forster) | Connecticut |  |
| Helochara communis Fitch | Connecticut |  |
| Membracidae |  |  |
| Campylenchia latipes (Say) | Connecticut |  |
| Stictocephala lutea Kopp \& Yonke | Connecticut |  |
| Ceresa bubalus Fabricius | Connecticut |  |
| HYMENOPTERA |  |  |
| Anthophoridae |  |  |
| Xylocopa virginica (Linnaeus) | Connecticut 9 |  |
| Vespidae |  |  |
| Polistes sp. Latrielle | Connecticut ${ }_{\text {P }}$ |  |
| Vespula maculifrons Brysson | Connecticut ${ }_{\text {+ }}$ | 3 specimens |
| DIPTERA |  |  |
| Tabanidae |  |  |
| Tabanus sulcifrons Macquart | New York State |  |
| Calliphoridae |  |  |
| Phormia regina (Meigan) | Connecticut |  |

## Appendix two

## Characters, character subset, and states used in phenogram

## Anterior mesothoracic phragma

1

2

3

4

5
Cuticle density: 0 thin; 1 thick; 2 anterior thinning of cuticle

## Anterior mesothoracic phragma lateral keel

6
7

8

## Anterior mesothoracic phragma medial keel

10
Size: 0 absent; 1 small; 2 large
Modification: 0 finlike; 1 bladelike; 2 scimitarshape

Anterior mesothoracic phragma ventral apodeme

11

12

Size: 0 absent; 1 present
Modification: 0 filament; 1 fingerlike; 2 cupped;
3 peglike; 4 hooked; 5 lobed

## Anterior mesothoracic ventral bridge

13
14
Size: 0 absent; 1 small; 2 large
Modification: 0 square; 1 round; 2 arching; 3
bladelike; 4 flat; 5 double rings of cuticle; 6 narrow

Anterior mesothoracic ventral bridge apodeme
15

16
Size: 0 absent; 1 small; 2 large; 3 extremely large

Modification: 0 lobed; 1 fingerlike; 2 filament; 3 square-shape; 4 anvil-shape; 5 spinelike; 6 toothlike; 7 hooked; 8 square; 9 flat

## Anterior mesothoracic shelf

17

## Apodeme alpha

18

19

Size: 0 absent; 1 small; 2 large
Modification: 0 short fingerlike; 1 long fingerlike; 2 filament; 3 square; 4 lobes variously shaped; 5 bladelike; 6 tonguelike; 7 head with ventral spine; 8 hooking

## Apodeme beta

22
23

Size: 0 absent; 1 present
Modification: 0 fingerlike; 1 hooked; 2 filament
Base modification: 0 anvil-shape; 1 square; 2
saddle-shape; 3 domed; 4 triangular; 5 small; 6 dorsally flat

Head modification: 0 absent; 1 cone-shape; 2 arrow-shape; 3 disc-shape; 4 flat; 5 funnelshape; 6 fan-shape; 7 3-cornered star-shape; 8 featherlike; 9 scallop-shape

Contact with other structures: 0 p ms ph foot touching apodeme dorsum; 1 pms ph foot touching apodeme dorsum; 2 p ms ph foot fusing with apodeme dorsum

## Metathoracic ventral bridge

27
28

## Metathoracic ventral bridge apodeme

## Metathoracic ventral bridge extension

Size: 0 absent; 1 small; 2 large
Modification: 0 domed; 1 with dorsal ridge; 2 arching; 3 with extension; 4 flat; 5 broad; 6 fusing with bladder

Size: 0 absent; 1 small; 2 large
Modification: 0 triangular, 1 hooking; 2 toothlike; 3 ring-shape; 4 fingerlike; 5 filamentous; 6 saddle-shape; 7 C-shape; 8 rectangular; 9 anvil-shape;

Ornamentation: 0 with palisades; 1 with filaments; 2 with additional lobes/apodemes; 3 fusing with apodeme beta or posterior coxa II Head modification: 0 pointed; 1 bulbous; 2 posterior arm snakelike; 3 scoop-shape; 4 square

Size: 0 absent; 1 small; 2 large
Modification: 0 curving; 1 flat; 2 meandering; 3
triangular; 4 crescent-shape; 5 dog bone-shape; 6 linear

Ornamentation: 0 with folds; 1 fusing with
segma coria; 2 with palisades; 3 lobed; 4 fusing with ridges

## Posterior mesothoracic phragma: shape and arch (subset)

36
37

38

39

## Posterior mesothoracic phragma: dorsal structures and foot (subset)

Size: 0 absent; 1 small; 2 large
Modification: 0 triangular; 1 tubular-shape; 2 hourglass-shape; 3 column; 4 rounded; 5 divided into more than one structure; 6 nearly rectangular Fusing: 0 fusing with ventral surfaces; 1 touching ventral surfaces; 2 fusing with ventral surfaces

Lateral arch: 0 absent; 1 present; 2 with extension; with apodeme

Crown: 0 wide; 1 narrow
41

42

43
40
 trough or rugose region; 2 with lateral window; 3 multiple lobes

Flat foot shapes: 0 absent; 1 round; 2 pointing; 3 scoop-shape; 4 boat-shape; 5 scallop-shape; 6 spoon-shape; 7 dorsoventrally straight sided; 8 variable

Round foot shapes: 0 absent; 1 bulbous; 2 knob-
shape; 3 club-shape; 4 humanlike foot-shape; 5 with posterior hook; 6 with semi-circular anterior frill; 7 hooking; 8 variable

## Posterior mesothoracic phragma medial ridge (subset)

44
45

## Posterior mesothoracic ventral bridge

46
47

48

## Ridge 1

Size: 0 absent; 1 small; 2 large
Modification: 0 suture; 1 medial trough; 2 domed; 3 with folds; 4 linear; finlike

Size: 0 absent; 1 small; 2 large
Modification: 0 linear; 1 dividing; 2 square; 3
short; 4 arching; 5 slightly round; 6 broad; 7 triangular

Ornamentation: 0 with palisades; 1 with dorsal ridge; 2 with lobes; 3 with extension; 4 spooonshape extension

Size: 0 absent; 1 small; 2 large
Modification: 0 linear; 1 fusing with other ridges; 2 lobed; 3 anterior arm of 3 ridge " N " configuration; 4 flat; 5 narrow; 6 curving; 7 lobe; 8 anterior arm of 3 ridge triangle formation; 9 anterior arm of 3 ridge fan configuration

## Ridge 2

## Ridge 3

## Spiracle 1

## Spiracle 2

Size: 0 absent; 1 small; 2 large
Modification: 0 linear, 1 fusing with other ridges; 2 trough; 3 lobed; 4 medial arm of 3 ridge " $N$ " configuration; 5 flat; 6 posterior arm of 3 ridge triangle formation; 7 curving; 8 with hook; 9 medial arm of 3 ridge fan configuration

Size: 0 absent; 1 small; 2 large Modification: 0 linear; 1 fusing with other ridges; 2 lobed; 3 posterior arm of 3 ridge " N " configuration; 4 flat; 5 bladelike; 6 ventral arm of 3 ridge triangle formation; 7 curving; 8 with hook; 9 posterior arm of 3 ridge fan configuration Modification: 0 oval; 1 round; 2 rectangular

Size: 0 absent; 1 small; 2 moderately small; 3 moderately large; 4 large; 5 extremely large

58
59

## Thoracic floor

60
61

62
63

64

65
66

67
68

## Thoracic wall modifications

69

## Thoracic wall

Position: 0 ventral; 1 lateral; 2 dorsal
Modification: 0 round; 1 oval; 2 cone-shape; 3 slit; 4 ballooned trachea

Surface: 0 smooth; 1 rough
Lobes: 0 absent; 1 small; 2 large; 3 with folds
Pores: 0 absent; 1 small; 2 large
Pits: 0 absent; 1 present
Modification: 0 with keel; 1 with tongue; 2 ventral linear ridges

Surface: 0 smooth; 1 rough
Lobes: 0 absent; 1 small; 2 large; 3 with folds; 4 elongate; 5 contiguous; 6 lobes separate Pores: 0 absent; 1 small; 2 large; 3 variable Pits: 0 absent; 1 present; 2 variable

Modification: 0 with tongue; 1 with secondary ridges; 2 patterned pubescence; 3 with glands; 4 with cavity(ies); 5 with $90^{\circ}$ angle; 6 with dorsal star configuration; 7 with narrow additional ridge; 8 with broad additional ridge

## Wing muscle opening

70
71

72

## Coxae

## Exoskeleton

77

Size: 0 absent; 1 small; 2 large
Modification: 0 round; 1 rectangular; 2 oval; 3 triangular; 4 with reduced tooth; 5 square Position: 0 ventral; 1 lateral; 2 dorsal; 3 very dorsal; 4 ?; 5 concealed by other structures

Invagination: $00-30^{\circ} ; 130-60^{\circ} ; 260-80^{\circ} ; 3$ variable

Cuticle density: 0 thin; 1 moderately thin; 2 moderately thick; 3 thick; 4 very thick; 5 thick ventrally, thin dorsally; 6 thin ventrally, thick dorsally; 7 distinct regions near coxae, very thick

## Prothorax

Size: 0 small; $11 / 3$ size of mesothorax; $21 / 4$ size of mesothorax; $31 / 2$ size of mesothorax; $43 / 4$ size of mesothorax; 5 same size as mesothorax Modification: 0 dorsoventrally compressed; 1 necklike; 2 with apodemes and lobes; 3 square; 4 dorsoventrally rectangular; 5 round

## Thorax contour

81
Cunate shape: 0 slight posterior narrowing; 1 acute posterior narrowing; 2 acute posterior broadening; 3 slight posterior broadening

82

83

84

## Extra characters

85

Filiform shape: 0 filiform; 1 slight posterior broadening; 2 slight posterior narrowing; 3 anterior narrowing Oval shape: 0 oval; 1 oval, at widest point fusing with abdomen; 2 oval, prothorax filiform Round and Pyriform shapes: 0 round; 1 round, at widest point fusing with abdomen; 2 pyriform, dorsally flat

Spiracle 1 ornamentation: 0 without palisades; 1 with palisades

Spiracle 2 ornamentation: 0 without palisades; 1 with palisades; 2 filamentlike palisades Spiracle 1 location: 0 fusing with segma coria; 1 fusing with anterior mesothorax; 2 fusing with posterior prothorax

Spiracle 2 orientation: 0 vertical; 1 horizontal; 2 semihorizontal
274
Appendix three
Character state matrix
The data matrix is unaltered from original version, except for italicizing of species names. Following some species, locations and
macropterous or apterous states are recorded.
Location abbreviations are: AZ Arizona; CA California; CO Colorado; CT Connecticut; FL Florida; MI Michigan; MN Minnesota;

[^0]\#Nexus begin data;
dimensions ntax $=159$ nchar $=89$;
format datatype=standard symbols="0123456789" gap=- interleave;
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Gerris_remigis_CA_macro
Halobates_robustus
Limnoporus_canaliculatus
Limnoporus_notabilis
Rheumatobates_palosi
Microvelia_americana

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| 12112200-0-1129023681-01122292125-22111-4-0-25420102511100000000000011520-0102 |

Microvelia_californiensis
Rhagovelia_distincta
Rhagovelia_obesa
Macrovelia_hornii
Hydrometra_martini
Hydrometra_stagnorum
Mesovelia_furcata_apt
Mesovelia_mulsanti_OR_CTapt
Mesovelia_mulsanti_CT_macro
Hebrus_buenoi
Hebrus_burmeisteri
Neoplea_striola
Paraplea_puella
Notonecta_undulata
Np._CT
Neta_irrorata
Nata

## N

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# Pelocoris_femoratus 

Pelocoris_femoratus
Gelastocoris_oculatus
Nerthra_hapaeformis
Gelastocoridae_sp_CT
Callicorixa_alaskensis
Callicorixa_wollastoni
Hesperocorixa_atopodonata
Hesperocorixa_interrupta
Hesperocorixa_sp
Retrocorixa_semistriata_UK
Tropocorixa_merdionalis
Trichocorixa_louisianae
Nepa_apiculata
Ranatra_fusca
Belostoma_flumineum
Lethocerus_americanus
$\stackrel{\infty}{N}$
100100001211161602138124801424-10--20011--41114-262727104110000-0000-25142022033-0--0---0
100100001211161602678124801424-10--20011-4-1414-262727114110000-0000-25142022033-0-0-00
$100100001211161602678124801424-10--20011-4-1314-262727114110000-0000-25142022033-0-0-00$
100100000-130-0-01510104001424-2410------0-15-0-0-0-301010000-000040--42023233-1--00002
100100000---0-0-00-00104000-0---2410-------0-0-0-0-0-301010000-000040-----3233-1-0000-

200100000-0-110-02482124102421-0--2001113-132411610101111100000000031-510-324240---0000
210100000-0-110-02468124102121--0--20011-3-1424116101011111000000400-12221-310243----0000 000)
20010120120-0-0-02678124102521--10-2001123-0-14-131413221111000-1000-10540-01353-1--0000
10010120120-0-0-02473124102221-21-2001123-0-14-131413221111000-1000-10540-01353-0---0000

20010211210-0-0-02473120301421--1212001124-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120301421-1212001124-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120301421--1212001124-2414-11111140411000000000610540-00033--2-0002
20010211210-0-0-02473120301421--1212001124-2414-11111140411000000000610540-00033---2-0002

Pentacora_hirta
Pentacora_sphacelata
Saldula_saltatoria
Cimex_lectularius
Oeciacus_vicarious
Orius_insidiosus
Anthocoridae_sp_Israel
Anthororidae_sp_NV
Nabis_rufusculus
Nabicula_subcoleoptrata
Adelphocoris_lineolatus
Capsus_ater
Collaria_oculata
Inacora_malina
Leptopterna_dolabrata
Cophes_frontifer
Cora

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20010211210-0-0-02473120301421--1212001123-2414-111111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--121200112-22414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--121200112-12414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--1212001123-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--1212001123-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--1212001122-2414-111111140411000000000610540-00033---2-0002
20010211210-0-0-02473120301421--121200112-42414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120301421--1212001124-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120301421--1212001123-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--1212001124-2414-11111140411000000000610540-00033---2-0002

20010211210-0-0-02473120301421--1212001123-2414-111111140411000000000610540-00033---2-0002
20010211210-0-0-02473120101421--1212001123-2414-111111140411000001000610540-00033---2-0002
20010211210-0-0-02473120101421--1212001123-2414-11111140411000000000610540-00033---2-0002
20010211210-0-0-02473120301421--1212001123-2414-11111140411000000000610540-00033---2-0002


| Lygidae_mendax |
| :---: |
| Lygidae_rosacea |
| Lygocoris_pabulinus |
| Lygus_lineolaris |
| Orthotylus_cruciatus |
| Poecilocapsus_lineatus |
| Prepops_fraternus |
| Prepops_insitivus |
| Prepops_nigricollis |
| Slaterocoris_atriitbialis |
| Tropidosteptes_amoenus |
| Tropidosteptes_cardinalis |
| Tropidosteptes_palmeri |
| Ceratocapsus_modestus |
| Lopidae_caesar |
| Lopidae_media |

20010211210-0-0-02473120101421--1212001123-2414-11111140411000001000610540-00033---2-0002



20010211210-0-0-02473120101421--1212001123-2414-11111140411000000020610540-00033---2-0002
20010211210-0-0-02473120101421-1212001123-2414-11111140411000000020610540-00033---2-0002



20010211210-0-0-02473120101421-1212001123-2414-11111140411000000000610540-00033---2-0002




100000000-0-110-024741-4602021-12-10001-1-1414-191919101110010-1200-112400064340--00000
100000000-0-110-023781-4602021--10-10011-1-0-24-190-19312110010-0001-112100064340---01000
Lopidae_robiniae
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s!ןeБә
Trigonotylus_ruficornis
Monalocoris_americanus

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Lopus_decolor
Orestoderus_obliquus Pilophorus_laetus
Plagiognathus_albatus
Plagiognathus politus
Plagiognathus_obscurus

Corythucha_caryae
Corythucha_marmorata
Melanorhopala_clavata
$100000000-0-2124024831-4312424--11-20001-2-0-25-101111313110000-1011-10540-03153---200000$

Aradus_quadrilineatus_CT
Aradus_quadrilineatus_TX

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Aradus_robustus_robustus

$$
\begin{aligned}
& \text { 10011000110-111502483124302021--0--20011-1-0-25-232423513111001-1001-10510-032333---00000 }
\end{aligned}
$$

20012121120-112122483120311411--2612011204-2415-102710303111200-1200-22212-02014--1-00100

20012000121412212247312031120---1212011204-2515-10271030411110001200-22212-02014--1-00100

1003200021111111224831201125230-2122011104-25240101010204111001-1100-10510202033-1-00100
1003200021111111224731201125230-2122011104-25240101010204111001-1100-10510202033-1-00100
202001201216222402483122111021--22120111-3-2514-101010204110000-0000-10210-020143---00000
200020000-11122702483120111022-1262201120-22514-101310203111000-1000-10500-02214--1-00010

200020000-11122702483120111022-1262201120-22514-101310203111000-1000-10500-02214--1-00010
200020000-11122702483120111022312622011203-2514-101310203110200-0400-10500-02214-1-00010
100110001111120-22483122111214--0--1010204-25140181010103010001-0001-105202010343---00120
201022202211142422483124111223--26-20111-3-1424-131413204110001-0001-222102010143--00100
201022202211142422483124111223--26-20111-3-14241131413204110101-0201-222102010143---00100
201022202211142422483124111223--26-20111-3-14241131413204110101-0201-222102010143--00100
201022202211142422483124111223--26-20111-3-14241131413204110001-0001-222102010143---00100
201022202211142422483124111223--26-20111-3-14241131413204110000-0000-222102010143---00100

201022202211142422483124111223--26-20111-3-14241131413204111000-1000-222102010143--00100
201022202211142422483124111223--26-20111-3-14241131413204110000-0000-222102010143---00100
201000002211161722783124112514-121120111-3-1410-131413303111011-1011-112122020340---10102
201000002211161722783124112514-121120111-3-1410-131413303111011-1011-112122020340---10102
$201000002211161722783124112514-121120111-3-1410-131413303110000-0000-112122020340---10102$
202010000-0-110-024831241122110122120111-3-14141131413404110000-06007155102021143---00100
202010000-0-110-024831241122110122120111-3-14141131413404110000-05008155102021143---00100 Megalotomus_quinquespinosus

Thyreocoridae_sp._FL<br>

Parastrachia_japonensis
 Anasa_tristis
Hygia_opaca
Leptoglossus_corculus
Leptoglossus_occidentalis
Leptoglossus_phyllopus
Thasus_gigas
Thasus_neocalifornicus
Alydus_eurinus
Alydus_pilosulus
Liorhyssus_hyalinus_AZ
Liorhyssus_hyalinus_Korea
$101110000-0-2624024831261222210016212212-3-0-14-131413304210000-0000-122102020143--00100$
10111000220-2624024831261121233-22220111-3-14140131413304211000-0400-125102020143---00200
10111000220-2624024831261121233-22220111-3-14140131413304211000-0400-122102020143---00200
20111130220-210-22483120122511--26112212-3-14140131413404210000-0000-125222020143--00102




203010000-0-0-17011571-1400-11-0--26001-1-0-0--131413203100200-0210-10500-020131---00000

203010000-0-0-17018571-1400-11-0--26001-1-0-0--131413203100200-0210-10500-020131---00000
10310000220-121102482126121211011622021232-14140131413404110000-0000-105202025042--01100



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Largidae_sp._NC
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Jalysus_wickhami
Jalysus_sp._FL
Berytidae_sp._MI
Lygaeus_kalmii
smeposef-sməodosuo
Myodocha_serripes
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Philaenus_spumaria
Tibicen_canicularis
200000000-0-1110024941-081120---0--11102-3-0-15-101010101010001-0100-0-30-010043---10002
200000000-0-1110024941-081120---0--11102-3-0-15-101010101010001-0100-0--30-010043---10002
100000000-0-110-024741-021140---1641113233-0-15-111110101210100-0101-0--22-02004-1--00002
100000000-0-110-024741-021140---1641113233-0-15-111110101210100-0101-0--22-02004-1--00002
Campylenchia_latipes

## Strictocephala_bisonia

Graphocephala_coccinea
Helochara_communis
 ;

# Adult Heteropteran Thoracic Endoskeleton (Insecta: Hemiptera) <br> A Family-Level Study <br> Tables 

## Book 1 (Part II)

## Gale Elinore Ridge

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M.S., Southern Connecticut State University, 1998

A Dissertation<br>Submitted in Partial Fulfillment of the<br>Requirements for the Degree of<br>Doctor of Philosophy<br>at the<br>The University of Connecticut

2008

# Part II: Tables 

## Appendix four

## Character state tables for endoskeletal structures

## Introduction

The tables were complied from character state matrix data (Appendix 3). There is a table for each character with species on the Y axis and states on the X axis. Each dot identifies a specific character state present in a specific species. The dashes are species too damaged in the critical point drying stage of SEM preparation to be use. The extra characters table at section end are supplemental features not inserted into the main tables, but worthy of inclusion.
Table 13: Anterior mesothoracic phragma


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| P. cinctus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
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| S. diadema | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Z. exsanguis | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| M. picipes | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| R. personatus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Stenopodainae sp. | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| T. dimidiata | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| R. prolixus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Phymatidae sp. Brazil | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Phymatidae sp. Texas | - | - | - | - | - | - | - | - | - |
| Phymatidae sp. Massachusetts | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Aradid sp. Costa Rica | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| A. crenatus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| A. quadrilineatus Connecticut | $\bullet$ | $\bullet$ | $\bullet$ |  |  |  |  |  |  |
| A. quadrilineatus Texas | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| A. robustus robustus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| A. similis | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Mezira sp. | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |


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| Amnestus sp. | - | - | - | - | - | - | - | - | - |
| Cydnidae sp. Brazil |  | $\bullet$ |  |  |  | $\bullet$ |  | $\bullet$ |  |
| Cydnidae sp. North Carolina |  | $\bullet$ |  |  |  | $\bullet$ |  | $\bullet$ |  |
| A. hilare |  | $\bullet$ |  |  |  | - |  |  | $\bullet$ |
| B. arborea | - | - | - | - | - | - | - | - | - |
| Codophila sp. |  | $\bullet$ |  |  |  | $\bullet$ |  |  | $\bullet$ |
| M. lugens |  | $\bullet$ |  |  |  | - |  |  | $\bullet$ |
| E. alternata | $\bullet$ |  |  | - |  |  |  | $\bullet$ |  |
| H. aeneifrons | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Edessa sp. | $\bullet$ |  |  | $\bullet$ |  |  |  | - |  |
| E. cruciatus | $\bullet$ |  |  | - |  |  |  | - |  |
| E. lateralis | $\bigcirc$ |  |  | - |  |  |  | $\bigcirc$ |  |
| T. javanica |  | $\bullet$ |  |  |  | $\bullet$ |  | $\bigcirc$ |  |
| G. aterrima | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| G. atra | $\bigcirc$ |  |  | - |  |  |  | $\bullet$ |  |
| P. japonensis | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Galgupha sp. Florida | $\bullet$ |  |  | $\bullet$ |  |  |  | - |  |
| Galgupha sp. Colorado | $\bullet$ |  |  | - |  |  |  | - |  |


| O. nigricornis India | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
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| Dysdercus sp. Arizona | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Dysdercus sp. California | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| A. terminalis |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| A. tristis |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| H. opaca |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| L. corculus |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| L. occidentalis |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| L. phyllopus |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| P. calcar | - | - | - | - | - | - | - | - | - |
| T. gigas |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| T. neocalifornicus |  |  | $\bullet$ |  |  | $\bullet$ |  | $\bullet$ |  |
| A. eurinus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| A. pilosulus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| M. quinquespinosus | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| L. hyalinus Korea | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| L. hyalinus Arizona | $\bullet$ |  |  | $\bullet$ |  |  |  | $\bullet$ |  |
| Largus sp. Texas | $\bullet$ | $\bullet$ |  | $\bullet$ |  |  |  |  |  |


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| P. hirta |  | $\bullet$ |  |  |  | $\bullet$ |
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| P. sphacelata |  | $\bullet$ |  |  |  | $\bullet$ |
| S. saltatoria |  | $\bullet$ |  |  |  | $\bullet$ |
| C. lectularius | $\bullet$ |  |  |  |  |  |
| O. vicarious | $\bullet$ |  |  |  |  |  |
| O. insidiosus | $\bullet$ |  |  |  |  |  |
| Anthocoridae sp. Israel | $\bullet$ |  |  |  |  |  |
| Anthocoridae sp. Nevada | $\bullet$ |  |  |  |  |  |
| N. americoferus | - | - | - | - | - | - |
| N. rufusculus |  | $\bullet$ |  |  |  | $\bullet$ |
| N. subcoleoptrata |  | $\bullet$ |  |  |  | $\bullet$ |
| A. lineolatus |  |  | $\bullet$ |  | $\bullet$ |  |
| C. ater |  |  | $\bullet$ |  | $\bullet$ |  |
| C. frontifer |  |  | $\bullet$ |  | $\bullet$ |  |
| L. mendax |  |  | $\bullet$ |  | $\bullet$ |  |
| L. rosacea |  |  | $\bullet$ |  | $\bullet$ |  |
| L. pabulinus |  |  | $\bullet$ |  | $\bullet$ |  |
| L. quercalbae |  |  |  |  |  |  |
| L. lineolaris |  |  |  |  |  |  |


| P. lineatus |  |  | $\bullet$ |  | $\bullet$ |  |
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| T. amoenus |  |  | $\bullet$ |  | $\bullet$ |  |
| T. cardinalis |  |  | $\bullet$ |  | $\bullet$ |  |
| T. palmeri |  |  | $\bullet$ |  | $\bullet$ |  |
| P. fraternus |  |  | $\bullet$ |  | $\bullet$ |  |
| P. insitivus |  |  | $\bullet$ |  | $\bullet$ |  |
| P. nigricollis |  |  | $\bullet$ |  | $\bullet$ |  |
| I. malina |  |  | $\bullet$ |  | $\bullet$ |  |
| C. modestus |  |  | $\bullet$ |  | $\bullet$ |  |
| L. caesar |  |  | $\bullet$ |  | $\bullet$ |  |
| L. media |  |  | $\bullet$ |  | $\bullet$ |  |
| L. robiniae |  |  | $\bullet$ |  | $\bullet$ |  |
| M. flavosparsus |  |  | $\bullet$ |  | $\bullet$ |  |
| P. regalis |  |  | $\bullet$ |  | $\bullet$ |  |
| O. cruciatus |  |  | $\bullet$ |  | $\bullet$ |  |
| S. atritibialis |  |  | $\bullet$ |  | $\bullet$ |  |
| D. rubi |  |  | $\bullet$ |  | $\bullet$ |  |
| M. americanus |  |  | $\bullet$ |  | $\bullet$ |  |

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| P. cinctus |  |  | - | - |  |  |
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| S. diadema |  |  | - | - |  |  |
| Z. exsanguis |  |  | - | - |  |  |
| M. picipes |  |  | - | - |  |  |
| R. personatus |  |  | - | - |  |  |
| Stenopodainae sp. |  |  | - | - |  |  |
| T. dimidiata |  |  | - | - |  |  |
| R. prolixus |  |  | - | - |  |  |
| Phymatidae sp. Brazil |  |  | - | - |  |  |
| Phymatidae sp. Texas | - | - | - | - | - | - |
| Phymatidae sp. Massachusetts |  |  | - | - |  |  |
| Aradid sp. Costa Rica |  |  | - |  | - |  |
| A. crenatus |  | $\bullet$ |  |  | - |  |
| A. quadrilineatus Connecticut |  | - |  |  | - |  |
| A. quadrilineatus Texas |  | - |  |  | - |  |
| A. robustus robustus |  | - |  |  | - |  |
| A. similis |  | - |  |  | - |  |
| Mezira sp. |  | - |  |  | - |  |

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| Largidae sp. North Carolina |  |  | - |  |  | - |
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| Largidae sp. California | - | - | - | - | - | - |
| P. analis Ghana |  |  | - |  |  | - |
| Jalysus sp. Florida | - |  |  |  |  |  |
| J. spinosus Connecticut | - |  |  |  |  |  |
| J. wickhami | - |  |  |  |  |  |
| Berytidae sp. Michigan | - |  |  |  |  |  |
| L. kalmii |  |  | $\bullet$ |  |  | - |
| O. fasciatus |  |  | $\bullet$ |  |  | $\bullet$ |
| M. serripes | - |  |  |  |  |  |
| I. bosqui | - |  |  |  |  |  |
| Auchenorrhyncha |  |  |  |  |  |  |
| P. spumaria | - |  |  |  |  |  |
| T. canicularis | - |  |  |  |  |  |
| G. coccinea | - |  |  |  |  |  |
| H. communis | - |  |  |  |  |  |
| S. bisonia | - |  |  |  |  |  |
| C. latipes | - |  |  |  |  |  |

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Table 16：Anterior mesothoracic phragma ventral apodeme

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| цuәsqy $\bullet^{\text {¢ }}$ |  |  |  |  |  |  |  |  |  |
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| Amnestus sp. | - | - | - | - | - | - | - | - |
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| Cydnidae sp. Brazil | - |  |  |  |  |  |  |  |
| Cydnidae sp. North Carolina | - |  |  |  |  |  |  |  |
| A. hilare | - |  |  |  |  |  |  |  |
| B. arborea | - | - | - | - | - | - | - | - |
| Codophila sp. | - |  |  |  |  |  |  |  |
| M. lugens | - |  |  |  |  |  |  |  |
| E. alternata |  | - |  |  |  |  | - |  |
| H. aeneifrons |  | - |  |  |  |  | - |  |
| Edessa sp. |  | - |  | - |  |  |  |  |
| E. cruciatus |  | - |  | - |  |  |  |  |
| E. lateralis |  | - |  | - |  |  |  |  |
| T. javanica |  | - |  |  |  |  |  | - |
| G. aterrima |  | - |  | - |  |  |  |  |
| G. atra |  | - |  | - |  |  |  |  |
| P. japonensis |  | $\bullet$ |  | - |  |  |  |  |
| Galgupha sp. Florida |  | - |  | - |  |  |  |  |
| Galgupha sp. Colorado |  | $\bullet$ |  | - |  |  |  |  |


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Table 17：Anterior mesothoracic ventral bridge

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| C. bubalus | - | - | - | - | - | - | - | - | - | - |

Table 18: Anterior mesothoracic ventral bridge apodeme


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| Amnestus sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
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| Cydnidae sp. Brazil |  | - |  |  |  |  |  |  | - |  |  |  |  |  |
| Cydnidae sp. North Carolina |  | - |  |  |  |  |  |  | - |  |  |  |  |  |
| A. hilare |  |  | - |  |  | - |  |  |  |  |  |  |  |  |
| B. arborea | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Codophila sp. |  |  | - |  |  | - |  |  |  |  |  |  |  |  |
| M. lugens |  |  | - |  |  | - |  |  |  |  |  |  |  |  |
| E. alternata |  |  | - |  |  | - |  |  |  |  |  |  |  |  |
| H. aeneifrons |  |  | - |  |  | - |  |  |  |  |  |  |  |  |
| Edessa sp. |  | - |  |  |  | - |  |  |  |  |  |  |  |  |
| E. cruciatus |  | - |  |  |  | - |  |  |  |  |  |  |  |  |
| E. lateralis |  | - |  |  |  | - |  |  |  |  |  |  |  |  |
| T. javanica |  |  | - |  |  |  |  |  | - |  |  |  |  |  |
| G. aterrima |  |  | - |  |  |  |  |  |  |  |  | - |  |  |
| G. atra |  |  | - |  |  |  |  |  |  |  |  | - |  |  |
| P. japonensis | - |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Galgupha sp. Florida |  |  | - |  |  |  |  |  |  |  |  | - |  |  |
| Galgupha sp. Colorado |  |  | - |  |  |  |  |  |  |  |  | - |  |  |


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Table 19: Anterior mesothoracic shelf







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Table 20: Apodeme alpha

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| әр!м : วseg |  |  |  |  |  |  |  |  |  |  |  |
| arenbs : aseg |  |  |  |  |  |  |  |  |  |  |  |
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Table 22: Metathoracic ventral bridge

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| N. americoferus | - | - | - | - | - | - | - | - | - |
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| Mezira sp. |  |  |  |  |  |  |  |  |  |
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| Amnestus sp. | - | - | - | - | - | - | - | - | - |
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| G. atra |  |  |  |  |  |  |  |  | - |
| P. japonensis |  |  |  |  |  |  |  |  | - |
| Galgupha sp. Florida |  |  |  |  |  |  |  |  | - |

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| Galgupha sp. Colorado |  |  | - |  |  |  |  |  | - |
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| A. terminalis |  | - |  |  |  |  |  | - |  |
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| Table 28：Posterior mesothoracic ventral bridge |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
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Table 30: Ridge 2


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| A. remigis MN CT WY ap. |  |  |  |  |  |  |  |  |  |
| A. remigis CA macro. |  |  |  |  |  |  |  |  |  |
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| R. distincta |  |  |  |  |  |  |  |  |  |
| R. obesa |  |  |  |  |  |  |  |  |  |
| M. hornii |  |  |  |  |  |  |  |  |  |
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| H. stagnorum |  |  |  |  |  |  |  |  |  |
| M. furcata apterous |  |  |  |  |  |  |  |  |  |
| M. mulsanti $\mathrm{OR}, \mathrm{CT}$ ap. |  |  |  |  |  |  |  |  |  |
| M. mulsanti CT macro. |  |  |  |  |  |  |  |  |  |
| H. buenoi |  |  |  |  |  |  |  |  |  |
| H. burmeisteri |  |  |  |  |  |  |  |  |  |
| N. striola | - |  |  |  |  |  |  |  |  |
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Table 37: Wing muscle opening

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Table 41: Thoracic contour

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## Most state rich characters，by family，with species included but not identified．

Table 43：Apodeme beta，posterior mesothoracic phragma with dorsal structures and foot

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Table 43: continued.







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Table 44: Apodeme alpha and posterior mesothoracic phragma form and arch


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Table 44: continued.


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## 658



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Table 45: continued.





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Table 46: Apodeme alpha, posterior mesothoracic phragma with dorsal structures and foot







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Table 46 continued.


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Table 48 continued.





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# Adult Heteropteran Thoracic Endoskeleton <br> (Insecta: Hemiptera) <br> A Family-Level Study <br> Illustrations and Scanning Electron Micrographs 

## Book 2

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B. A. Hons., Trinity College of Music, London, 1980
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A Dissertation
Submitted in Partial Fulfillment of the

Requirements for the Degree of
Doctor of Philosophy
at the

The University of Connecticut
2008

## Introduction

Drawings were oriented with head to left and aligned to an exact lateral view. No specimens are tilted to show hidden features, and so the 47 illustrations are identical. If there are important features, such as dorsal ridges, the dorsum is lifted, and this is noted on the drawing.

Sometimes artistic adjustments were taken with the posterior mesothoracic phragma having it slightly pulled back revealing spiracle 2 or other hidden structures without compromising proportions (Belostomatidae, Berytidae etc.). Though described in the text, spiracles in some drawings were not drawn (Enicocephalidae). They were concealed by other structures and to show them would have distorted the drawings. For accuracy, the majority of proportions and details were directly copied from the scanning electron micrographs, and final details rendered from direct observations of specimens. Labels and label-lines were kept small, so as not to obscure structures. Scanning electron micrographs were not edited, so fragments of trachea and muscle ligaments maybe present. The order of the drawings and scanning electron micrographs follows appendix one. Each drawing is numbered with accompanying scanning electron micrograph(s), identified by the number and a letter. Some drawings do not have scanning electron micrographs because these images lacked definition.

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a ms ph, anterior mesothoracic phragma; a ms ph Ik, anterior mesothoracic phragma lateral keel; a ms ph mk, anterior mesothoracic phragma medial keel; a ms ph vap, anterior mesothoracic phragma ventral apodeme; a ms vb, anterior mesothoracic ventral bridge; a ms vb ap, anterior mesothoracic ventral bridge apodeme; a ms sh, anterior mesothoracic shelf; apa, apodeme alpha; apb, apodeme beta; mt vb, metathoracic ventral bridge; mt vb ap, metathoracic ventral bridge apodeme; mt vb $\mathbf{e}$, metathoracic ventral bridge extension; $\mathbf{p} \mathbf{~ m s} \mathbf{p h}$, posterior mesothoracic phragma; $\mathbf{p}$ $\mathbf{m s} \mathbf{p h} \mathbf{m r}$, posterior mesothoracic phragma medial ridge; $\mathbf{p} \mathbf{~ m s} \mathbf{v b}$, posterior mesothoracic ventral bridge; $\mathbf{r} 1$, ridge $1 ; \mathbf{r} 2$, ridge $2 ; \mathbf{r} 3$, ridge $3 ; \mathbf{r} \mathbf{3} \mathbf{e}$, ridge 3 extension; $\mathbf{s p}$, spiracle; tf, thoracic floor; tw, thoracic wall; wmo, wing muscle opening.


Fig. 1. Generalized adult heteropteran endoskeleton; Anasa tristis (DeGeer) (Coreidae)


Fig. 1a. Generalized adult heteropteran endoskeleton; Anasa tristis (DeGeer) (Coreidae)
†

Fig. 2. Enicocephalidae


Fig. 2a. Enicocephalidae
$\because$


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Fig. 20c. Anthocoridae: anterior mesothoracic gland ducts


Fig. 20d. Anthocoridae: anterior mesothoracic gland ducts


Fig. 20e. Anthocoridae: anterior mesothoracic gland ducts


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\begin{aligned}
& \text { Appendix } 4 \\
& \text { Apodeme beta heads } \\
& \text { During the period when I was taking the scanning electron micrographs, some of the apodeme beta heads were well } \\
& \text { positioned for some good images; and so when possible, I made a series of images specifically of these heads. Some heads clearly } \\
& \text { show chitinous outlines of muscle bundles where the M. furca-plauralis attached (Fig. 9). } \\
& \text { These images illustrate a high level of detail, which might be found in the heteropteran endoskeleton, on structures } \\
& \text { smaller than a grain of sand. Species names are in alphabetical order. }
\end{aligned}
$$

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[^0]:    NC North Carolina; OR Oregon; NV Nevada; TX Texas; UK United Kingdom; WY Wyoming: apt. apterous; macro. macropterous.

[^1]:    Fig. 4d. Microvelia americana (Veliidae): eye facets

[^2]:    Fig. 15a. Ranatra fusca (Nepidae)

[^3]:    Fig. 31a. Tessaratoma javanica (Tessaratomidae)

[^4]:    Fig. 32a. Thyeocoridae

[^5]:    Fig. 6. Ilschnodemus bosqui (Slater \& Wilcox) (Blissidae)

