Handbook of Zoology
Arthropoda: Insecta

Coleoptera, Beetles
Volume 2: Morphology and Systematics
(Elateroidea, Bostrichiformia, Cucujiformia partim)

Handbook of Zoology

Founded by Willy Kükenthal
Continued by M. Beier, M. Fischer, J.-G. Helmcke, D. Starck, H. Wermuth

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Arthropoda: Insecta

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Editors' preface

Much of what had to be said in a preface was done so in the Editors' Preface of volume 1 and will not be repeated here. What follows is an annotation. There are two more installments to come, with volume 3 (Phytophaga) in progress and volume 4 which will cover special topics of morphology, natural history, and evolution.

The detailed family by family review of the groups of beetles covered in this volume turned out to be a challenging scientific project. The tremendous difficulty to find suitable authors for many chapters highlights a dramatic loss of expertise, which is in stark contrast with what gets published and discussed openly in the context of the ongoing biodiversity crisis, especially as it relates to systematics and taxonomy. Without the encyclopedic knowledge of an increasingly smaller circle of outstanding coleopterists, the completion of the 116 chapters of this volume would definitely not have been possible. The groups included are two recently described families of Adephaga (chapters 2–3) and the polyphagan superfamilies Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea, Cucujoidea and Tenebrionoidea.

Two introductory chapters are also included, one of which is an update on beetle classification, and the other a much-needed glossary of morphological terms. While classifications will change almost on a yearly basis due to new phylogenetic data, morphological terminology is an old calloused dog that is entrenched by tradition with many beetle specialists having their own sets of terms that are not used in other groups (the genitalic terminology of Coccinellidae is one example). During the course of editing and writing of the chapters the mix of terminology was frustratingly obvious, and not the fault of the authors themselves. Because homology is the ultimate scientific concept that underpins phylogeny and classification, the editors decided that a glossary would help to improve the communication among coleopterists and readers of the Handbook.

You will note that the editorship has changed since volume 1, a combination of editors that suit our expertise. In vol. 1, Rolf G. Beutel was lead editor because of his focus on Adephaga, and here, Richard A. B. Leschen takes lead as his work has been mainly on Cucujoidea. Then, it was decided to add John F. Lawrence for his broad expertise on much of the Polyphaga, a knowledge asset that pushed volume 2 towards its logical and most successful limit. Meanwhile, Adam Ślipiński was also brought to the fold to assist with the management of Cucujoidea and as associate editor of Tenebrionoidea. Apart from chapter author and co-author, Adam, with the help of Anne Hastings, had managed hundreds of illustrations for many of the family chapters.

Since we had begun work on volume 2, several key coleopterists have passed away, among them Alistair S. Ramsdale (Montana State University) who had contributed elateroid chapters to this volume. Another great loss was the untimely death of the outstanding staphylinid specialist Dr. Steve Ashe (University of Kansas) to whom we dedicate this volume. He was advisor to Richard A. B. Leschen and supervisor of Marc A. Branham, who is one of our vol. 2 authors. Shortly before this volume was completed, Robert E. Roughley passed away; he was a specialist on Adephaga and was coauthor on the Gyrinidae chapter in Volume 1. Lastly we remember Hiroyuki Sasaji, whose main works concerned Cucujoidea and Tenebrionoidea, especially Coccinellidae, which are covered in this volume.

First of all, our greatest thanks go to the authors who have contributed to volume 2, without you coleopteran systematics would not be such a vibrant field of study and this project would have not been completed. Second, we would like to thank our institutions and funding agencies and naturally we would like to express our gratitude to our friends, colleagues, and families who supported us during the writing and editing of volume 2. We lastly thank Stephanie Dawson at De Gruyter by assisting with the overall editorial process and especially the final stages of proofing. Though Stephanie politely kept asking us about deadlines which were off by almost two years, she had to succumb to the nuances of coleopterists with patience and respect and we were happy to work alongside her in this demanding and large project.

Richard A. B. Leschen
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John F. Lawrence
Adam Ślipiński (associate editor of
Tenebrionoidea)

Contents

Editors' preface V

Contributors XI

1. Changes in classification and list of families and subfamilies
John F. Lawrence, Rolf G. Beutel, Richard A. B. Leschen and Adam Ślipiński 1

2. Glossary of Morphological Terms
John F. Lawrence, Rolf G. Beutel, Richard A. B. Leschen and Adam Ślipiński 9

3. Adephaga (Addendum) Introduction and Phylogeny
Rolf G. Beutel, Ignacio Ribera and Michael Balke 21

3.1. Aspidytidae Ribera, Beutel, Balke and Vogler, 2002
Rolf G. Beutel, Michael Balke and Ignacio Ribera 21

3.2. Meruidae Spangler and Steiner 2005
Rolf G. Beutel, Michael Balke and Warren E. Steiner 28

4. Elateroidea Introduction, Phylogeny
John F. Lawrence, Ladislav Bocak, Milada Bocakova, Rolf G. Beutel and Jyrki Muona 35

4.1. Rhinorhipidae Lawrence, 1988
John F. Lawrence 38

4.2. Artematopodidae Lacordaire, 1857
John F. Lawrence 42

4.3. Brachypsectridae Horn, 1881
Cleide Costa, Sergio A. Vanin, John F. Lawrence, Sergio Ide and Marc A. Branham 47

4.4. Cerophytidae Latreille, 1834
Cleide Costa, Sergio A. Vanin, John F. Lawrence and Sergio Ide 54

4.5. Eucnemidae Eschscholtz, 1829
Jyrki Muona 61

4.6. Throscidae Laporte, 1840
Jyrki Muona, John F. Lawrence and Adam Ślipiński 69

4.7. Elateridae Leach, 1815
Cleide Costa, John F. Lawrence and Simone Policena Rosa 75

4.8. Plastoceridae Crowson, 1972
Marc A. Branham 103

4.9. Family Drilidae Blanchard, 1845
Ladislav Bocak, Marc A. Branham and Robin Kundrata 104

4.10. Family Omalisidae Lacordaire, 1857
Ladislav Bocak and Milada Bocakova 110

4.11. Lycidae Laporte, 1836
Ladislav Bocak and Milada Bocakova 114

4.12. Telegeusidae Leng, 1920
John F. Lawrence 123

4.13. Phengodidae LeConte, 1861
Cleide Costa and Santiago Zaragoza-Caballero 126

4.14. Rhagophthalmidae Olivier, 1907
Itsuro Kawashima, John F. Lawrence and Marc A. Branham 135

4.15. Lampyridae Latreille, 1817
Marc A. Branham 141

4.16. Omethidae LeConte, 1861
Alistair S. Ramsdale 149

4.17. Cantharidae Imhoff, 1856
Alistair S. Ramsdale 153

4.18. Elateriformia *Incertae Sedis*
John F. Lawrence, Itsuro Kawashima and Marc A. Branham 162

5. Derodontiformia Introduction, Phylogeny
John F. Lawrence, Rolf G. Beutel and Richard A. B. Leschen 179

5.1. Derodontidae LeConte, 1861
Richard A. B. Leschen and Rolf G. Beutel 180

5.2. Nosodendridae Erichson, 1846
Richard A. B. Leschen and Rolf G. Beutel . . . 185

5.3. Jacobsoniidae Heller, 1926
John F. Lawrence and Richard A. B. Leschen 190

6. Bostrichiformia Latreille 1802
John F. Lawrence, Richard A. B. Leschen and Rolf G. Beutel 197

6.1. Dermestidae Latreille, 1804
John F. Lawrence and Adam Ślipiński 198

6.2. Endecatomidae LeConte, 1861
John F. Lawrence 206

6.3. Bostrichidae Latreille, 1802
John F. Lawrence 209

6.4. Ptinidae Latreille, 1802
T. Keith Philips and Karen L. Bell 217

7. Cucujiformia Lameere, 1938
Introduction, Phylogeny
Richard A. B. Leschen and
Adam Ślipiński 227

8. Lymexloidae Fleming, 1821
John F. Lawrence 229

9. Cleroidea Latreille, 1802
Introduction and Phylogeny
Richard A. B. Leschen. 237

9.1. Phloiophilidae Kiesenwetter, 1863
John F. Lawrence and
Richard A. B. Leschen. 239

9.2. Trogossitidae Fabricius, 1801
Jiří Kolibáč and Richard A. B. Leschen 241

9.3. Chaetosomatidae Crowson, 1952
Richard A. B. Leschen. 247

9.4. Metaxinidae Kolibáč, 2004
Jiří Kolibáč and Richard A. B. Leschen 250

9.5. Thanerocleridae Chapin, 1924
Jiří Kolibáč and Richard A. B. Leschen 253

9.6. Cleridae Latreille, 1802
Jiří Kolibáč 257

9.7. Acanthocnemidae Crowson, 1964
John F. Lawrence and
Richard A. B. Leschen. 262

9.8. Phycosecidae Crowson, 1952
Richard A. B. Leschen and
Rolf G. Beutel. 265

9.9. Prionoceridae Lacordaire, 1857
John F. Lawrence and
Richard A. B. Leschen. 268

9.10. Mauroniscidae Majer, 1994
John F. Lawrence 271

9.11. Melyridae Leach, 1815
John F. Lawrence and
Richard A. B. Leschen. 273

10. Cucujoidea, Latreille, 1802
Introduction, Phylogeny
Richard A. B. Leschen and
Adam Ślipiński 281

10.1. Boganiidae Sen Gupta and Crowson, 1966
John F. Lawrence and
Adam Ślipiński 282

10.2. Byturidae Jacquelin duVal, 1858
Andrew R. Cline, Michael A. Goodrich
and Richard A. B. Leschen 286

10.3. Helotidae Reitter, 1876/Chapuis, 1876
John F. Lawrence, Adam Ślipiński and
Chi-Feng Lee 292

10.4. Protocucujidae Crowson, 1954
Adam Ślipiński and Rolf G. Beutel 296

10.5. Sphindidae Jacquelin du Val, 1861
Juanita A. Forrester and
Joseph V. McHugh 300

10.6. Biphyllidae LeConte, 1861
Andrew R. Cline and Floyd W. Shockley . . . 306

10.7. Erotylidae Leach, 1815
Richard A. B. Leschen, Paul E. Skelley and
Joseph V. McHugh 311

10.8. Monotomidae Laporte, 1840
Yves Bousquet. 319

10.9. Hobartiidae Sen Gupta and Crowson, 1966
Wioletta Tomaszewska and
Adam Ślipiński 324

10.10. Cryptophagidae Kirby, 1837
Richard A. B. Leschen. 327

10.11. Agapythidae Sen Gupta and Crowson, 1969
Richard A. B. Leschen and
John F. Lawrence 334

10.12. Priasilphidae Crowson, 1973
Richard A. B. Leschen and
John F. Lawrence 336

10.13. Phloeostichidae Reitter, 1911
John F. Lawrence and Adam Ślipiński. 340

10.14. Silvanidae Kirby, 1837
Michael C. Thomas and
Richard A. B. Leschen. 346

10.15. Cucujidae Latreille, 1802
Michael C. Thomas and
Richard A. B. Leschen. 350

10.16. Myraboliidae Lawrence and Britton, 1991
Adam Ślipiński, Wioletta Tomazsewska
and John F. Lawrence. 354

10.17. Cavognathidae Sen Gupta and
Crowson, 1966
Adam Ślipiński and
Wioletta Tomaszewska 357

10.18. Lamingtoniidae Sen Gupta and
Crowson, 1969
John F. Lawrence and
Richard A. B. Leschen. 360

10.19. Passandridae Blanchard, 1845/
Erichson, 1845
Daniel Burckhardt and
Adam Ślipiński 363

10.20. Phalacridae Leach, 1815
John F. Lawrence, Matthew L. Gimmel
and Warren E. Steiner, Jr. 368

10.21. Propalticidae Crowson, 1952
John F. Lawrence 374

10.22. Laemophloeidae Ganglbauer, 1899
Michael C. Thomas and Richard A. B. Leschen. 376

10.23. Tasmosalpingidae Lawrence and Britton, 1991
John F. Lawrence and Adam Ślipiński 381

10.24. Cyclaxyridae Gimmel, Leschen & Ślipiński, 2009
Richard A. B. Leschen, Matthew L. Gimmel and Adam Ślipiński 383

10.25. Kateretidae Erichson in Agassiz, 1846
Josef Jelínek and Andrew R. Cline 386

10.26. Nitidulidae Latreille, 1802
Josef Jelínek, Chris Carlton, Andrew R. Cline and Richard A. B. Leschen. . . 390

10.27. Smicripidae Horn, 1879
Andrew R. Cline 407

10.28. Bothrideridae Erichson, 1845
Adam Ślipiński, Nathan Lord and John F. Lawrence 411

10.29. Cerylonidae Billberg, 1820
Adam Ślipiński and John F. Lawrence 422

10.30. Alexiidae Imhoff, 1856
Adam Ślipiński and Wioletta Tomaszewska 432

10.31. Discolomatidae Horn, 1878
Andrew R. Cline and Adam Ślipiński 435

10.32. Endomychidae Leach, 1815
Wioletta Tomaszewska 442

10.33. Coccinellidae Latreille, 1802
Adam Ślipiński and Wioletta Tomaszewska 454

10.34. Corylophidae LeConte, 1852
Adam Ślipiński, John F. Lawrence and Andrew R. Cline 472

10.35. Latridiidae Erichson, 184
Christopher S. Hartley and Joseph V. McHugh 481

11. Tenebrionoidea Introduction, Phylogeny
John F. Lawrence, Darren A. Pollock and Adam Ślipiński. 487

11.1. Mycetophagidae Leach, 1815
John F. Lawrence and Richard A. B. Leschen. 491

11.2. Archeocrypticidae Kaszab, 1964
John F. Lawrence 496

11.3. Pterogeniidae Crowson, 1953
John F. Lawrence 501

11.4. Ciidae Leach in Samouelle, 1819
John F. Lawrence and Cristiano Lopes-Andrade. 504

11.5. Tetratomidae Billberg, 1820
John F. Lawrence and Richard A. B. Leschen 514

11.6. Melandryidae Leach, 1815
Nikolai B. Nikitsky and Darren A. Pollock 520

11.7. Mordellidae Latreille, 1802
John F. Lawrence and Adam Ślipiński 533

11.8. Ripiphoridae Gemminger and Harold, 1870 (Gerstaecker, 1855)
John F. Lawrence, Zachary H. Falin and Adam Ślipiński 538

11.9. Zopheridae Solier, 1834
Adam Ślipiński and John F. Lawrence 548

11.10. Ulodidae Pascoe, 1869
Richard A. B. Leschen and Adam Ślipiński 559

11.11. Promecheilidae Lacordaire, 1859
John F. Lawrence, Adam Ślipiński and Mario Elgueta 563

11.12. Chalcodryidae Watt, 1974
John F. Lawrence and Richard A. B. Leschen. 567

11.13. Trachelostenidae Lacordaire, 1859
John F. Lawrence and Adam Ślipiński 571

11.14. Tenebrionidae Latreille, 1802
Eric G. Matthews, John F. Lawrence, Patrice Bouchard, Warren E. Steiner, Jr. and Adam Ślipiński. 574

11.15. Prostomidae G. G. Thomson, 1859
Ainsley Seago and Rolf G. Beutel 659

11.16. Synchroidae Lacordaire, 1859
Adam Ślipiński and John F. Lawrence 667

11.17. Stenotrachelidae C. G. Thomson, 1859
John F. Lawrence and Adam Ślipiński 670

11.18. Oedemeridae Latreille, 1810
John F. Lawrence and Adam Ślipiński 674

11.19. Meloidae Gyllenhal, 1810
Marco A. Bologna, Federica Turco and John D. Pinto 681

11.20. Mycteridae Blanchard, 1845
Darren A. Pollock. 693

11.21. Boridae C. G. Thomson, 1859
Darren A. Pollock 699

11.22. Trictenotomidae Blanchard, 1845
Darren A. Pollock and Dmitry Telnov 704

11.23. Pythidae Solier, 1834
Darren A. Pollock 708

11.24. Pyrochroidae Latreille, 1807
Daniel K. Young and Darren A. Pollock 715

11.25. Salpingidae Leach, 1815
John F. Lawrence, Adam Ślipiński, Darren A. Pollock and Hermes Escalona . . . 722

11.26. Anthicidae Latreille, 1819
Donald S. Chandler 729

11.27. Aderidae Winkler, 1927
John F. Lawrence and Adam Ślipiński 741

11.28. Scraptiidae Mulsant, 1856
John F. Lawrence and Adam Ślipiński 746

11.29. Tenebrionoidea Incertae sedis
John F. Lawrence, Hermes Escalona and Richard A. B. Leschen 750

Taxonomic Index 761

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1. Changes in classification and list of families and subfamilies

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The classification used in Handbook of Zoology, part 38.1 (Coleoptera, Beetles, Vol. 1) was based primarily on that of Lawrence & Newton (1995) and Lawrence *et al.* (1999), with a few additions or modifications based on subsequent work. Further changes and additions to that family list based on more recent publications are listed below:

Artematopodidae. The tribe Allopogonini Crowson was elevated to subfamily level by Lawrence (2005a).

Eucnemidae. The subfamily Anischiinae Fleutiaux, recognized at the family level in 38.1, was moved into the family Eucnemidae by Lawrence *et al.* (2007) and considered to be a subfamily well within the major eucnemid clade (excluding Perothopinae, Phyllocerinae, Palaeoxeninae, Pseudomeninae and Phlegoninae).

Elateridae. The subfamily Tetralobinae was reduced to a tribe within Agrypninae by Costa *et al.* (1992, 1994). Campyloxeninae Costa (1975) and Morostominae Dolin (2000) were added as subfamilies.

Lycidae. The new subfamily and tribal classification proposed by Bocak & Bocakova (2008) and based in part on Bocakova *et al.* (2007) was used in Chapter 4.11.

Phengodidae. Mastinocerinae LeConte and Penicillophorinae Paulus were recognized at the subfamily level.

Rhagophthalmidae. Although treated as a separate family here, as in 38.1, some molecular evidence (Bocakova *et al.* 2007) suggests that this group does belong within Phengodidae, as suggested by Crowson (1972).

Lampyridae. The constitution of this family used in Chapter 4.15 is based on cladograms produced by Branham & Wenzel (2001, 2003); thus several formerly included taxa within Pterotinae, Ototretinae and Ototretadrilinae have been discussed in a separate Chapter (4.18) dealing with Elateriformia *incertae sedis.* Subfamilies remaining in Lampyridae are the Psilocladinae (= Cyphonocerinae; Jeng *et al.* 1998), Amydetinae, Lampyrinae, Photurinae and Luciolinae.

Elateriformia *incertae sedis.* Chapter 4.18 includes elateriform taxa whose family-group relationships are in doubt. All of these taxa belong within Elateroidea with the exception of Podabrocephalidae, which appears to be related to Ptilodactylidae. All of the taxa excluded from Lampyridae by Branham & Wenzel (2001, 2003) are also included here, as well as the doubtful throscid genus *Neocrowsonium* Kistner & Abdel-Galil and the subfamily Cydistinae Paulus (1972), formerly included in Karumiidae.

Derodontiformia. The placing of Derodontidae, Nosodendridae and Jacobsoniidae in a separate superfamily increases the likelihood that Bostrichoidea is a monophyletic group. It is not at all certain, however, that the three families placed here form a single clade. This is discussed in Chapters 5 and 6.

Dermestidae. New data on the phylogeny of Dermestidae have been published by Lawrence & Ślipiński (2005) and Kiselyova & McHugh (2006). In the former work, Dermestinae and Trinodinae were redefined to include Marioutinae and Thylodriinae, respectively.

Ptinidae. The priority of Ptinidae Latreille 1802 over Anobiidae Fleming 1821 was pointed out by Lawrence & Newton (1995); the family name has been changed in this volume.

Lymexylinae. Atractocerinae is recognized a subfamily separate from Lymexylinae and containing several genera following Paulus (2004).

Trogossitidae. A new family-group classification involving only two subfamilies was proposed by Kolibáč (2005, 2006) and is followed in Chapter 9.2.

Thanerocleridae. The clerid subfamily Thaneroclerinae was elevated to family rank by Kolibáč (1992, 1998) and a new subfamily Zenodosinae was proposed.

Metaxinidae. The genus *Metaxina* Broun, tentatively included in Thaneroclerinae by Crowson (1964) was made the type of this new family by Kolibáč (2004).

Mauroniscidae. This family was proposed by Majer (1994 b, 1995) and recognized in Lawrence *et al.* (1999).

Melyridae. The subfamily Gietellinae, recognized by Lawrence & Newton (1995), was reduced to tribal level within Dasytinae.

Cucujoidea. A new arrangement of cucujoid families was proposed by Leschen *et al.* (2005). These authors also noted that Cucujoidea was probably paraphyletic if the cleroids are excluded, and similar statements have been made in other recent works (Beutel & Pollock 2000; Hunt *et al.* 2007).

Cryptophagidae. The subfamily Hypocoprinae was considered to be a tribe within Atomariinae by Leschen (1996).

Phloeostichidae. The subfamilies Agapythinae Sen Gupta & Crowson, Myraboliinae Lawrence & Britton, Priasilphinae Crowson and Tasmosalpinginae Lawrence & Britton were all raised to family rank by Leschen *et al.* (2005), leaving only Phloeostichinae and Hymaeinae within this family. See Chapters 10.11, 10.12, 10.13, 10.16 and 10.23.

Nitidulidae. Three additional subfamilies were proposed by Kirejtshuk: Amphicrossinae (1986), Epuraeinae (1986) and Maynipeplinae (1998).

Endomychidae. A reanalysis of the subfamilies of Endomychidae (Tomaszewska 2005) confirmed the classification presented in 38.1.

Coccinellidae. A new classification involving only two subfamilies, with almost all currently recognized subfamilies considered to be tribes within Coccinellinae, was proposed by Ślipiński (2007) and is used in Chapter 10.33.

Corylophidae. A new subfamily and tribal classification was proposed by Ślipiński *et al.* (2009). Only two subfamilies, Periptyctinae and Corylophinae are recognized, with all other supergeneric groups included within the latter.

Tetratomidae. The melandryid subfamilies Hallomeninae and Eustrophinae were transferred to this family by Nikitsky (1998, 2004 a, b).

Melandryidae. A new classification based in part on Nikitsky (2002) is included in Chapter 11.6.

Ripiphoridae. A new classification with the subfamilies Pelecotominae and Ptilophorinae redefined was proposed by Falin (2004). See Chapter 11.8.

Zopheridae. In the classification proposed by Ślipiński & Lawrence (1999) only two subfamilies are recognized, with both Usechinae and Monommatinae being downgraded to tribes within Zopherinae.

Promecheilidae. With the addition of the genus *Promecheilus* Solier to this family, the name Perimylopidae St. George (1939) has been replaced by the older name Promecheilidae Lacordaire (1959).

Tenebrionidae. The major changes at the subfamily level in in Tenebrionidae are the recognition of the Nilioninae (including only *Nilio* Latreille) and the use of Stenochiinae as a senior synonym of Coelometopinae (Bouchard *et al.* 2005). See Chapter 11.14.

Oedemeridae. A new subfamily Polypriinae was proposed by Lawrence (2005 b) to include *Polypria* Chevrolat (Tenebrionoidea incertae sedis in Lawrence & Newton 1995) and *Dasytomima* Lawrence.

Meloidae. The subfamily Tetraonycinae Böving & Craighead (1931) was added by Bologna & Pinto (2001).

Mycteridae. As pointed out by Lawrence & Newton (1995), Eurypinae Thomson has priority over Lacconotinae and is used in Chapter 11.20.

Anthicidae. The subfamilies Afreminae, Lagrioidinae and Ischaliinae were removed from Anthicidae and included in the next Chapter. With their removal a much stronger case can be made for the monophyly of this family. Ischaliidae was recognized at the family level by Nikitsky & Egorov (1992) and Nikitsky (1996), and doubts have been expressed about the inclusion of *Afremus* Levey and *Lagrioida* Fairmaire & Germain in Anthicidae (Lawrence & Britton 1991; Costa *et al.* 1995; Werner & Chandler 1995; Chandler 2002).

Tenebrionoidea *incertae sedis*. Chapter 11.29 includes three family-group taxa listed in the previous paragraph plus the genera *Rhizonium* Sharp and *Aprostomis* Grouvelle.

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List of Families and Subfamilies

Adephaga

Meruidae Spangler & Steiner, 2005
Aspidytidae Ribera *et al.* 2002

Polyphaga

Elateriformia
Elateroidea

Rhinorhipidae Lawrence, 1988
Artematopodidae Lacordaire, 1857
  Electribiinae Crowson, 1975
  Allopogoniinae Crowson, 1973
  Artematopodinae Lacordaire, 1857
Brachypsectridae LeConte & Horn, 1883
Cerophytidae Latreille, 1834
Eucnemidae Eschscholtz, 1829
  Perothopinae Lacordaire, 1857
  Phyllocerinae Reitter, 1905
  Pseudomeninae Muona, 1933
  Palaeoxeninae Muona, 1993
  Phlegoninae Muona, 1993
  Anischiinae Fleutiaux, 1936
  Melasinae Fleming, 1821
  Eucneminae Eschscholtz, 1829
  Macraulacinae Fleutiaux, 1923
Throscidae Laporte, 1840
Elateridae Leach, 1815
  Cebrioninae Latreille, 1802
  Agrypninae Candèze, 1857 (incl. Tetralobinae)
  Thylacosterninae Fleutiaux, 1920
  Lissominae Laporte, 1835
  Semiotinae Jacobson, 1913
  Campyloxeninae Costa, 1975
  Pityobiinae Hyslop, 1917
  Oxynopterinae Candèze, 1857
  Denticollinae Stein & Weise, 1877 (1856)
  Negastriinae Nakane & Kishii, 1956
  Elaterinae Leach, 1815
  Cardiophorinae Candèze, 1860
  Hemiopinae Fleutiaux, 1941
  Physodactylinae Lacordaire, 1857
  Eudicronychinae Girard, 1971

- Subprotelaterinae Fleutiaux, 1936
- Morostominae Dolin, 2000

Plastoceridae Crowson, 1972
Drilidae Blanchard, 1845
Omalisidae Lacordaire, 1857
Lycidae Laporte, 1836
- Libnetinae Bocak & Bocakova, 1990
- Dictyopterinae Kleine, 1928
- Lypropaeinae Bocak & Bocakova, 1989
- Ateliinae Kleine, 1928
- Lycinae Laporte, 1836
- Dexorinae Bocak & Bocakova, 1989

Telegeusidae Leng, 1920
Phengodidae Leconte, 1861
- Phengodinae LeConte, 1861
- Mastinocerinae LeConte, 1881
- Penicillophorinae Paulus, 1974

Rhagophthalmidae Olivier, 1907
Lampyridae Latreille, 1817
- Psilocladinae McDermott, 1964
- Lampyrinae Latreille, 1817
- Luciolinae Lacordaire, 1857
- Photurinae Lacordaire, 1857

Omethidae Leconte, 1861
- Omethinae LeConte, 1861
- Matheteinae LeConte, 1881
- Driloniinae Crowson, 1972

Cantharidae Imhoff, 1856 (1815)
- Cantharinae Imhoff, 1856 (1815)
- Silinae Mulsant, 1862
- Dysmorphocerinae Brancucci, 1980
- Malthininae Kiesenwetter, 1852
- Chauliognathinae Leconte, 1861

Elateriformia Incertae Sedis
Podabrocephalidae Pic, 1930
- *Neocrowsonia* Kistner & Abdel-Galil, 1986
- Cydistinae Paulus, 1972
- Pterotinae LeConte, 1861
- *Harmatelia* Walker, 1858
- *Stenocladius* Fairmaire, 1878
- Ototretinae McDermott, 1964

Derodontiformia
Derodontoidea
Derodontidae LeConte, 1861
- Peltasticinae Leconte, 1861
- Derodontinae LeConte, 1861
- Laricobiinae Mulsant & Rey, 1863–4

Nosodendridae Erichson, 1846
Jacobsoniidae Heller, 1926

Bostrichiformia
Bostrichoidea
Dermestidae Latreille, 1804
- Dermestinae Latreille, 1804 (incl. Marioutinae)
- Thorictinae Agassiz, 1846
- Orphilinae LeConte, 1861
- Trinodinae Casey, 1900 (incl. Thylodriinae)
- Attageninae Laporte, 1840
- Megatominae Leach, 1815

Endecatomidae Leconte, 1861
Bostrichidae Latreille, 1802
- Dysidinae Lesne, 1921
- Polycaoninae Lesne, 1936
- Bostrichinae Latreille, 1802
- Psoinae Blanchard, 1851
- Dinoderinae C. G. Thomson, 1863
- Lyctinae Billberg, 1820
- Euderiinae Lesne, 1934

Ptinidae Latreille, 1802
- Eucradinae LeConte, 1861
- Ptininae Latreille, 1802
- Dryophilinae LeConte, 1861
- Ernobiinae Pic, 1912
- Anobiinae Fleming, 1821
- Ptilininae Shuckard, 1840
- Alvarenganiellinae Viana & Martinez, 1971
- Xyletininae Gistel, 1956
- Dorcatominae Thomson, 1859
- Mesocoelopodinae Mulsant & Rey, 1864

Cucujiformia
Lymexyloidea
Lymexylidae Fleming, 1821
- Hylecoetinae Gistel, 1856
- Lymexylinae Fleming, 1821
- Atractocerinae Laporte, 1840
- Melittommatinae Wheeler, 1986

Cleroidea
Phloiophilidae Kiesenwetter, 1863
Trogossitidae Latreille, 1802
- Peltinae Kirby, 1837
- Trogossitinae Latreille, 1802

Chaetosomatidae Crowson, 1952
Metaxinidae Kolibáč, 2004 (from Cleridae)
Thanerocleridae Chapin, 1924 (from Cleridae)
- Zenodosinae Kolibáč, 1992
- Thaneroclerinae Chapin, 1924

Cleridae Latreille, 1802
- Tillinae Leach, 1815
- Hydnocerinae Spinola, 1844
- Clerinae Latreille, 1802
- Korynetinae Laporte, 1836 (incl. Epiphloeinae, Enopliinae, Tarsosteninae)

Acanthocnemidae Crowson, 1964
Phycosecidae Crowson, 1952
Prionoceridae Lacordaire, 1857
Mauroniscidae Majer, 1994
Melyridae Leach, 1815
- Rhadalinae LeConte, 1861 (incl. Aplocneminae)
- Melyrinae Leach, 1815
- Dasytinae Laporte, 1840 (incl. Gietellinae)
- Malachiinae Fleming, 1821 (incl. Attalomiminae)

Cucujoidea (arrangement is new)
Boganiidae Sen Gupta & Crowson, 1966
- Paracucujinae Endrödy-Younga & Crowson, 1986
- Boganiinae Sen Gupta & Crowson, 1966

Byturidae Jacquelin Du Val, 1858
- Platydascillinae Pic, 1914
- Byturinae Jacquelin Du Val, 1858

Helotidae Reitter, 1876/Chapuis, 1876
Protocucujidae Crowson, 1954
Sphindidae Jacquelin Du Val, 1860
    Protosphindinae Sen Gupta & Crowson, 1979
    Odontosphindinae Sen Gupta & Crowson, 1979
    Sphindiphorinae McHugh, 1993
    Sphindinae Jacquelin Du Val, 1860
Biphyllidae LeConte, 1861
Erotylidae Latreille, 1802
    Xenoscelinae Ganglbauer, 1899
    Pharaxonothinae Crowson, 1952 (incl. Setariolinae)
    Loberinae Bruce, 1951
    Languriinae Crotch, 1873
    Cryptophilinae Casey, 1900 (incl. Toraminae)
    Erotylinae Latreille, 1802 (incl. Tritominae, Dacninae, Megalodacninae, Encaustinae)
Monotomidae Laporte, 1840
    Rhizophaginae Redtenbacher, 1845
    Monotominae Laporte, 1840
Hobartiidae Sen Gupta & Crowson, 1966
Cryptophagidae Kirby, 1837
    Cryptophaginae Kirby, 1837
    Atomariinae LeConte, 1861 (incl. Hypocoprinae, Alfieriellinae)
Agapythidae Sen Gupta & Crowson, 1969
Priasilphidae Crowson, 1973
Phloeostichidae Reitter, 1911
Silvanidae Kirby, 1837
    Brontinae Erichson, 1845/Blanchard, 1845
    Silvaninae Kirby, 1837
Cucujidae Latreille, 1802
Myraboliidae Lawrence & Britton, 1991
Cavognathidae Sen Gupta & Crowson, 1966
Lamingtoniidae Sen Gupta & Crowson, 1966
Passandridae Erichson 1845/Blanchard, 1845
Phalacridae Leach, 1815
    Phaenocephalinae Matthews, 1899
    Phalacrinae Leach, 1815
Propalticidae Crowson, 1952
Laemophloeidae Ganglbauer, 1899
Tasmosalpingidae Lawrence & Britton, 1991
Cyclaxyridae Gimmel *et al.,* 2009
Kateretidae Erichson, 1846
Nitidulidae Latreille, 1802
    Calonecrinae Kirejtshuk, 1982
    Maynipeplinae Kirejtshuk, 1998
    Epuraeinae Erichson, 1843
    Carpophilinae Erichson, 1842
    Amphicrossinae Kirejtshuk, 1986
    Meligethinae C. G. Thomson, 1859
    Nitidulinae Latreille, 1802
    Cillaeinae Kirejtshuk & Audisio in Kirejtshuk, 1986
    Cryptarchinae C. G. Thomson, 1859
    Cybocephalinae Jacquelin Du Val, 1858
Smicripidae Horn, 1879
Bothrideridae Erichson, 1845
    Teredinae Seidlitz, 1888
    Xylariophilinae Pal & Lawrence, 1986
    Anommatinae Ganglbauer, 1899
    Bothriderinae Erichson, 1845
Cerylonidae Bilberg, 1820
    Euxestinae Grouvelle, 1908
    Loeblioryloninae Ślipiński, 1990
    Ostomopsinae Sen Gupta & Crowson, 1973
    Murmidiinae Jacquelin Du Val, 1858
    Ceryloninae Bilberg, 1820
Alexiidae Imhoff, 1856
Discolomatidae Horn, 1878
    Notiophyginae Jacobson, 1915
    Discolomatinae Horn, 1878
    Aphanocephalinae Grouvelle, 1912
    Cephalophaninae John, 1954
    Pondonatinae John, 1954
Endomychidae Leach, 1815
    Merophysiinae Seidlitz, 1872
    Pleganophorinae Jacquelin Du Val, 1885
    Anamorphinae Strohecker, 1953
    Leiestinae C. G. Thomson, 1863
    Mycetaeinae Jacquelin Du Val, 1857
    Eupsilobiinae Casey, 1895
    Xenomycetinae Strohecker in Arnett, 1962
    Danascelinae Tomaszewska, 2000
    Endomychinae Leach, 1815
    Epipocinae Gorham, 1873
    Stenotarsinae Chapuis, 1876
    Lycoperdininae Redtenbacher, 1844
Coccinellidae Latreille, 1807
    Microweiseinae Leng, 1920 (= Sticholotidinae part)
    Coccinellinae Latreille, 1807 (incl. Sticholotidinae part, Chilocorinae, Coccidulinae, Scymninae, Ortaliinae, Epilachninae)
Corylophidae Leconte, 1852
    Periptyctinae Ślipiński *et al.,* 2001
    Corylophinae LeConte, 1852
Latridiidae Erichson, 1842
    Latridiinae Erichson, 1852
    Corticariinae Curtis, 1829

Tenebrionoidea

Mycetophagidae Leach, 1815
    Esarcinae Reitter, 1882
    Mycetophaginae Leach, 1815
    Bergininae Leng, 1920
Archeocrypticidae Kaszab, 1964
Pterogeniidae Crowson, 1953
Ciidae Leach in Samouelle, 1819
    Sphindociinae Lawrence, 1974
    Ciinae Leach in Samouelle, 1819
Tetratomidae Billberg, 1820
    Tetratominae Billberg, 1820
    Piseninae Miyatake, 1960
    Penthinae Lacordaire, 1859
    Hallomeninae Mulsant 1856/Gistel, 1856 (from Melandryidae)
    Eustrophinae Gistel, 1856 (from Melandryidae)
Melandryidae Leach, 1815
    Melandryinae Leach, 1815
    Osphyinae Mulsant, 1856 (1840)

Mordellidae Latreille, 1802
  Ctenidiinae Franciscolo, 1951
  Mordellinae Latreille, 1802
Ripiphoridae Gemminger & Harold, 1870 (1853)
  Ptilophorinae Gerstaecker, 1855
  Pelecotominae Seidlitz, 1875 (incl. Micholaeminae)
  Hemirhipidiinae Heller, 1921
  Ripidiinae Gerstaecker, 1855
  Ripiphorinae Gemminger & Harold, 1870 (1853)
Zopheridae Solier, 1834
  Colydiinae Erichson, 1842
  Zopherinae Solier, 1834 (incl. Monommatinae, Usechinae, Pycnomerinae)
Ulodidae Pascoe, 1869
Promecheilidae Lacordaire, 1859 (= Perimylopidae)
Chalcodryidae Watt, 1974
Trachelostenidae Lacordaire, 1859
Tenebrionidae Latreille, 1802
  Lagriinae Latreille, 1825 (1820)
  Nilioninae Lacordaire, 1859
  Cossyphodinae Wasmann, 1899
  Phrenapatinae Solier, 1834
  Zolodininae Watt, 1974
  Pimeliinae Latreille, 1802
  Tenebrioninae Latreille, 1802
  Alleculinae Laporte, 1840
  Diaperinae Latreille, 1802
  Stenochiinae Kirby, 1837 (= Coelometopinae)
Prostomidae C. G. Thomson, 1859
Synchroidae Lacordaire, 1859
Stenotrachelidae C. G. Thomson, 1859
  Stenotrachelinae C. G. Thomson, 1859
  Cephaloinae LeConte, 1862
  Nematoplinae Leconte, 1862
  Stoliinae Nikitsky, 1985
Oedemeridae Latreille, 1810
  Polypriinae Lawrence, 2005
  Calopodinae Costa, 1852
  Oedemerinae Latreille, 1810 (incl. Nacerdinae)
Meloidae Gyllenhal, 1810
  Eleticinae Wellman, 1910
  Meloinae Gyllenhal, 1810
  Tetraonycinae Böving & Craighead, 1931
  Nemognathinae Laporte, 1840
Mycteridae Blanchard, 1845
  Mycterinae Blanchard, 1845
  Eurypinae J. Thomson, 1860 (= Lacconotinae)
  Hemipeplinae Lacordaire, 1854
Boridae C. G. Thomson, 1859
  Borinae C. G. Thomson, 1859
  Synercticinae Lawrence & Pollock, 1994
Trictenotomidae Blanchard, 1845
Pythidae Solier, 1834
Pyrochroidae Latreille, 1807
  Tydessinae Nikitsky, 1986
  Pilipalpinae Abdullah, 1964
  Pedilinae Lacordaire, 1859
  Pyrochroinae Latreille, 1807
  Agnathinae Lacordaire, 1859
Salpingidae Leach, 1815
  Othniinae LeConte, 1861
  Prostominiinae Grouvelle, 1914
  Agleninae Horn, 1878
  Inopeplinae Grouvelle, 1908
  Dacoderinae LeConte, 1862
  Aegialitinae LeConte, 1862
  Salpinginae Leach, 1815
Anthicidae Latreille, 1819
  Eurygeniinae LeConte, 1862
  Macratriinae LeConte, 1862
  Steropinae Jacquelin Du Val, 1863
  Copobaeninae Abdullah, 1969
  Lemodinae Lawrence & Britton, 1991
  Tomoderinae Bonadona, 1961
  Anthicinae Latreille, 1819
Aderidae Winkler, 1927
Scraptiidae Mulsant 1856/Gistel, 1856
  Scraptiinae Mulsant, 1856/Gistel, 1856
  Anaspidinae Mulsant, 1856

Tenebrionoidea *Incertae Sedis*
  Lagrioidinae Abdullah & Abdullah, 1968 (from Anthicidae)
  Afreminae Levey, 1985 (from Anthicidae)
  Ischaliinae Blair, 1920 (from Anthicidae)
  Rhizonium Sharp, 1876
  Aprostomis Grouvelle, 1912

2. Glossary of Morphological Terms

John F. Lawrence, Rolf G. Beutel, Richard A. B. Leschen and Adam Ślipiński

Although a brief overview of beetle morphology may be found in Crowson (1955, 1981), Lawrence (1991), Lawrence & Britton (1991), Lawrence *et al.* (1999 a, b) and Beutel & Lawrence (2005), the following set of definitions and discussions represents a preliminary attempt to standardize nomenclature within the order, especially with respect to terminology introduced in relatively recent publications and not included in general textbooks or dictionaries. This is not meant to be a complete glossary, and a detailed treatment of beetle morphology will be included in a later volume of this series. The terms discussed below are, in general, those which turn up regularly in adult and larval descriptions of the beetle families included in this volume, and commonly used words found in general insect morphology texts are included only when their use within the order Coleoptera requires some explanation or elaboration. Terms or topics are arranged alphabetically under each of eight subheadings: head, prothorax, pterothorax, hind wing and abdomen for adults and head, thorax and abdomen for larvae.

Adult Head

Antennae: Clavate. Antennomeres gradually broader towards the apex; synonymous with incrassate.

Antennae: Capitate. One or more apical antennomeres are abruptly broader than and/or distinctly longer than those preceding them.

Antennal Fossa. Saucer-like concavity surrounding the countersunk antennal insertion (not to be confused with the antennal insertion or socket).

Antennal Insertion. Point of attachment of the antenna. Antennal insertions are considered to be exposed when at least some portion of each antennal socket is visible from above the long axis of the head (without regard to head orientation with respect to the body).

Cervical Sclerite. Compound sclerite in Polyphaga joining the ventrolateral edge of the occipital foramen with the lateral portion of the prosternum on each side. Each sclerite is usually divided into an anterior and posterior section separated by membrane.

Corpotentorium. Transverse bridge (tentorial bridge) connecting the posterior tentorial arms, often arched and occasionally bearing an anteriorly projecting median process (Stickney 1923).

Corporotentorium (**see** Corpotentorium).

Epistomal Suture (or Sulcus) (**see** Frontoclypeal Suture).

Frontoclypeal Suture. Transverse suture representing an invagination between the frons and clypeus to form the epistomal ridge beneath with the anterior tentorial pits at either end.

Laminatentoria. Mesal expansions of the anterior tentorial arms, which may meet at the midline to form a secondary bridge anterior to the corpotentorium, if present (Stickney 1923).

Median Occipital Endocarina. Internal longitudinal ridge extending anteriorly from the dorsal edge of the occipital foramen.

Subantennal Groove. Groove or concavity lying below the antennal insertion and housing the base of the antenna. Placed between the eye (if present) and the mandibular articulation, and sometimes extends below or behind the eye.

Transverse Occipital Ridge. Any transverse line, carina or elevated ridge extending across the occipital region between the eyes and the occipital foramen. Usually indicates the extent to which the head is retracted into the prothorax; an elevated ridge may abut the anterior edge of the pronotum.

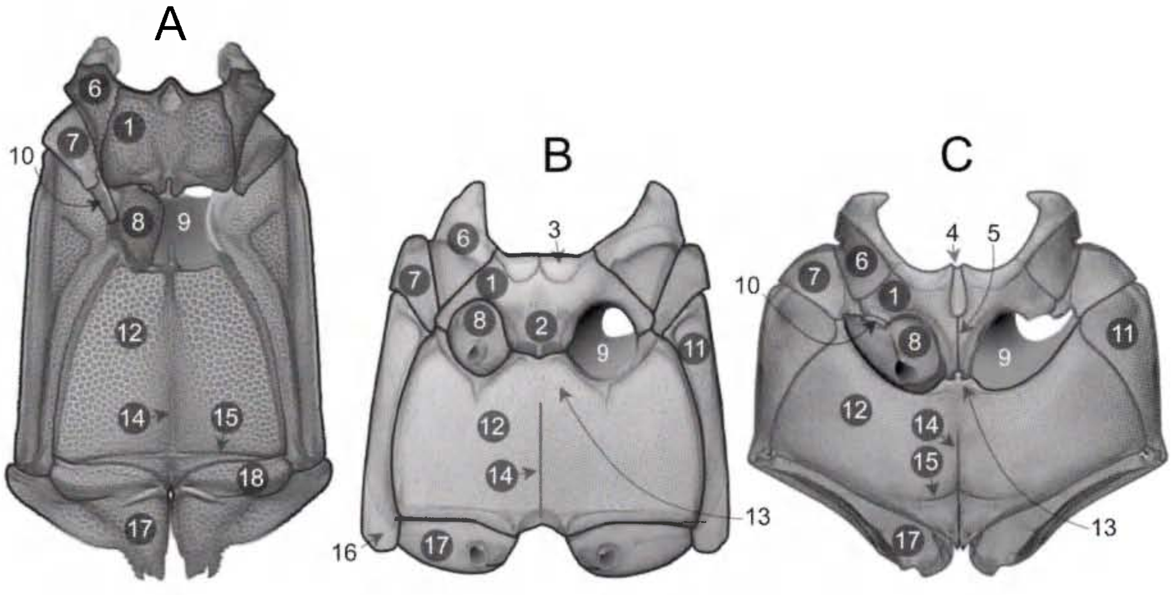
Vertexal Line (**see** Transverse Occipital Ridge).

Adult Prothorax

Cryptopleuron (**see** Endopleuron).

Endopleuron. Portion of the propleuron beneath the pronotum; not visible externally. In Archostemata, Adephaga and some Myxophaga this is a relatively minor part of the pleuron, but in almost all Polyphaga the pleuron is entirely internalized.

Hypomeron. Ventral portion of pronotum below the lateral pronotal carinae when these are present. In many Polyphaga, the two hypomera extend mesally behind the coxae partly or completely closing the procoxal cavities externally (**see** Postcoxal Process).



1. Mesoventrite
2. Mesoventral Process
3. Procoxal Rest
4. Mesoventral Cavity
5. Mesothoracic Discrimen
6. Mesanepisternum
7. Mesepimeron
8. Mesocoxa
9. Mesocoxal Cavity
10. Mesotrochantin
11. Metanepisternum
12. Metaventrite
13. Metaventral Process
14. Metathoracic Discrimen
15. Metakatepisternal Suture
16. Metepimeron
17. Metacoxa
18. Metatrochantin

Fig. 2.1. Coleopteran pterothoraces, ventral: A, *Distocupes varians* (Lea) (Archostemata: Cupedidae); B, *Episcaphula australis* (Boisduval) (Polyphaga: Cucujoidea: Erotylidae); C, *Sclerocyphon* sp. (Polyphaga: Byrrhoidea: Psephenidae). (© CSIRO Australia).

Lateral Pronotal Carina. Distinct edge separating the pronotal disc from the pronotal hypomeron on each side. Equivalent to the lateral edge of the prothorax (but not the pronotum, which terminates only at the notopleural or notosternal suture). The lateral carina may be raised to form a margin or bead, but that is not always the case.

Postcoxal Process. Mesal extension of the posterior part of the propleuron (Archostemata and Adephaga) or hypomeron (Myxophaga and Polyphaga) behind the procoxa, which may meet the prosternal process or the opposing postcoxsal process, thus closing the procoxal cavitiy externally.

Pronotal Disc. Dorsal portion of the pronotum, lying above the lateral pronotal carinae when these are present.

Procoxal Cavity. Countersunk prothoracic housing into which the procoxa fits. Formed in part by the prosternum (but **see** Prosternum) and in part by the propleuron (Archostemata, Adephaga and Myxophaga) or pronotal hypomeron (Polyphaga). This is an autapomorphy of the order Coleoptera but is secondarily reduced in a number of soft-bodied beetles.

Procoxal Cavities: External Closure. Externally closed when the postcoxal processes of the hypomera meet the prosternal process or meet one another.

Procoxal Cavities: Internal Closure. Internally closed when a narrow or broad bridge connects a portion of the internal lining of the cavity (usually in the vicinity of the sternal apophysis) with the internal wall of the postcoxal process.

Prosternal Process. Posterior projection of the mesal portion of the prosternum which extends between the procoxae and may overlap the mesoventrite or fit into the mesoventral cavity. The term "spinasternum" has been used by those studying Curculionoidea for the posterior end of the prosternal process, when the central portion of that process has been obliterated to accommodate the enlarged and contiguous procoxae.

Prosternum. Used for the entire ventral plate lying in front of and between the procoxae and between the notosternal or pleurosternal sutures, although it is likely that this sclerite has a complex origin, like comparable structures in the mesothorax and metathorax (**see** Mesoventrite and Metaventrite).

Spinasternum (**see** Prosternal Process).

Sublateral Pronotal Carina. Applied to various longitudinal carinae lying mesad of the lateral carinae. These may extend the length of the pronotal disc, as in Laemophloeidae, or be restricted to the posterior angles, as in many Elateridae.

Adult Pterothorax

Elytral Sutural Flange: Deflection. Deflected when the apical portion of the flange is expanded and thus visible when the elytra are in the closed position. Characteristic of certain families of Cucujoidea (Leschen *et al.* 2005) but may occur elsewhere.

Lateral Closure of Mesocoxal Cavity. Laterally open when the lateral wall is formed partly by one or more pleural sclerites and laterally closed when the lateral wall is formed entirely by the meeting of the mesoventrite and metaventrite.

Mesanepisternum. Anterior pleural sclerite of the mesothorax.

Mesendosternite. A pair of internal apodemes formed by invaginations within the mesocoxal cavities and representing the original furca.

Mesepimeron. Posterior pleural sclerite of the mesothorax.

Mesocoxal Cavity. Countersunk pterothoracic housing into which the mesocoxa fits. Formed by portions of the mesoventrite and metaventrite, often with the addition of mesopleural sclerites and less commonly the metanepisternum. This autapomorphy of the order Coleoptera is secondarily reduced in a number of soft-bodied beetles.

Mesofurca (**see** Mesendosternite).

Mesometathoracic Joint. Joint between mesothorax and metathorax which is visible only within the mesocoxal cavities; membranous in Archostemata and Adephaga and some families of Polyphaga, but either consists of a solid joint or is completely absent in Myxophaga and most Polyphaga.

Mesometaventral Joint (**see** Mesometaventral Junction).

Mesometaventral Junction. Meeting of the mesoventrite and metaventrite between the mesocoxal cavities. The junction may involve the abutment of the two sclerites, the overlapping of one by the other, or a complex, monocondylic or dicondylic joint. In some instances the two sclerites are fused together with or without a visible joint.

Mesosternal Cavity (**see** Mesoventral cavity).

Mesosternum (**see** Mesoventrite).

Mesothoracic Discrimen. Median line on the mesoventrite representing the invagination of the true mesosternum. This line is rarely complete and often absent in the mesothorax, where the single invagination or furca is replaced by well separated endosternal apodemes.

Mesoventral Cavity. Cavity on the mesoventrite into which the prosternal process fits.

Mesoventral Process. Mesal lobe at the posterior edge of the mesoventrite which usually extends between the mesocoxal cavities and meets the metaventral process (**see** Mesometaventral Junction).

Mesoventrite. Applies to the ventral plate lying in front of and between the mesocoxal cavities; delimited laterally by the mesothoracic pleurosternal sutures. Although called the mesosternum in most earlier works on Coleoptera, this sclerite is equivalent to the paired mesothoracic preepisterna and paired mesokatepisterna, the true mesosternum having been largely invaginated and represented only by the area in the immediately vicinity of the bases of the mesendosternites). The transverse suture separating the katepisterna from the preepisterna is never complete in the mesothorax of beetles (indicated by an internal transverse ridge in a few Archostemata) and the discrimen, representing the invagination of the original mesosternum, is present in most Archostemata, Gyrinidae, most Scirtoidea, most Buprestidae, a number of byrrhoid families and the elateroid family Artematopodidae.

Metacoxal Cavity. Countersunk abdominal housing into which the metacoxa fits. Usually formed by abdominal sternites II and III combined with the posterior wall of the metaventrite. This autapomorphy of the order Coleoptera is secondarily reduced in a number of soft-bodied beetles.

Metafurca (**see** Metendosternite).

Metakatepisternal Suture. Transverse suture on the metaventrite which separates the paired metathoracic preepisterna from the paired metakatepisterna. Although a complete suture, extending from the discrimen to the lateral edges of the mesoventrite on each side, is part of the groundplan of Coleoptera, it is often shortened so that it extends for only a short distance on either side of the discrimen.

Metanepisternum. Anterior pleural sclerite of the metathorax, which in Coleoptera is laterad of the metaventrite and mesoventrad of the metepimeron. Because the lateral (dorsal) portion of the metanepisternum is often concealed beneath the elytral epipleura, its shape in descriptions is based on the visible portion only.

Metathoracic Discrimen. Median line extending forward from the posterior edge of the metaventrite, internally corresponding with a more or less high median ridge representing the invagination of the true metasternum. The ridge is usually connected with the metendosternite. The discrimen is often relatively long and may extend anteriorly to or beyond the base of the metaventral process, but it is reduced or absent in a number of groups.

Metaventral Process. Mesal lobe at the anterior end of the metaventrite which often extends forward between the mesocoxae and meets the mesoventral process (**see** Mesometaventral junction).

Metaventrite. Ventral plate lying behind and between the mesocoxal cavities and delimited laterally by the metanepisterna. Although called the metasternum in most earlier works on Coleoptera, this sclerite is equivalent to the paired metapreepisterna and paired metakatepisterna, the true metasternum having been invaginated along the midline. The transverse suture separating the katepisterna from the preepisterna is often complete, but may be shortened (extending for a short distance on either side of the discrimen) or absent, and the discrimen, representing the invagination of the original metasternum, is often very long, sometimes completely dividing the metaventrite into halves, but may be shortened or absent in various taxa. [Ferris 1940; Campau 1940; Matsuda 1960; Lawrence 1999; Lawrence *et al.* 1999 b; Beutel & Haas 2000.]

Metendosternite. Complex internal apodeme equivalent to the metafurca. Arises at or near the posterior edge of the metaventrite usually at the junction of the discrimen and the metakatepisternal suture and projecting anterodorsally. It usually consists of a median stalk, two short to long lateral arms and an anterior process from which a pair of tendons arise; however a lamina may be associated with each of the lateral arms and a pair of anteroventral processes may arise from the point where the lateral arms meet the stalk. In some taxa the stalk may be short or absent and the anterior tendons often arise on the arms. [Crowson 1938, 1944, 1955.]

Metepimeron. Posterior pleural sclerite of the metathorax, which in Coleoptera is located laterad of and above the metanepisternum and mostly concealed by the elytral epimeron. In most beetle groups a small portion of this sclerite is visible near the lateral edge of the metacoxa.

Prepectus. Anterior portion of mesoventrite and combined mesanepisterna, especially when set off from remainder of ventrite.

Pretarsus. The terminal segment of the leg, consisting of a pair of claws in most adults or rarely a single claw.

Postcoxal Lines of Metaventrite. Slightly raised ridges or abrupt edges of impressions at the anterior edge of the metaventrite. Sometimes these lines delimit crural impressions, but this is not always the case.

Procoxal Rests of Mesoventrite. Pair of impressions at the anterior edge of the mesoventrite into which the procoxae fit; these impressions may be almost horizontal in lateral view, but more often they are distinctly inclined or occasionally almost vertical. The procoxal rests sometimes extend laterally beyond the mesoventrite and onto the mesanepisterna.

Prosternal Rest of Mesoventrite. Median elevation at the anterior edge of the mesoventrite which fits against the underside of the prosternal process; in those elateroid taxa utilizing the clicking maneuver this process blocks the prosternal process from sliding into the mesoventral cavity until sufficient pressure is built up to overcome the inertia. In some other taxa the process may be flattened and abut the underside of the prosternal process.

Prothoracic Rest of Mesoventrite. Refers to a condition in which the entire anterior edge of the mesoventrite and flanking mesanepisterna form a peduncle over which the prothorax fits; this is usually correlated with a broad external closure of the procoxal cavities.

Scutellar Shield. Exposed portion of the mesoscutellum which lies between the bases of the elytra.

Scutellum. Posterior portion of mesotergum. Often referring only to that portion of the scutellum which is visible between the bases of the elytra (**see** Scutellar Shield).

Transverse Metasternal Suture (**see** Metakatepisternal Suture).

Transverse Metaventral Suture (**see** Metakatepisternal Suture).

Trochantin. Precoxal remnant articulating with the coxa, sternum and pleuron.

Trochantin (Prothorax). Used in Myxophaga and Polyphaga for the exposed portion of the trochantinopleuron.

Trochantinopleuron. Fusion product of the prothoracic trochantin with the propleuron.

Hind Wing

The terms for wing veins and related structures used in this volume are based primarily on that of Kukalová-Peck & Lawrence (1993, 2004). Some changes in wing vein terminology listed on p. 144

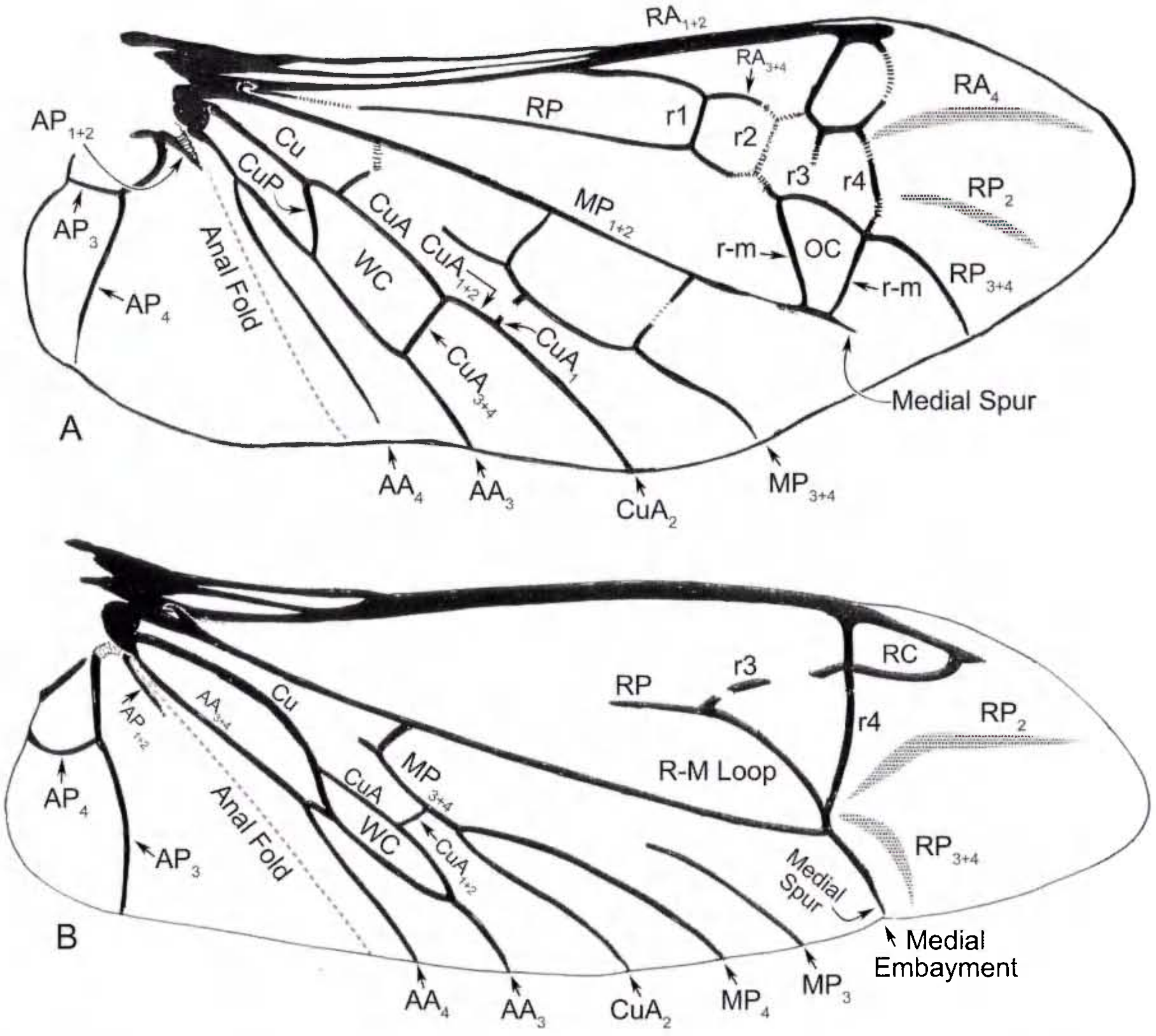


Fig. 2.2. Coleopteran hind wings: A, *Omma stanleyi* Newman (Archostemata: Ommatidae); B, *Notodascillus sublineatus* Carter (Polyphaga: Dascilloidea: Dascillidae). (Modified from Lawrence & Britton 1991; © CSIRO Australia.) RC = Radial cell; OC = Oblongum cell; WC = Wedge cell.

of the latter work and based in part on the study by Haas & Kukalová-Peck (2001) have been overlooked in some subsequent studies. The most important of these deal with venation in the medial field and will be repeated here: CuA = Cu, CuA_{1+2} = CuA, CuA_{3+4} = CuP, CuA_2 = CuA_{3+4}, AA = AA_{3+4}, AA_{1+2} = AA_3, AA_{3+4} = AA_4.

Anal Area (**see** Anal Lobe).

Anal Embayment. Embayment in the wing margin at the end of the anal fold which may be weak and gradual or consist of a deep notch.

Anal Field (**see** Anal Lobe).

Anal Fold. Fold between AA_{3+4} and AP; delimiting the anal lobe.

Anal Lobe. Portion of the wing basad of the anal fold. The anal lobe (actually homologous with the ano-jugal lobe but the jugal component is highly reduced in beetle wings) usually contains AP_{3+4} (which may be forked to form AP_3 and AP_4) and occasionally a small AP_{1+2} may also be present. In Lawrence *et al.* (1999 b) the term "anal lobe" was used in narrower sense for those instances where the anal field was separated from the remainder of the wing by a deep notch.

Anal Notch. Deep and usually narrow anal embayment.

Ano-Jugal Lobe (**see** Anal Lobe).

Anterior Wing Strut (**see** Radial Bar).

Apical Area (**see** Apical Field).

Apical Extensions of RP. Branches of RP (usually RP1 and RP2) extending apicad of the R-M loop. In some taxa there may be two or three branches, in others only RP2 remains and branches may be vaguely indicated or absent. Linear, often oblique sclerotizations in the apical field of various elateroid wings (Crowson 1961; Dolin 1975) may represent remnants of these radial extensions, but this is uncertain.

Apical Field. Portion of the wing membrane lying apicad of the radial cell (Polyphaga), cross-vein r4, the R-M loop (Polyphaga), the oblongum cell (most Archostemata, Myxophaga and Adephaga) and medial spur, and often containing terminal branches of RA and RP or the elateroid sclerites possibly derived from them.

Basal Portion of RP. Portion of RP between its origin (usually obliterated) and its junction with an R-M cross-vein forming the R-M loop or the base of the oblongum cell. Rarely complete and very short or even absent in some taxa.

Bending Zone. Area of weakness in the radial and medial bars which allows them to be curved towards one another when the bar is rotated in a certain way (by movements of the axillary sclerites). The weakness may be caused by a series of transverse impressions or by a flattening of the strut. Bending zones may be relatively broad so that bending is gradual or may be shortened to the point where they are more like a sharp hinge. Bending zones are found in only a few of the polyphagan families included in this volume.

Cross-vein r3. Subapical cross-vein between RA_{3+4} and RP; transverse (perpendicular to long axis of wing) or strongly oblique in Archostemata, Myxophaga and Adephaga and often slightly oblique to longitudinal (parallel to long axis of wing) in Polyphaga; rarely complete and often absent. Termed the "radial recurrent vein" in some older systems of nomenclature.

Cross-vein r4. Apical cross-vein between RA_{3+4} and RP; always more or less transverse and usually complete.

Cubito-Anal Remnant. Occasionally used when a single compound vein consisting of Cu, CuP and AA_3 remains in the medial field.

Deflexion Zone (**see** Bending Zone).

Free Veins. Veins not joined apically to another vein and often extending to the wing margin; in the medial field usually consisting of MP_{3+4} (or MP_3 and MP_4), CuA_2, AA_3 and AA_4.

Medial Area (see Medial Field).

Medial Bar. Posterior wing strut, consisting entirely of MP_{1+2}.

Medial Binding Patch (see Medial Fleck).

Medial Bridge. Bridge at the base of the wing connecting RA with MP_{1+2}; important in the folding and unfolding of the wing.

Medial Embayment. Emargination of the wing membrane at or beyond the end of the medial spur.

Medial Field. Portion of the wing membrane between medial bar (MP_{1+2}) and the anal fold and usually containing branches of MP_{3+4}, Cu and AA_{3+4}. Veins in the medial field, referred to by Crowson (1955, p. 91) as "anal veins in the main group", tend to anastomose in various ways and reduction of free veins from five to one or none is relatively common, especially in small species.

Medial Fleck. Binding patch located in the medial field. In Polyphaga this is located in front of MP_{3+4}. In some Adephaga a non-homologous fleck is located behind MP_{3+4}. and usually containing MP_{3+4}, Cu and AA_{3+4} and their branches.

Medial Spur. Apical extension of MP_{1+2} beyond the R-M loop or oblongum cell. Very short and straight or absent in Archostemata, Myxophaga and Adephaga and usually longer and posteriorly curved in Polyphaga.

Median Area. Error in Lawrence *et al.* (1999 b) (**see** Medial Field).

Median Bar. Error in Lawrence *et al.* (1999 b) (**see** Medial Bar).

Medio-Cubital Brace. Reinforced cross-vein joining MP_{1+2} and Cu near their bases, but usually broken in the middle by a fold.

MP_{3+4}: Cross-vein and Basal Spur. Sub-basal cross-vein joining MP_{3+4} to MP_{1+2} and often accompanied by a basal spur, which is a remnant of the true base of the vein. When the spur is absent, the cross-vein may appear to be the base of MP_{3+4}, but in a more apical position.

Oblongum Cell. Cell in most Archostemata, Adephaga and Myxophaga formed between two R-M cross-veins.

Posterior wing strut (**see** Medial Bar).

Radial Bar. Anterior wing strut consisting of an alignment and fusion of ScP and RA.

Radial Cell. Forking of RA into RA_{1+2} and RA_{3+4} and a subsequent rejoining of these two branches near the anterior wing margin in Polyphaga. Not homologous with cells formed by cross-veins between RA_{1+2} and RA_3 or RA_{3+4} in Archostemata, Myxophaga and Adephaga.

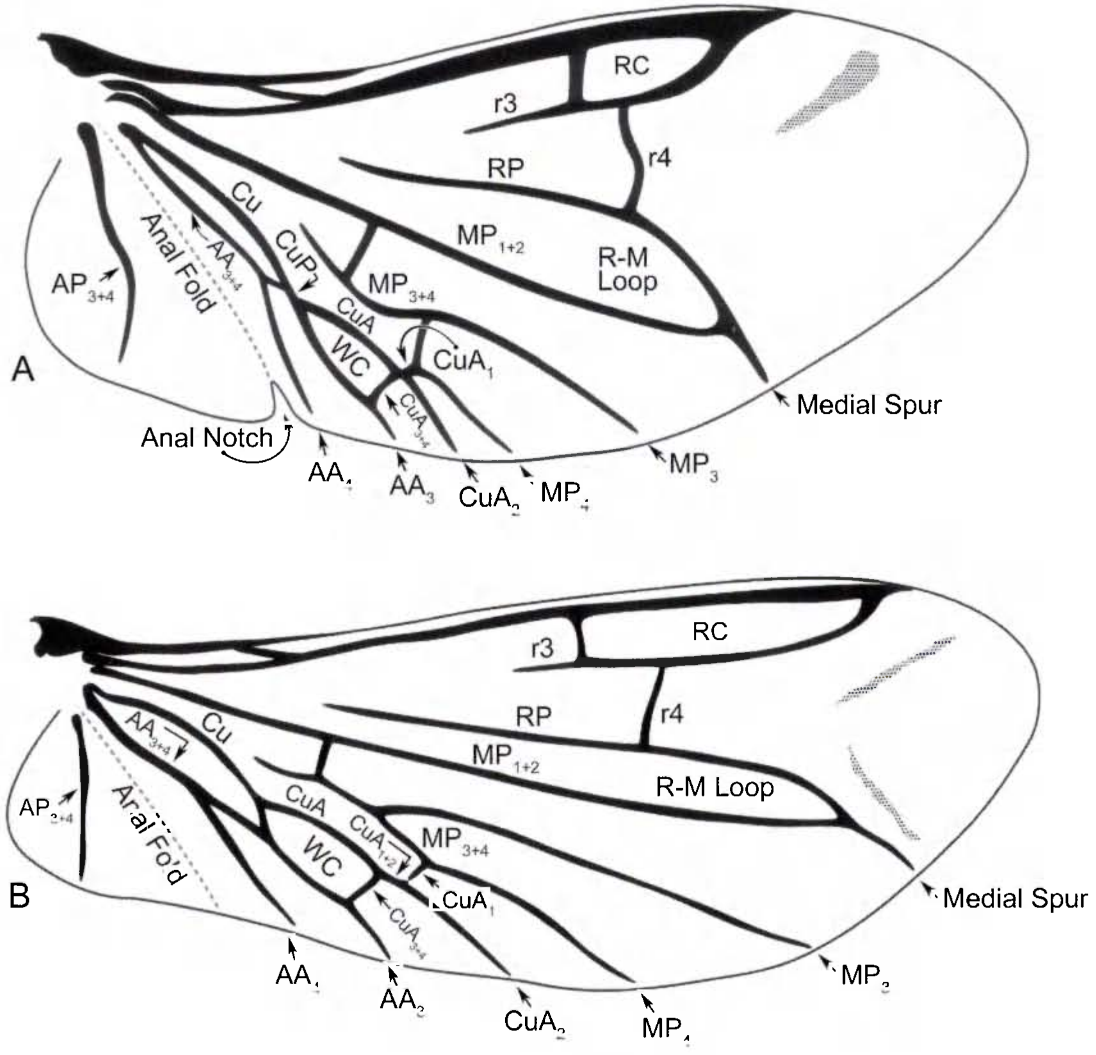


Fig. 2.3. Coleopteran hind wings: A, *Osslimus freyi* (Cobos) (Polyphaga: Elateroidea: Elateridae); B, *Stichotomus* sp. (Polyphaga: Elateroidea: Elateridae). (Modified from Calder 1996; © CSIRO Australia.)

Radio-Medial Loop (**see** R-M Loop).

R-M Loop. Apically arched R-M cross-vein joining the basal portion of RP and MP_{1+2}. Homologous to the apical side of the oblongum cell. Often forming a continuous curve between RP and MA, but sometimes narrowed so that an acute angle is formed.

Second Cubito-Anal Cell (**see** Wedge Cell).

Subcubital Fleck (**see** Medial Fleck).

Transverse Folds. More or less obliquely transverse folds; involved in the shortening of the wing length.

Wedge Cell. Cell formed by CuA anteriorly, CuP basally, AA_3 posteriorly, and CuA_{3+4} apically and usually giving rise apically or subapically to one or more branches of Cu and to the terminal portion of AA_3. This cell is also referred to as the 2nd cubito-anal cell, the first being formed at the wing base between Cu and AA_{3+4}, with CuP at its apex.

Adult Abdomen

Accessory Lobes. Paired lobes articulated with the apicale in the aedeagus of various Tenebrionoidea.

Aedeagus. Combined structure consisting of phallobase, parameres and penis.

Apicale. Formed by the fusion of the two parameres.

Baculum. Sclerotized bar or strut which serves to support a membranous ovipositor. Paired longitudinal baculi are often present on the proctiger and paraprocts, and a transverse baculum often occurs at the base of the coxite.

Basal Piece (**see** Phallobase).

Basale (**see** Phallobase).

Bursa. Enlargement of the female genital tract, which is often a blind sac at the anterior end of the tract (anterior bursa), but may be an enlarged section of the tract in the vicinity of the common oviduct (vaginal bursa).

Connate Ventrites. Visible sternites which are not freely movable. This is not always easy to determine in lightly sclerotized abdomens, and there tends to be a continuum from sclerites which are capable of some limited movement to those which are solidly fused together. In rare cases the sutures between connate ventrites may be partly to almost entirely effaced.

Coxite (**see** Gonocoxite).

Cucujiform Aedeagus. That type of aedeagus in which the phallobase forms a sheath or ring partly or entirely enclosing the penis.

Double Tegmen. Referring to a type of cucujiform aedeagus found in a number of Cleroidea plus the cucujoid families Biphyllidae and Byturidae in which the tegmen bears a pair of anterior struts and an opposing median anterior strut.

Endophallus. Inverted membranous tube within the penis and sometimes armed with a variety of sclerotized structures.

Epiproct (**see** Proctiger).

Genital Ring. Ring-like structure surrounding the aedeagus and consisting of segments IX and X, which may be partly or entirely fused together.

Gonangulum (**see** Gonocoxite).

Gonocoxite. One of two coxites associated with segment IX in female Coleoptera. The coxite is often divided into a basal and apical lobes, the first of which may have a transverse or oblique baculum which articulates with the paraproctal baculum. The apical lobe is further subdivided in some taxa. The basal coxital lobe may be homologous to the gonangulum of Scudder (1961).

Gonostylus (**see** Stylus).

Hemitergite IX (**see** Laterotergite IX, Paraproct).

Internal Sac (**see** Endophallus).

Lateral Lobes (**see** Parameres).

Laterotergite IX. Paired plates formed when tergite IX is divided into two parts in either male or female (**see** Paraproct).

Median Lobe (**see** Penis).

Ovipositor. In female Coleoptera usually referring to the combined proctiger, paraprocts, gonocoxites and styli. One or more of these elements may be absent in certain groups and in a few families there is no distinct ovipositor, but just a vulva surrounded by membrane.

Parameral Piece (**see** Apicale).

Parameres. Paired structures articulated with the posterior end of the phallobase in aedeagi of the trilobate type; sometimes fused to the phallobase, fused together in various ways or fused to the anterior end of the penis.

Paraproct. Referring to one of the two hemitergites or laterotergites of segment IX in most female beetles in which segment IX has become entirely divided into two parts which lie on either side of tergite X.

Penis. Major intromittent organ containing the inverted endophallus and the opening of the ejaculatory duct; enclosed by the phallobase and parameres or the tegmen.

Phallobase. Anterior or basal portion of the aedeagus to which the parameres are attached in aedeagi of the trilobate type. In aedeagi of the cucujiform type, the phallobase forms most of the sheath or ring enclosing the penis.

Postcoxal Lines of First Abdominal Ventrite. Slightly raised ridges of abrupt edges of impressions at the anterior edge of ventrite 1. Usually delimiting crural impressions.

Proctiger. Referring to tergite X in both male and female; lies immediately above the anal opening and may become membranous in some groups.

Spermatheca. Usually referring to a sac-like structure, often sclerotized; attached by a slender duct to the genital tract.

Spermathecal Gland. Gland associated with the spermatheca, usually either joined directly to it or to the spermathecal duct.

Spiculum Gastrale. Slender strut formed by an anterior extension of the subgenital plate.

Spiculum Relictum. Anterior strut on sternite VIII in the male.

Spiculum Ventrale. Anterior strut on sternite VIII in the female.

Stylus. Small lobe articulated apically or subapically to the coxite in the ovipositor of most Coleoptera.

Subgenital Plate. Ventral portion of the genital ring, formed by a fusion of sternite IX and anteroventral extensions of tergite IX or laterotergites IX.

Tegmen. Usually synonymous with the phallobase in aedeagi of the cucujiform type, in which the phallobase forms a sheath or ring partly or entirely surrounding the penis (**see** Cucujiform Aedeagus). When the parameres are fused to the end of the phallobase, the term tegmen is often used for the entire combined structure.

Tegmenite. Slender sclerite articulated with sternite IX or in the connecting membrane between the sternite IX and the phallobase.

Tergite X (**see** Proctiger).

Trilobate Aedeagus. Basal type of aedeagus in Coleoptera, which consists of a penis lying dorsad of a phallobase and paired, articulated parameres. In many Coleoptera, including most Archostemata, Adephaga and Myxophaga, as well as a variety of Polyphaga, the phallobase appears to be absent, having become membranous or fused to the parameres.

Vaginal Palp. Combined gonocoxite and stylus (Mikoleit 1973).

Valvifer. Used inconsistently by Tanner (1927) but in general homologous with the paraproct (**see** Paraproct).

Ventral Sclerite. Slender longitudial sclerite lying ventrally between the coxites and below the vulva.

Ventrite: Abdominal sternite exposed in intact specimens; not concealed by the metacoxae or enclosed within the abdominal apex. The first ventrite in most Polyphaga and in Myxophaga and Archostemata is sternite III, but it is sternite II in Adephaga and in some groups of Polyphaga.

Vulvar Sclerite (**see** ventral sclerite).

Larval Head

Coronal suture (**see** Epicranial Stem).

Ecdysial lines. Lines of weakness on the dorsal head surface where the cuticle separates during moulting.

Epicranial Stem. Median ecdysial line, which forks to form the frontal arms.

Epicranial suture (**see** Ecdysial Lines, Epicranial Stem, Frontal Arms).

Frontal Arms. Paired ecdysial lines either arising from the epicranial stem or independently joined to the posterior edge of the head capsule.

Frontal Sutures (**see** Frontal Arms).

Gula. Sclerotised region posterad of the posterior tentorial pits.

Hypopharyngeal Bracon. More or less sclerotized (but not usually pigmented) bridge joining the ventral mandibular articulation on each side with the hypopharynx.

Hypopharyngeal Sclerome. Sclerotized bar or tooth-like structure on the hypopharynx; acts in conjunction with the mandibular molae.

Hypostomal Cavity. Excavation of the ventral portion of the head capsule enclosing the retracted maxillae and labium.

Hypostomal Ridges. Sclerotized lateral edges of the hypostomal cavity.

Hypostomal Rods. Posterior continuations of the hypostomal ridges beyond the maxillary bases and onto the ventral portion of the head capsule.

Ligular Sclerome. Sclerotized wedge-like sclerite formed from the ligula. Not equivalent to the hypopharyngeal sclerome, which is located well posterad of this on the surface of the hypopharynx.

Maxillolabial Complex. The combination of maxillae and labium when these are closely associated and mainly or exclusively moved in a nearly vertical direction (without an intervening maxillary articulating area).

Medial Endocarina. Dorsal internal ridge on the head usually lying beneath the epicranial stem, when present, and often extending forward between the frontal arms. May also be present when ecdysial lines are absent.

Mola. Usually basal and armed with asperities, tubercles or transverse ridges. In some groups somewhat reduced and sub-basal.

Paired Endocarinae. Pair of dorsal internal ridges on the head, usually lying beneath the bases of the frontal arms.

Prostheca. Located distad of the basal mola and either membranous, sclerotized but hyaline, or consisting of hair-like structures of various kinds. Similar structures in the absence of a mola are not referred to as prosthecae.

Sensorium. Usually refers to a large sensillum located on the preapical antennomere. Although it is usually conical or palpiform, it may be dome-like or occasionally multiple or complex (consisting of several dome-like sections). Occasionally located on the apical palpomere or very rarely (some Phalacridae) on the basal one.

Sensory Appendage (**see** Sensorium).

Ventral Epicranial Ridges. Pair of ridges extending posteriorly from the ventral mandibular articulations; located laterad and ventrad of the hypostomal ridges and more or less supporting the maxillolabial complex.

Ventral Mouthparts. Refers to the maxillae plus the labium or the maxillolabial complex when these structures form a single unit.

Ventral Mouthparts: Retraction. The retraction of the ventral mouthparts is the distance between the ventral mandibular condyles and the basal attachments of the cardines or the depth of the hypostomal cavity. In larvae with protracted ventral mouthparts, this distance or depth is minimal or zero, and the mandibles and maxillae are attached approximately at the same level.

Larval Thorax

Basisternum. Anterior part of the larval sternum, anterad of the sternal pits.

Cervicosternum. Small anteromesal sclerite, separate from the presternum.

Laterotergite. One of the sclerotized plates lying between the inflected part of the tergum and the pleural sclerites (precoxale and postcoxale); one of the mesothoracic laterotergites may contain the spiracle.

Precoxale. Pleural (episternal) sclerotised area anterolaterad of the coxal articulation.

Postcoxale. Pleural (epimeral) sclerotised area posterolaterad of the lateral part of the coxal articulation.

Presternum. Separate anteromedian sclerite anterad of the basisternum; sometimes large and more or less triangular, but often vaguely defined or absent.

Pretarsus. The terminal segment of the larval leg, consisting of a pair of claws in most Adephaga and a few Archostemata or a single claw in some Adephaga, most Archostemata and all Myxophaga and Polyphaga.

Tarsungulus. The terminal of claw segment of the larval leg in Polyphaga as used by those who maintain that this segment represents a fusion of the tarsus and pretarsus (**see** Pretarsus and Tibiotarsus).

Tibiotarsus. Formed by the fusion of the tibia and tarsus in larvae of Myxophaga and Polyphaga.

Larval Abdomen

Interurogomphal Pit. Pit or one of a pair of pits lying between the urogomphi.

Laterosternite. Sclerotized plate lying between the main sternal plate and the tergosternal fold.

Laterotergite. Sclerotized plate lying between the inflected part of the tergum and the tergosternal fold. One of the laterotergites usually contains the spiracle.

Pygopods. Paired projections on segment X which may or may not bear hooks and usually assist in locomotion.

Tergosternal Fold. Fold or membrane connecting the abdominal terga and sterna.

Urogomphi. General term used for a number of non-homologous, doubtfully homologous or rarely clearly homologous paired cuticular outgrowths arising from the posterior end of tergum IX. The basally articulated urogomphi occurring in some Adephaga and Staphyliniformia were formerly homologized with cerci, which occur on segment X or XI in some other orders, but these, like the fixed urogomphi, have clearly evolved on several occasions within Coleoptera.

Larval Spiracles

Spiracular Closing Apparatus. Apodeme attached to the trachea at or near the base of the spiracular atrium. It is involved in the closure of the trachea.

Annular-biforous Spiracle. Type of spiracle with the main spiracular opening accompanied by a pair of accessory openings. In some families (e.g., Histeridae, Nitidulidae), these accessory openings are much longer than the main opening, so that they resemble the biforous type of spiracles; however the spiracular scar is always absent.

Annular-multiforous Spiracle. Type of spiracle with a number of accessory openings around the perimeter of the main opening.

Annular-uniforous Spiracle. Type of spiracle with the main spiracular opening accompanied by a single accessory opening.

Bicameral Spiracle (**see** Annular-biforous Spiracle).

Biforus Spiracle. Spiracular opening entirely blocked by a medium septum with a narrow, slit-like opening on either side. Biforous spiracles have evolved in connection with the elateroid ecdysial process (Hinton 1947) and are always associated with a spiracular scar.

Bilabiate Spiracle (**see** Biforous Spiracle).

Cribriform Spiracle. Spiracular opening entirely or partly blocked by a sieve plate. Three or four types of cribriform spiracles have evolved in connection with the elateroid ecdysial process (Hinton 1947) and are associated with a spiracular scar, and another two or three in which normal ecdysis occurs and the spiracular scar is absent.

Ecdysial Scar (**see** Spiracular Scar).

Stigmatic Scar (**see** Spiracular Scar).

Spiracular Scar. Collapsed opening of a tube through which the spiracular lining is removed at ecdysis. Occurs only in those larvae which have biforous or cribriform spiracles and which undergo the elateroid type of ecdysis.

Unicameral Spiracle (**see** Annular-uniforous Spiracles).

Multicameral Spiracle (**see** Annular-multiforous Spiracle).

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3. Adephaga (Addendum)

Introduction and Phylogeny

Rolf G. Beutel, Ignacio Ribera and Michael Balke

The recent discoveries of two new families – Aspidytidae and Meruidae – were doubtlessly rare highlights in adephagan studies. Aspidytidae is a monogeneric family with two species with a remarkable distribution in China and South Africa, respectively. It was described by Ribera *et al.* (2002). Specimens of *Meru phyllisae* Spangler & Steiner, the only species of Meruidae, were first collected in 1985, but only described and assigned to a new family 20 years later (Spangler & Steiner 2005). The adults of both groups and at least the larvae of *Aspidytes niobe* Ribera *et al.* inhabit different hygropetric habitats. Within a short time a considerable amount of morphological and molecular data was accumulated and the systematic position of both groups appears to be largely clarified. Both belong to the complex of dytiscoid families. Meruidae is likely the sistergroup of Noteridae, and Aspidytidae belongs to a clade which also includes Amphizoidae, Hygrobiidae and Dytiscidae (Beutel *et al.* 2006; Balke *et al.* 2008; see also **2 –3.1.** and **3.2.**).

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3.1. Aspidytidae Ribera, Beutel, Balke and Vogler, 2002

Rolf G. Beutel, Michael Balke and Ignacio Ribera

Distribution. Aspidytidae is a monogeneric family with only two known species with a widely disjunct distribution: *Aspidytes niobe*, discovered in 2001 in the Western Cape Province of South Africa and described by Ribera *et al.* (2002); and *Aspidytes wrasei*, described one year later (Balke *et al.* 2003) although already discovered in 1995 by David Wrase and Michael Schülke in the Chinese province Shaanxi (Qin Ling Shan, Hua Shan, 34.27N 110.06E).

Biology and Ecology. Adults of both species and the larvae of *Aspidytes niobe* live in hygropetric habitats and are very likely predacious. *A. niobe* is known from two neighboring permanent water seepages flowing over exposed, nearly vertical rocks almost without vegetation, although areas around the seeps have a highly diverse plant cover. Adults were mostly resting on the rock surface, and walked rapidly when disturbed. Larvae were mostly found actively creeping over exposed rock surfaces in densely shaded areas (Alarie & Bilton 2005; I. Ribera & A. Cieslak pers. obs.). *Aspidytes wrasei* is known from a single locality, and was collected among stones and various plants at the base of a vertical hygropetric surface (Balke *et al.* 2003).

Morphology, Adults (Ribera *et al.* 2002; Balke *et al.* 2003). Total length 4.8–7.0 mm. Body streamlined, without pronoto-elytral angle, convex dorsally. Dorsal side almost entirely black; parts of head and lateral margins of pronotum and elytra ferrugineous; ventral side rufous. Cuticle shiny.

Head (Fig. 3.1.1 A) prognathous, distinctly shortened, wedge-shaped in lateral view. Compound eyes completely integrated in outline of laterally rounded head. Foramen occipitale wide. Posterior part of head distinctly retracted into prothorax, but without narrowed neck region. Tactile setae absent from head capsule. Clypeus distinctly narrowing towards labral articulation; frontoclypeal suture broadly interrupted medially. Clypeolabral suture almost straight. Labrum transverse, with wide median concavity. Anterior epipharynx with pair of large, sclerotized sensorial pegs. Antennae without pubescence or longer setae; inserted laterally, anterior to compound eyes, articulation not visible from above; scapus with globular basal piece and globular distal part separated by a distinct circular incision; distal part largely enclosing small pedicellus; length of 9-segmented flagellum ca. 0.8 mm (*A. wrasei*); segments 3 and 11 longer than other antennomeres, 4–9 very slightly expanded, 6–10 with unusual fields of sensorial pores on ventral side; sensorial field present but vestigial on antennomere 5. Mandibles fairly short and compact, with semicircular outer margin; ventral condyle and dorsal socket strongly developed; dorsal side convex and ventral side flat; setae absent; dense row of hairs on ventral side extends from base to anterior edge close to mesal margin; apical part with pointed tooth and axe-like dorsal cutting edge;

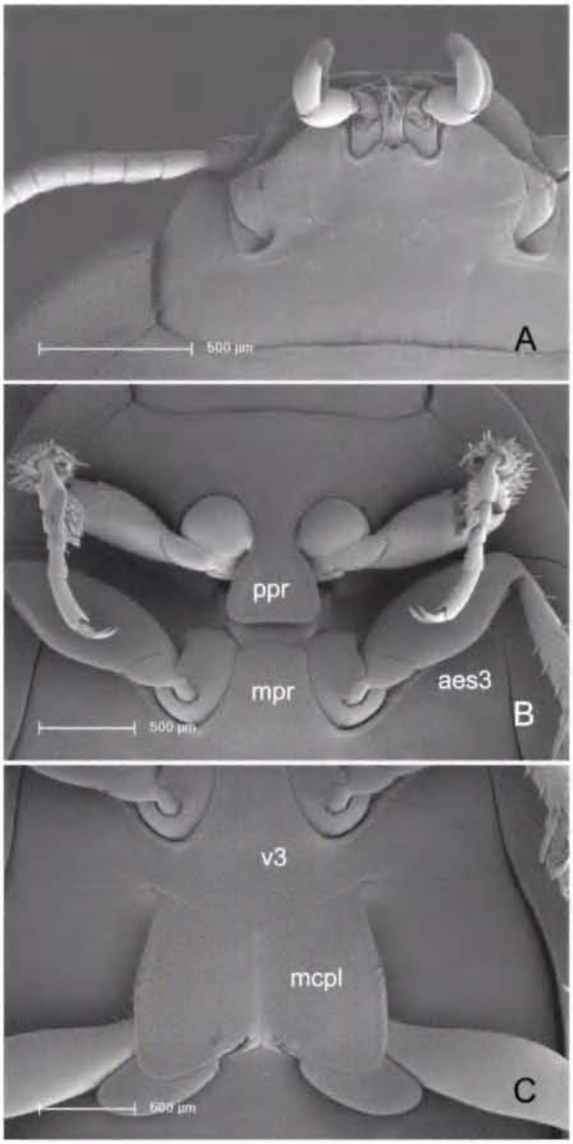

Fig. 3.1.1. SEM micrographs. *Aspidytes niobe*, adult; A, head, ventral view; B, pro- and mesothorax, ventral view; C, metathorax and abdominal base, ventral view.

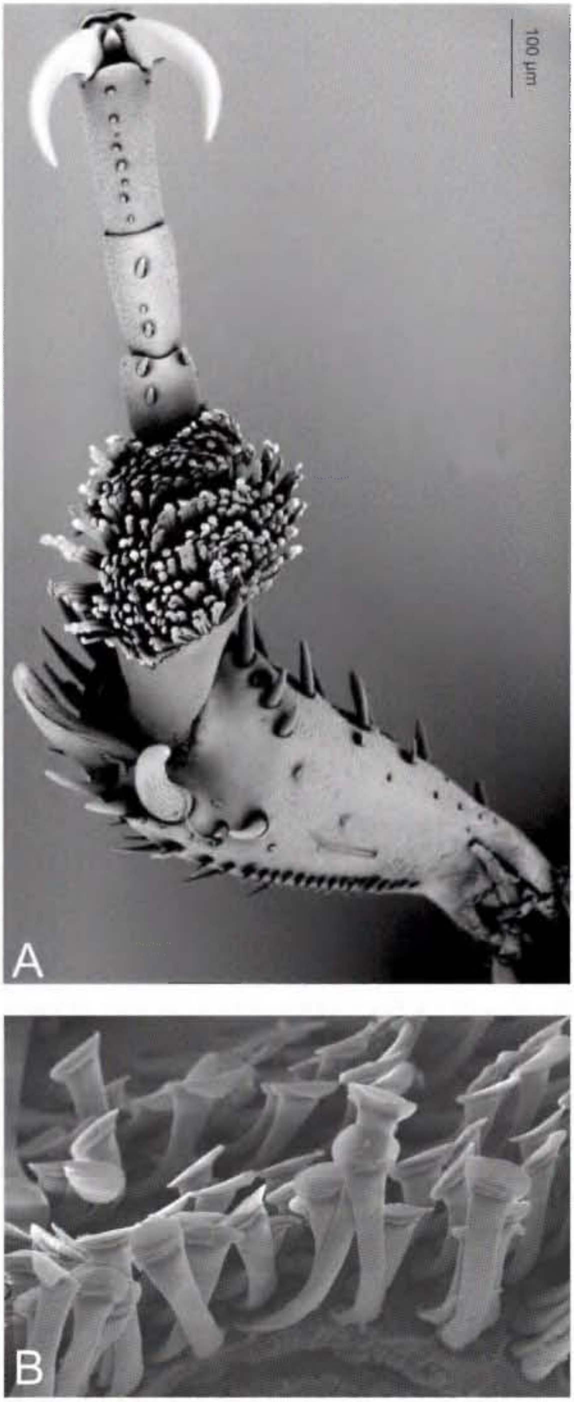

Fig. 3.1.2. SEM micrographs. *Aspidytes niobe*, male paratype; A, foreleg, ventral view, with attachment devices; B, modified adhesive hairs.

semicircular emargination separates apical tooth from small retinaculum; mola and prostheca absent. Maxilla inserted in maxillary groove between submentum and compound eye; composed of semicircular cardo, basistipes, dististipes, lacinia, galea, palpifer and palp; most parts covered by mental lobes; galea palp-like, 2-segmented; palp 5-segmented, fairly short, scarcely overtopping labial palp. Submentum fused with gula posteriorly; border between both sclerites marked by small but distinct posterior tentorial pits; lateral margin rounded; posterior part largely smooth, with transverse meshes, distinctly convex like anterior gula. Anterior part flat, narrowing towards median line, laterally covered by stiff, anteriorly directed setae; mentum with well developed parabolic lateral lobes enclosing deep median emargination for reception of prementum; mental lobes with group of anteriorly directed setae; prementum with prominent median part and distinctly developed palpigers; palpiger with distinct lateral emargination; palpomere 1 short, curved, with deep lateral concavity for reception of base of palpomere 2; palpomere 2 longer, with curved outer margin, extended distally, with two short but distinct spines at anterior margin; palpomere 3 larger than 2, with strongly convex outer margin and apical field of sensilla. Anterior tentorial grooves long, fissure-shaped. Gular ridges high, with posterior apodeme for attachment of extrinsic head muscles; connected by thin tentorial bridge; medially fused laminatentorium and mid-gular apodeme absent.

Pronotum laterally equally rounded, with distinct lateral and posterior beads; disc black, lateral and posterior margin rufous; inflected pronotal margin distinctly widening posteriorly; posterior edge with dense row of hairs. Proventrite separated from propleura by distinct pleurosternal suture; anterior margin with fringe of thin hairs. Trochantin completely covered by propleural lamella. Prosternal process well developed, posteriorly rounded (*A. wrasei*) or truncate, with rounded posterolateral edges (*A. niobe*) (Fig. 3.1.1 B). Procoxal cavities open, with sclerotized, rufous internal bridge. Profurca short but extensive. Foreleg fairly short; procoxae globular, with short ventral condyle; femora with short row of stiff hairs at anterior margin (profemoral cleaning device); tibia with truncate apex and two curved terminal spurs; external spur slightly stronger; tarsomeres 1–4 short; tarsomere 5 ca. 2.5 times as long as basal tarsal segments; male tarsomeres 1 and 2 laterally slightly dilated and ventrally with numerous adhesive hairs with minute apical discs (Fig. 3.1.2); claws equal. Mesothorax slightly shorter than prothorax. Scutellum exposed. Elytra with lateral bead extending to apex; epipleura broad anteriorly, strongly narrowing towards abdominal apex; with polygonal meshes of different size and few punctures. Distinct pentagonal groove of mesoventrite articulates with prosternal process anteriorly (prothorax in retracted position) and with anteromedian process of metaventrite posteriorly (Fig. 3.1.1 C). Faintly impressed pleural suture separates anepisternum from moderately broad epimeron. Mesocoxal cavity laterally bordered by mesal edge of epimeron and narrow apical part of metathoracic anepisternum (= complex type cf. Bell 1967). Middle legs similar to front legs; femur without tuft of spines; tibia and tarsus slightly longer; tibia only very slightly extended distally; tarsomeres 1 and 2 of males laterally slightly dilated and ventrally with numerous adhesive hairs with minute apical discs (as in Fig. 3.1.2). Metathorax slightly longer than prothorax. Anepisternum triangular, with distinct bead along lateral and mesal margin. Epimeron covered by elytral epipleura. Ventrite, composed of praeepisternum and katepisternum, moderately shortened, not reaching lateral metacoxal margin laterally; metaventral process well developed, with rounded anterolateral edges. Transverse suture present as faintly impressed line and internal ridge or as internal ridge only (*A. niobe*); about as long as width of internal lamina of metacoxa, separating posterior katepisternum from anterior praeepisternal part of ventrite. Median longitudinal suture (= discriminal line or discrimen) very short, not surpassing posterior half of katepisternum. Metacoxa moderately extended, slightly longer than ventrite; lateral margin broadly contiguous with epipleural margin; mesal walls extensively fused, forming large intercoxal septum; anterior paramedian angle absent; inner lamina and coxal plates distinct, broadened posteriorly, distinctly curved outwards anteriorly (Fig. 3.1.1 C); metatrochanter larger than pro- and mesotrochanter; tibia and tarsus longer than those of middle leg, appearing thin and longish (length of femur 0.80 mm, tibia 1.05 mm, tarsus 0.95 mm; ratio total body length/length of tibia + tarsus = 2.4 (ratio in *Hygrotus impressopunctatus* 1.7; *Amphizoa lecontei* 2.0; *Carabus auratus* 1.5). Wings well developed (examined in *A. niobe*), with distinct oblongum cell and moderately elongate medial setal binding patch (Beutel *et al.* 2006: fig. 11) (Fig. 3.1.3).

Abdomen with six exposed ventrites equivalent to sternites II, III, IV, V, VI, VII (= last visible

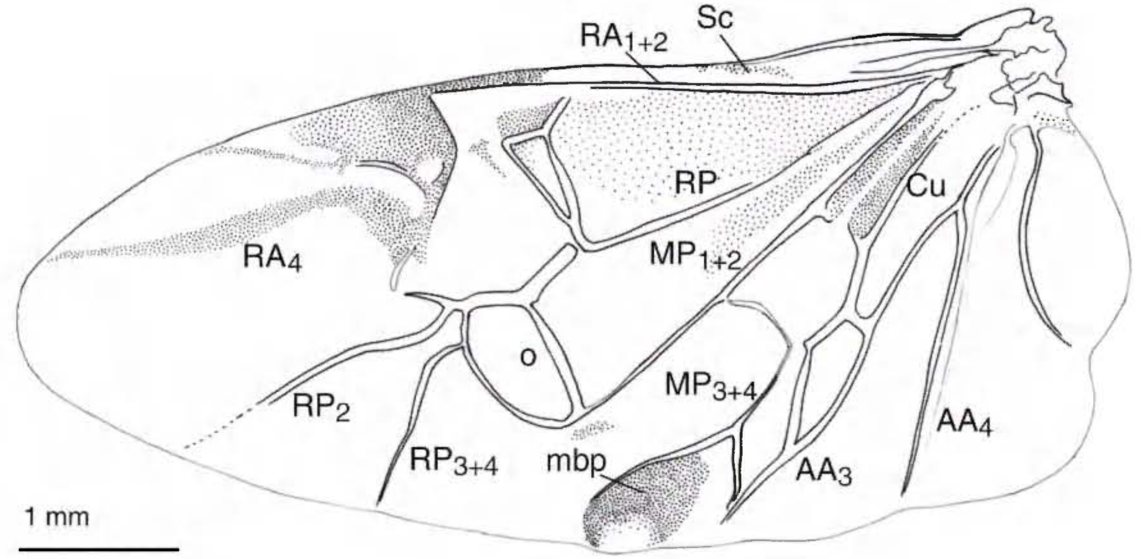

Fig. 3.1.3. *Aspidytes niobe*, hind wing. From: Beutel *et al.* 2006 (modified, nomenclature of venation following Kukalová-Peck & Lawrence 2004).

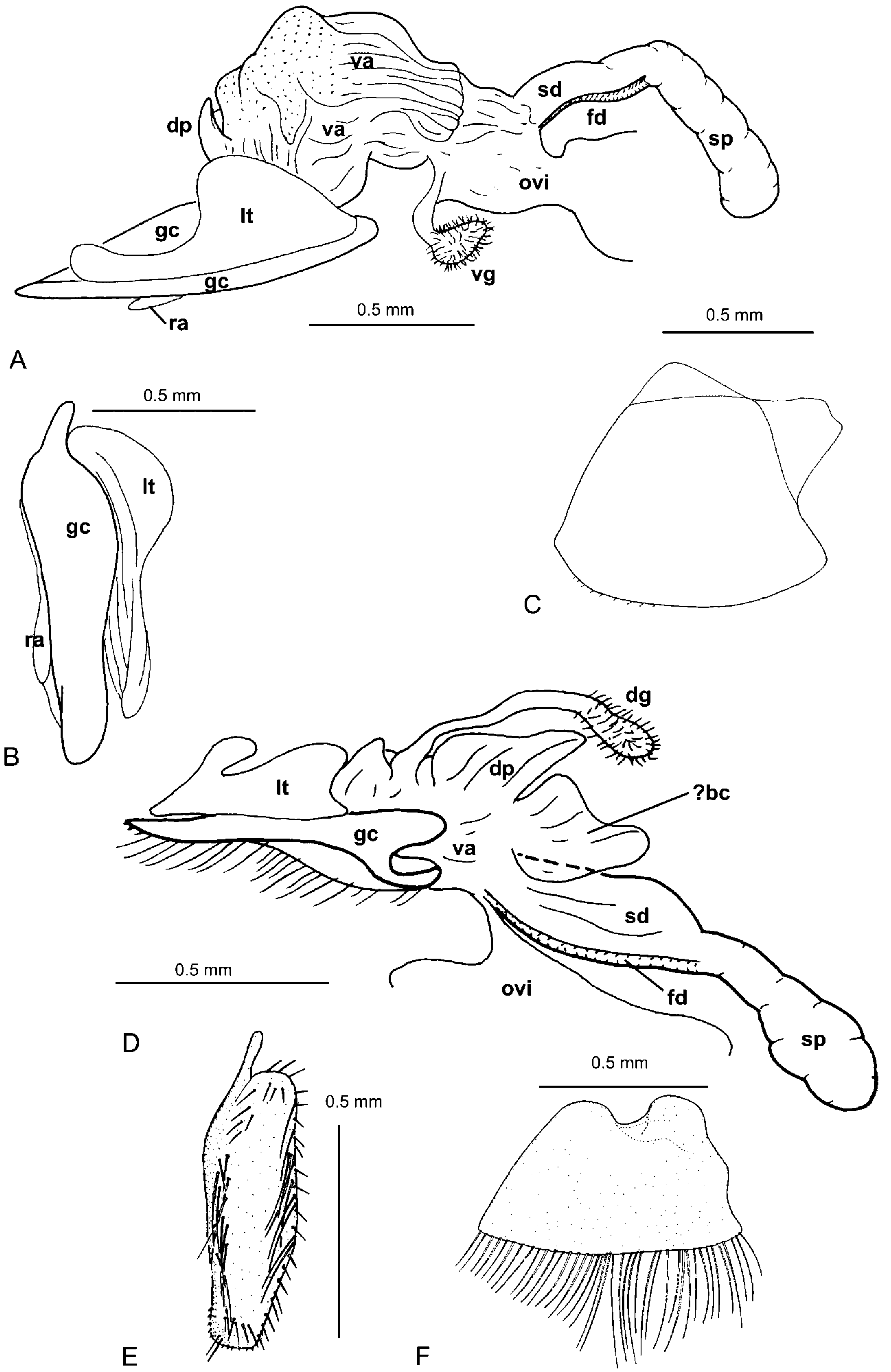

Fig. 3.1.4. A–C, *Aspidytes niobe,* female paratype genitalia. A, genital tract, lateral view: ra, ramen; gc, gonocoxa; lt, laterotergite; dp, dorsal pocket; va, vagina; vg, ventral gland; ovi, common oviduct; fd, fertilisation duct; sd, spermathecal duct; sp, spermatheca; B, gonocoxa, ramen and laterotergite (gc, ra, lt) in ventral view; C, gonocoxosternum, ventral view. D–F, *Aspidytes wrasei* female paratype genitalia. D, genital tract in lateral view, simplified (bc, bursa copulatrix; dg, dorsal gland; dp, dorsal pocket; fd, fertilization duct; gc, gonocoxa; lt, laterotergite; ovi, common oviduct; sd, spermathecal duct; sp, spermatheca; va, vagina); E, gonocoxa, ventral view, some setae omitted; F, gonocoxosternum, ventral view. From: Balke, M., Ribera, I. & Beutel, R. G. (2003) in Water Beetles of China Vol. III, with kind permission.

sternite); length decreasing from III to VI. Sternite II only visible laterally of metacoxa (Fig. 3.1.1 C). Sternites III and IV partly fused, but with very distinct separating suture. Lateral bead present on all sternites, most prominent along lateral margin of sternite VII. Shape of sternite VII roughly semicircular, evenly rounded posteriorly, and devoid of modifications of its surface or hind margin. Male and female genitalia distinctly different between species. *A. wrasei* with median lobe of aedeagus simply curved. Symmetrical parameres of roughly triangular shape; apex stylus-like, with few short setae anteriorly; margin devoid of setae (see Balke *et al.* 2003: figs. 16, 17). *A. niobe* with median lobe of aedeagus composed of several lobes and membranous sacs (ultrastructural features could not be assessed due to lack of fully sclerotized specimens). Parameres broadly oval; apex rounded with few short setae. Gonocoxae (Fig. 3.1.4.) (nomenclature of Miller 2001) (= genital appendages IX) of females of *A. wrasei* roughly rectangular in ventral view, with very slightly curved lateral margins and blunt apex; cranially with short external apodeme; laterally with rather long setae; distally with shorter setae. Proximal portion rather broad in lateral view. Gonocoxa of *A. niobe* elongate in ventral view, with apex broadly rounded; cranially with short external apodeme; devoid of recognisable setation. Laterotergite (= tergite IX; "Tergumhälften IX" or "Tergum IX" of Burmeister 1976) of both species articulated with cranial tip of gonocoxa, extended caudally, shorter than gonocoxa. Gonocoxosternite (Coxosternum; = invaginated sternum VIII; "Gonocoxosternum" of Burmeister 1976) of *A. wrasei* somewhat rectangular, with short anterior lobe (= antero-external angle) and median anterior concavity; antero-internal angle also forming lobe equally in size to anterior lobe; posterior margin with fringe of conspicuous long setae, comparable in length to height of gonocoxosternite. Ramen of *A. wrasei* ("Vulvarsklerite": Burmeister 1976) short, triangular, rufous. Of similar shape in *A. niobe*, with only few short, scarcely visible setae along posterior margin. Vagina of *A. wrasei* rather short and sac-like, with cranial expansion (probably representing bursa copulatrix) and conspicuous, approximately triangular dorsal pocket (Fig. 3.1.4 D: dp). Vagina and sac-like expansion not distinctly separated. Longish gland located in dorsomesal position ("dorsal gland", dg). Spermathecal duct (sd) comparatively short and broad, originating very close to opening of common oviduct (co) into bursa or vaginal expansion; spermatheca (sp) without any obvious modifications (50x) in both species; spermathecal gland always absent. Spermatheca and insertion of oviduct connected by narrow fertilisation duct (fd). Vagina of *A. niobe* with short, triangular caudal pocket on dorsal side (dp); caudal part of vagina covered with numerous spiny scales (dotted in Fig. 3.1.4 A); compact gland located in ventromesal position ("ventral gland", vg); spermathecal duct (sd) originating dorsally to opening of ommon oviduct (ovi) into vagina.

Morphology, Larvae (Alarie & Bilton 2005; Balke *et al.* 2005) (Figs. 3.1.5–3.1.7). Total length of mature larvae (excl. urogomphi) ca. 7 mm. Robust, almost denisciform anteriorly, but abdomen more subcylindrical towards apical segment IX. Head and body strongly pigmented on dorsal side. Cuticle smooth. Sclerites set with short setae and also setae of medium length (see Alarie & Bilton [2005] for a detailed account of the distribution of setae and pores).

Head prognathous, very slightly inclined (Fig. 3.1.6 A, B). Posteriorly retracted into prothorax but without distinct neck region. Moderately flattened, slightly broader than long, distinctly narrower than prothorax. Greatest width (ca. 1 mm) at posterior 1/3 of head; head capsule abruptly narrowing towards foramen occipitale and gradually narrowing towards clypeal region. Foramen

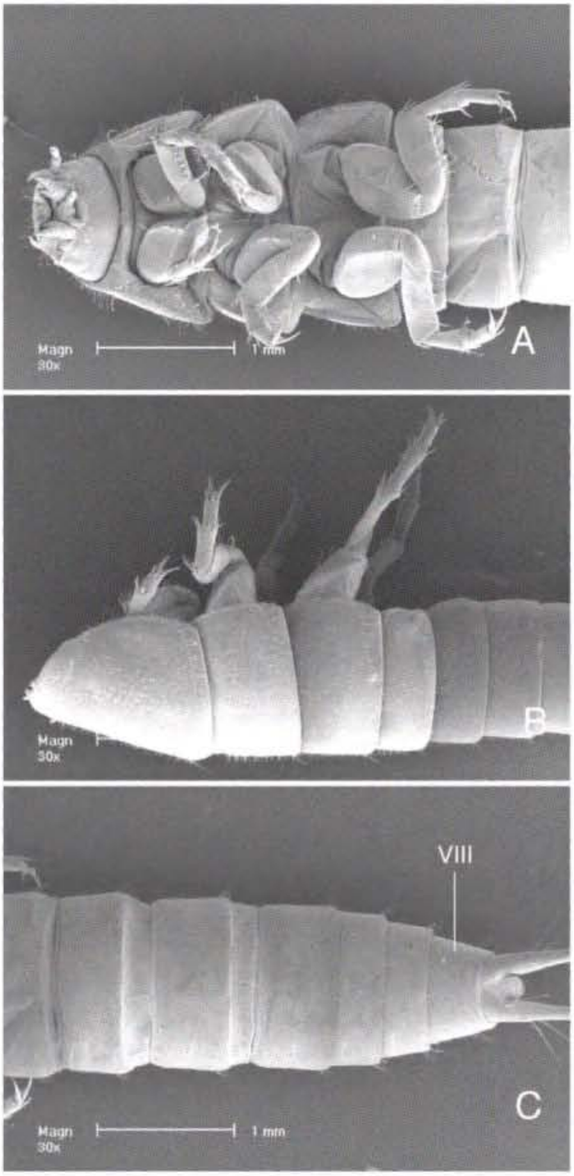

Fig. 3.1.5. SEM micrographs. *Aspidytes niobe*, larvae; A, head and thorax, ventral view; B, thorax, dorsolateral view; C, abdomen, dorsal view. From: Balke *et al.* 2005 (modified).

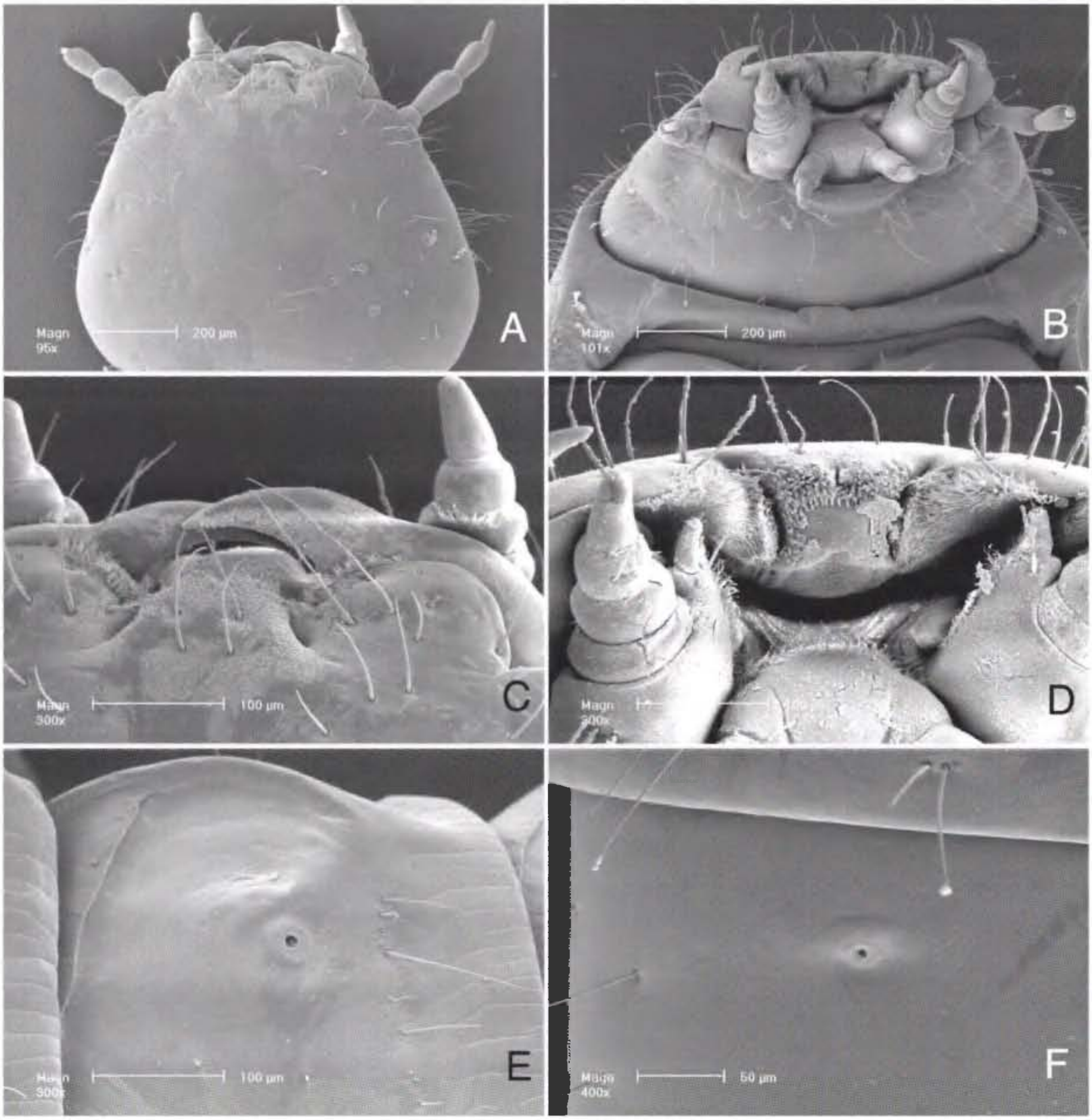

Fig. 3.1.6. SEM micrographs. *Aspidytes niobe,* larva; A, head, dorsal view; B, head, ventral view; C, clypeolabral region, dorsal view; D, clypeolabrum and mouthparts, frontal view; E, abdominal tergite I, with spiracle; F, abdominal tergite IV, with spiracle.

occipitale fairly large, broadly oval. Six moderately sized stemmata present posterad of antennal articulatory region, nearly arranged in a circle. Frontal suture (=frontal arms) present, lyriform, but with very indistinct indentation. Frons distinctly elongated posteriorly. Coronal suture accordingly shortened, ca. 1/3 as long as entire head capsule. Labrum fused with frontoclypeus; adnasalia (=epistomal lobes) distinct, slightly asymmetric; with several long setae and dense brush of microtrichia along mesal part of anterior margin and ventral surface; nasale without teeth, separated from adnasalia by very deep grooves; with several major sensilla (probably six) embedded in very dense field of smaller sensilla and microtrichia (Fig. 3.1.6 C, D). Antennae 4-segmented; antennomere 1 short; antennomere 2 ca. 4 times as long as wide, slightly extended distally; antennomere 3 slightly shorter than 2, also extended distally, with distinct sensorial appendage on ventral side of apical part; antennomere 4 very small and spindle-shaped, inserted on apex of segment 3. Mandibles moderately long, with fairly broad basal part; sickle-shaped distal part distinctly marked-off, with deep mesal concavity enclosed by ventral and dorsal cutting edge; retinaculum small but distinct; mola and prostheca absent. Maxillae inserted in shallow groove at anterior margin of head capsule, between anterior labium and mandibular articulation; cardo slightly narrower than stipital base, almost vertically oriented; stipes fairly short, with three long setae close to lateral margin; lacinia absent; galea inserted on stipital apex, 2-segmented. Submentum completely fused with gula posteriorly and with ventrolateral

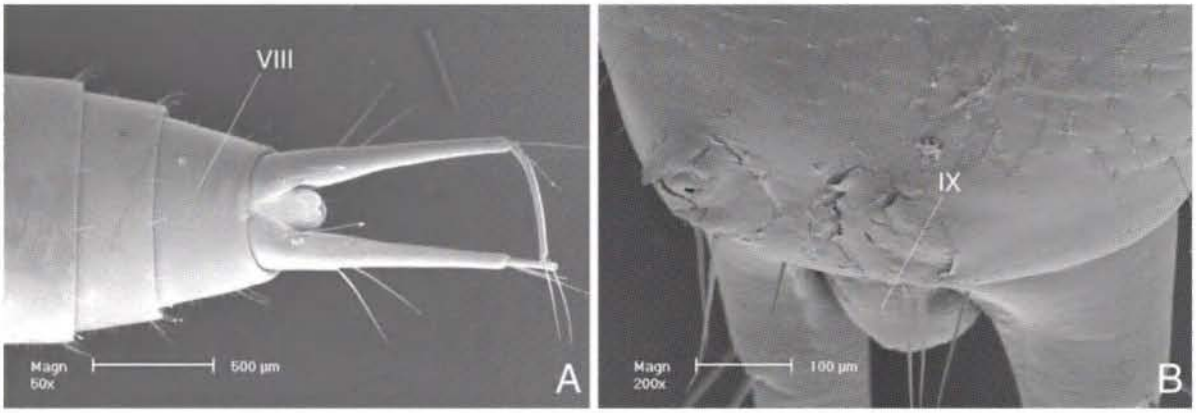

Fig. 3.1.7. SEM micrographs. *Aspidytes niobe*, larva; A, abdominal apex with urogomphi, ventral view; B, segments VIII and IX, dorsal view. From: Balke *et al.* 2005 (modified).

wall of head capsule laterally; mentum membranous, short; prementum short, without ligula; palpiger well developed; palp ventrally directed, 2-segmented; both segments about equally long, but basal segment distinctly wider. Posterior tentorial pits small but distinct, widely separated, distant from posterior margin of head capsule. Gula moderately long and broad. Tentorium with elongate caudal arms serving as attachment area of strongly developed M. tentoriopharyngalis. Prepharynx fairly short but not transverse; M. clypeopalatalis composed of several subcomponents; M. tentoriobuccalis anterior present and large; precerebral and postecerebral pharyngeal dilators strongly developed. Cerebrum located in posterior head region; suboesophageal ganglion large, located below well developed, nearly straight tentorial bridge and ventral wall of anterior pharynx.

Prothorax largest segment of body (Fig. 3.1.5); cuticle smooth and shiny, with numerous short setae inserted in small pores and longer setae along lateral margin and anterior margin of posterior collar. Pronotum shield-like, rounded anteriorly and laterally, with a distinct bead along lateral margin; epipleura, i. e., inflected part of pronotum (paratergal lobe) distinctly developed; posterior collar fairly broad, with parallel longitudinal riffles. Presternum not separated from epipleura laterally. Basisternum small, with narrow transverse anterior part and narrow median part between procoxae. Procoxae large and prominent, cone-shaped; distinct lateral concavity for reception of profemora in repose delimited by sharp anterior edge and less conspicuous posterior edge; anterior edge with several long setae; trochanter well developed; femur rather short, ca. 2 times as long as wide, with 4 spines along ventral edge; tibia shorter and narrower, moderately extended distally, with several apical setae; tarsus shorter than tibia, cylindrical, with two equal, strongly developed claws; single seta present between claws. Mesothorax shorter than prothorax, otherwise similar. Paratergal lobes slightly broader. Anterior margin straight, overlapped by posterior pronotum. Trochanters and femora slightly larger than on prothorax. Metathorax very similar to mesothorax. Coxae larger; femora and tibiae slightly longer.

Abdominal (Figs. 3.1.5–3.1.7) segment I approximately half as long as metathorax; with lateral bead, narrow paratergal lobes and posterior collar; spiracle small, located on lateral part of tergite. Sternal part with two distinct oblique ridges. Tergites of segments II–VIII laterally fused, forming ring-shaped structure; paratergal lobes absent; small spiracles positioned on tergites, close to posterior margin. Segments II–V distinctly longer than I, about equally broad. Segments VI and VII shorter; VI narrower than V, and VII narrower than VI; VII about as long as V and distinctly narrowing posteriorly. Strongly developed urogomphi inserted on segment VIII ventrolaterally, enclosing small but distinctly developed segment IX (visible in ventral and dorsal view); basal segment of urogomphi (Fig. 3.1.7) ca. 1.5 times as long as segment VIII; with broad bases almost contiguous ventromedially; evenly tapering towards apex; with several long setae; distal segment very slender, cylindrical, slightly more than half as long as basal segment; with long setae inserted on apex.

Pupa. Unknown

Eggs. Unknown.

Phylogeny and Taxonomy (Ribera *et al.* 2002; Balke *et al.* 2005). Combined analyses of morphological and molecular data strongly support a position of *Aspidytes* within a clade which also comprises Hygrobiidae, Amphizoidae and Dytiscidae. Typical dytiscoid features are the extensive fusion of the mesal metacoxal walls, the loss of two of three metathoracic furcacoxal muscles (Mm 81, 83), and the loss of the abdominal segment X in larvae. A feature less derived than in other dytiscoid groups is the incomplete reduction of the larval abdominal segment IX (Alarie & Bilton 2005). The phylogenetic relationships among the families of this clade are much less understood (Balke *et al.* 2005; Beutel *et al.* 2006). The most complete analyses to date (Balke *et al.* 2005, with fifty-three morphological characters of adults and larvae and ca. 6 Kb from six nuclear and mitochondrial genes) placed *Aspidytes* as sister to *Amphizoa*, although with relatively low support.

Acknowledgements

We are grateful to Hans Fery for many valuable comments and corrections.

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3.2. Meruidae Spangler and Steiner 2005

Rolf G. Beutel, Michael Balke and Warren E. Steiner

Distribution. The only known species *Meru phyllisae* Spangler & Steiner 2005 occurs in Venezuela, district of Amazonas, at El Tobogán de la Selva, 40 km south of Puerto Ayacucho, 5.23.1461 N, 67.36.5995 W, c. 140 m elevation.

Biology and Ecology (Spangler & Steiner 2005). The type series of *Meru phyllisae* was collected on the broad, shallow surface and margins of a cascade flowing over open bedrock. The cascade is fed by a white-water stream, the Río Coromoto. Leaves adhering to the wet rock are present in the slowly flowing sections. A water analysis provided the following data: pH 5; oxygen 12 ppm; hardness 0. The water temperature was 28°C when most of the specimens were collected.

Some specimens of *M. phyllisae* were taken by collecting leaves from the seepage areas into a fine-mesh dip-net. Most specimens were found in partly submerged root mats, which held decaying leaves, sticks and other debris at the edges of the open or semi-shaded stream margins. Species of the following groups were collected in the same microhabitat: Dytiscidae (e.g., *Copelatus, Laccodytes, Desmopachria,* various Bidessini), Noteridae (*Notomicrus*), Elmidae (many genera, e. g., *Cylloepus, Gyrelmis, Heterelmis, Austrelmis*), Hydraenidae (*Adelphydraena orchymonti* Perkins, *Hydraena* spp.), Hydrophilidae (*Anacaena, Berosus, Chaetarthria, Notionotus, Oocyclus, Phaenonotum*), Hydroscaphidae (*Scaphydra*), Sphaeriusidae (*Sphaerius*), Torridincolidae (*Hintonia*).

In captivity, beetles spent most of the time sitting still or crawling about on dead leaves. They were not observed feeding. Rarely beetles floated after becoming detached from the leaves and were observed walking along under the surface film as has been observed in Hydraenidae and some small hydrophilids. To submerge, the beetles turn over with the head directed downward and 'kick' (with an alternating leg motion as in walking) their way downward until finding a foothold on the substrate; if a beetle stopped 'kicking' on the way down, it would immediately float back to the surface, then start another descent. While the beetles were moving about, a silvery bubble-like area seemed to be present under each elytron. No mortality was noted until almost 4 months after capture, when two dead beetles were found. The last two specimens held in captivity lived in the glass finger bowl for 196 days.

Morphology, Adults (Spangler & Steiner 2005; Beutel *et al.* 2005) (Figs. 3.2.2 A, 3.2.3, 3.2.4). Total length 0.85–0.9 mm, width c. 0.4 mm. Body form ovate, with indistinct pronoto-elytral angle; widest at basal 1/4th of elytra; convex dorsally, slightly less so on ventral side. Colour dark brown to yellowish brown. Most surfaces bearing flat, wrinkled, unsclerotized setae arising from anterior side of large, shallow punctures.

Head (Figs. 3.2.1, 3.2.2 A) prognathous, not shortened and broadened. Neck region moderately narrowed, round in cross section, covered by anterior collar of prothorax. Compound eyes broadly elliptic, moderately prominent; large ommatidia

Fig. 3.2.1. *Meru phyllisae*, SEM micrograph, habitus. From: Spangler & Steiner 2005 (modified).

numbering 5 X 9 across axes of eye. Frons smooth, slightly convex, with reticulate microsculpture; laterally and basally with scattered shallow punctures and fine setae; frontoclypeal suture recognisable, nearly straight, not interrupted medially. Labrum trapezoidal, with scale-like microsculpture; connected with nearly straight anterior clypeal margin by an internal membranous fold; with a shallow median concavity covered by opposing, overlapping, spatulate setae and with three tapered setae originating from small pits lateral to base of spatulate setae; pair of small, flat, tooth-like setae imbedded in anterior margin of concavity. Antenna (Fig. 3.2.3 A–C) longer than head, filiform, glabrous, 11-segmented; scapus very short and almost completely concealed; pedicellus almost globular, urn-shaped, bearing a few slender setae; antennomere III as long as pedicellus but more narrow, nearly twice as long as wide, subcylindrical, thickest toward apex; antennomeres 4–10 of similar form, but 5, 7 and 9 longer and thicker than adjacent ones; antennomeres 7 and 9 bearing a plate-like sensorial patch ventrally; antennomere 11 longer than preceding two combined, thickest at middle and obliquely tapering to a narrow apex, with two plate-like sensorial patches near apex on ventral side (Fig. 3.2.3 C). Mandibles asymmetrical (Fig. 3.2.4 A), nearly twice as long as wide, with single, blunt, falcate, apical incisor and mesal terebral tooth; brushes of trichia, mola and retinaculum absent; left mandible slightly longer than right, terebral tooth broadly angular; inferior terebral ridge with one or two minute teeth; right mandible with terebral tooth truncate and closer to apex than that of left mandible; basal face with several small wrinkles. Maxilla (Figs. 3.2.3 E, F, 3.2.4 B) with small and wedge-shaped cardo; mediostipes and lacinia fused; basistipes well developed, triangular, narrowing toward base of palp; lacinia stout, elongate, glabrous, with a curved, robust apical spine and seven spines on inner side; galea palp-like, 2-segmented, shorter than lacinia, with apical segment elongate, cylindrical, smoothly rounded at apex; palpifer not recognisable as separate element of maxilla; palpus 4-segmented; apical palpomere slightly longer than combined length of segments 1–3, with sensory structures on distal part. Submentum broad, with distinct posterior tentorial pit at basolateral corner (Fig. 3.2.2 A); mentum flat, smooth, slightly more than half as wide as head, with two long setae on each side at about middle; prementum recessed, inserted between anterolateral rounded lobes of mentum; base of palpiger with single small seta; ligula moderately extended and rounded apicomedially, with 12–14 apical setae (Fig. 3.2.3 D); labial palp 3 segmented; apical segment swollen and slightly longer than combined length of segments 1 and 2, with apical sensory structures similar to those of maxillary palp (Fig. 3.2.3 E). Gular ridges high; tentorium well developed except for reduced dorsal arms; laminatentorium extensive, Y-shaped in cross section. Head musculature

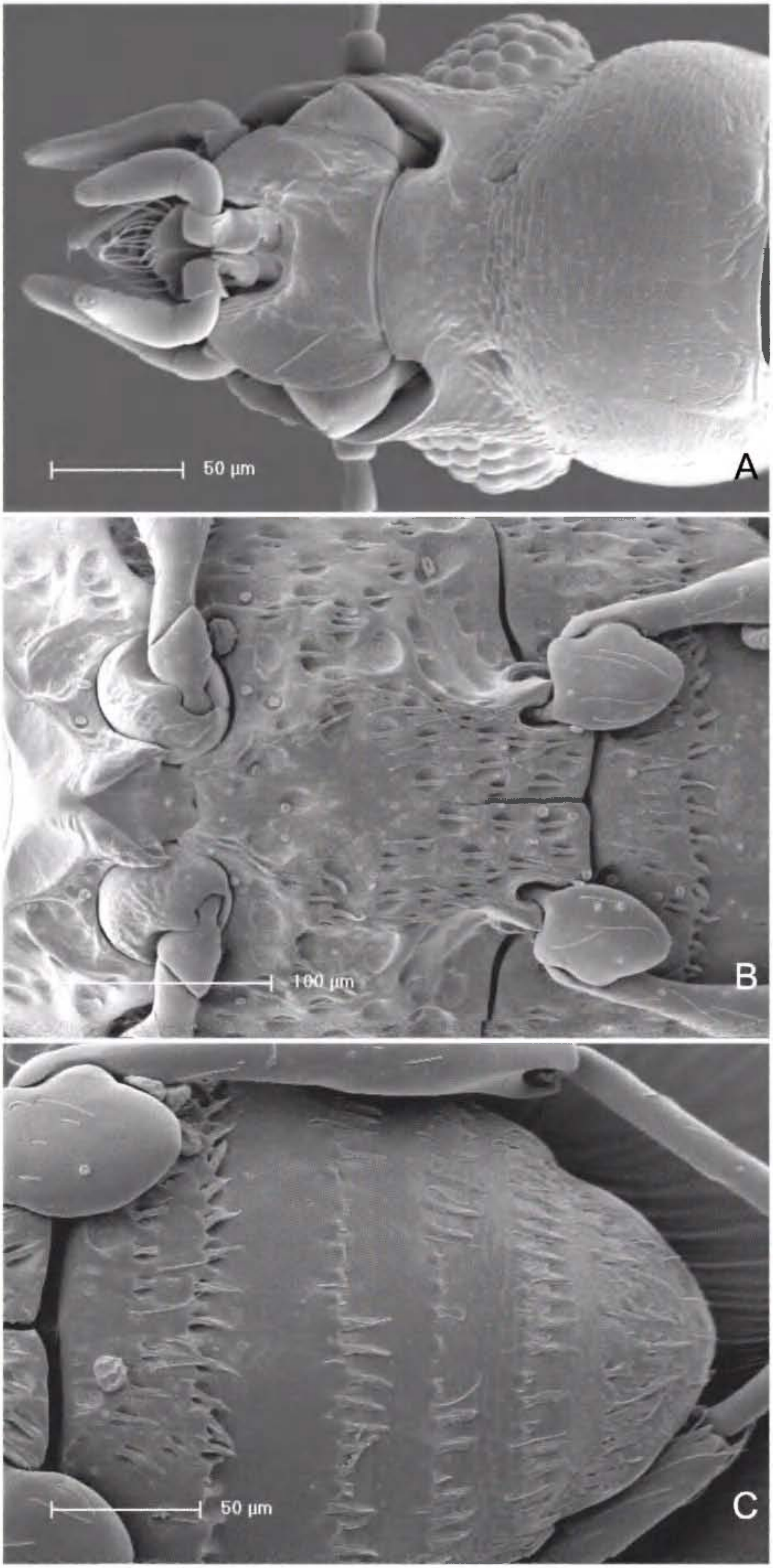

Fig. 3.2.2. *Meru phyllisae,* SEM micrographs. A, head and prothorax, ventral view; B, pterothorax, ventral view; C, abdomen, ventral view. From: Beutel *et al.* 2006 (modified).

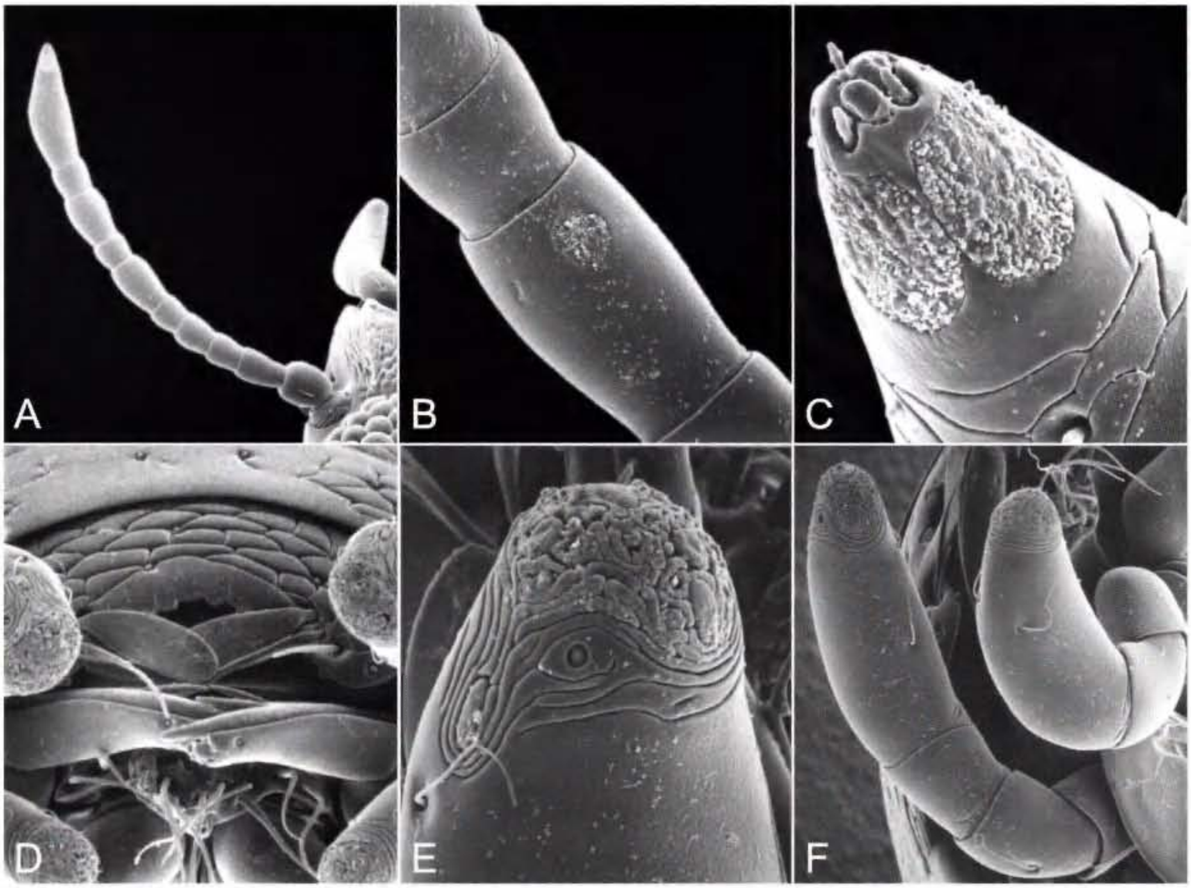

Fig. 3.2.3. *Meru phyllisae*, SEM micrographs. A, antenna, dorsal view; B, antennomeres 6–8, with sensorial patch on segment 7; C, apex of antennomere 11, ventral view; D, labrum and mouthparts, frontal view; E, maxillary and labial palp; F, apex of maxillay palp. From: Spangler & Steiner 2005 (modified).

well developed, not distinctly affected by miniaturisation. Prepharynx, pharynx and oesophagus extremely wide, round in cross section. Brain large in relation to head size; largest part located in posterior head region; circumoesophageal connectives short; suboesophageal ganglion enclosed by gular ridges. Cervical sclerites absent.

Prothorax (Fig. 3.2.2 A) about 4/5 as wide as elytra. Pronotum widest at base, slightly wider than long; lateral margin sinuate, not beaded; anterior margin straight, anterior corners narrowly rounded; posterior corners angled; posterior margin nearly straight between corner and middle, tightly fitted against base of elytron and forming an angle of about 125° with other side at middle; disc evenly convex, with four shallow depressions on each side; coarsely, densely punctate; each puncture with a long, robust, flattened and wrinkled seta, pleated at base, arising from anterior edge of puncture and recumbent across it; length of seta about twice diameter of a puncture; scattered, hair-like setae also present, arising from smooth areas between large punctures. Thoracic ventrites with similar combination of setae and punctures, but larger and more sparsely placed laterally. Prosternum (Fig. 3.2.2 A) with notopleural and pleurosternal sutures visible; anterior prosternal margin evenly arcuate, with fine fringe of micro-setae along edge and on each side with one large, anteriorly directed, club-shaped seta, with apex flattened and toothed, brush-like. Prosternal process very narrow between procoxae but wider and truncate behind them. Propleuron large, extending behind coxa. Procoxal cavity closed internally. Procoxa globular; trochanter smooth, unmodified. Musculature of prothorax normally developed. Mesoventrite fused with metaventrite and with lateral pleural parts; pentagonal groove present, partly covered by prosternal process. Mesocoxa globular. Musculature well developed. Scutellar shield not exposed. Elytra convex, twice as wide as long, dorsally with setae and punctures like those on pronotum (Spangler & Steiner 2005: fig. 5 A, B) in addition to rows of large, deep, strial punctures without setae; sutural stria absent and sutural edge not beaded; lateral margin arcuate in lateral view; epipleuron indistinct; inner surface smooth, laterally with large, locking pit at about mid length and round patch of granular surface (presumably for wing-folding) anterior to it (Spangler & Steiner 2005: fig. 5 C, D). Metaventrite fused with anepisternum and metacoxae, without discernable sutures; transverse ridge absent. Mesal wall of metacoxa extensively fused (intercoxal septum); metacoxal plates very reduced, not covering base of trochanter, with lateral margins indistinct anteriorly; median lamina of metacoxae

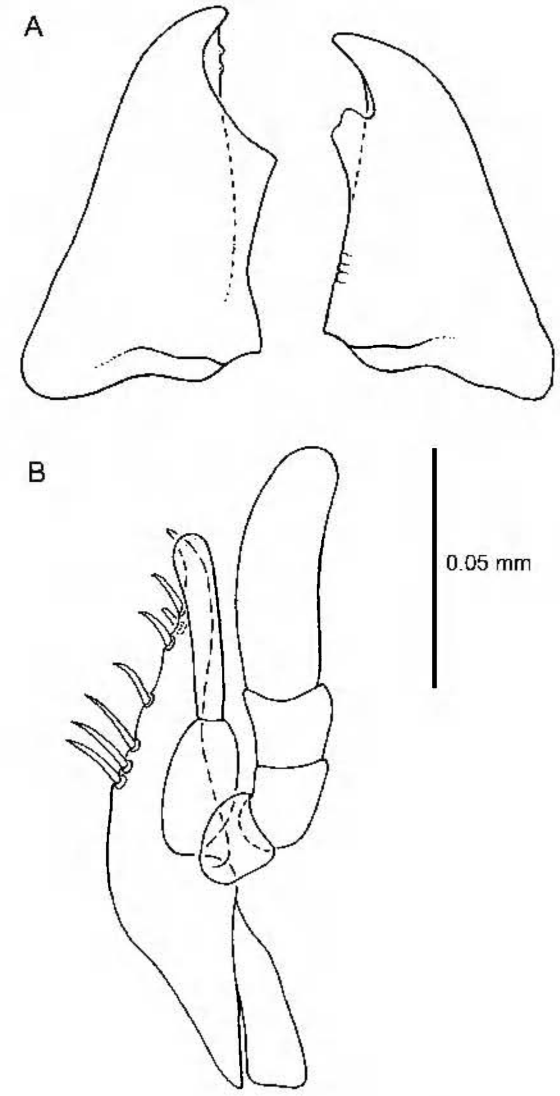

Fig. 3.2.4. *Meru phyllisae,* mouthparts. A, mandibles; B, maxilla. From: Spangler & Steiner 2005 (modified).

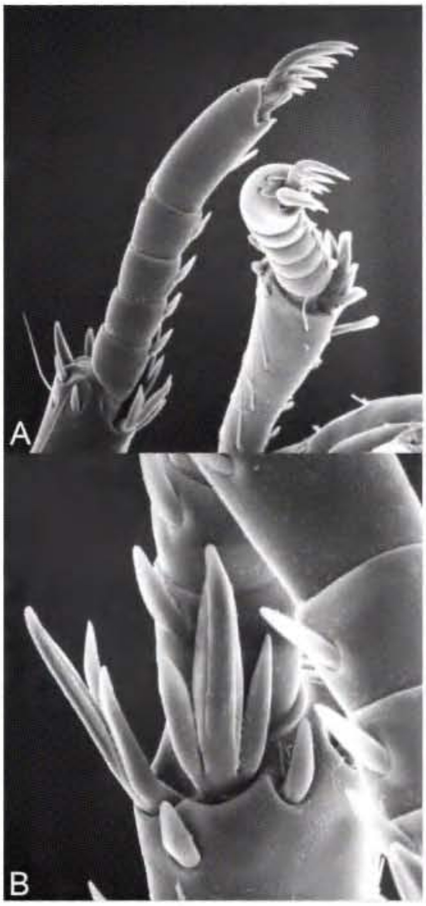

Fig. 3.2.5. *Meru phyllisae,* SEM micrographs. A, front and middle legs, posterior view; B, mesotibial spurs. From: Spangler & Steiner 2005 (modified).

not distinctly separated from lateral part; posterior margin straight, with small median emargination and deep incisions for trochanteral articulations (Fig. 3.2.2 B); metatrochanter large, about twice size of pro- and mesotrochanter, globular, swollen posteriorly; junction with metafemur oblique and sinuate. Metafurca simplified, Y-shaped, without lateral arms (Fig. 3.2.6 B); attached to extensive intercoxal septum and to metaventrite for two-thirds of its length. Mm. furcacoxalis anterior and posterior absent; large indirect flight muscles also reduced in both specimens examined and large parts of metathorax filled with fat body tissue. Hind wings dimorphic (3.2.6 A; Spangler & Steiner 2005: figs. 10–12), either fully developed with venation moderately developed and distal half folded, or brachypterous, as long as elytron, with venation very reduced and distal half appearing shrunken; margins with fringe of long hairs; medial binding patch (katastigma) absent; oblongum cell not discernable. Distal parts of legs (Fig. 3.2.5 A) with femora smooth, club-shaped, widest at about apical 1/3, with scattered sparse hair-like setae, some brush-tipped, and row of five to seven thick, branched setae on dorsal surface; metafemur very slender basally, attached dorsolaterally to trochanter; distal two-thirds swollen; tibiae simple, straight, gradually thickening from base to near apex, with sparse, thin setae, irregularly distributed, becoming more stout toward apex of tibia; each tibia bearing paired, toothed apical spurs; both spurs trident on pro- and mesotibia, one trident and one laterally pectinate on metatibia (Fig. 3.2.5 B); tarsal formula 5-5-5; last tarsomeres longer than combined lengths of preceding two; tarsomeres 1 and 2 each with four stout, ventral setae, 3 and 4 with two setae, and 5 with one seta; hind tarsus with basal tarsomere longest; length equals combined length of tarsomeres 2–4; tarsal claws large, pectinate, with 4–5 teeth; empodium small, smooth, pad-like. Proventriculus present (Spangler & Steiner 2005: fig. 16), with four larger plates smooth, each with single median acuminate and serrulate flap seemingly capable of folding against base; smaller four plates vase-shaped in lateral view, smooth, with fringe of fine hairs.

Abdomen with six visible ventrites (morphological sternites II–VII) (Fig. 3.2.2 B, C). Ventrites 1, 2 and 3 completely fused (=sternites II–IV),

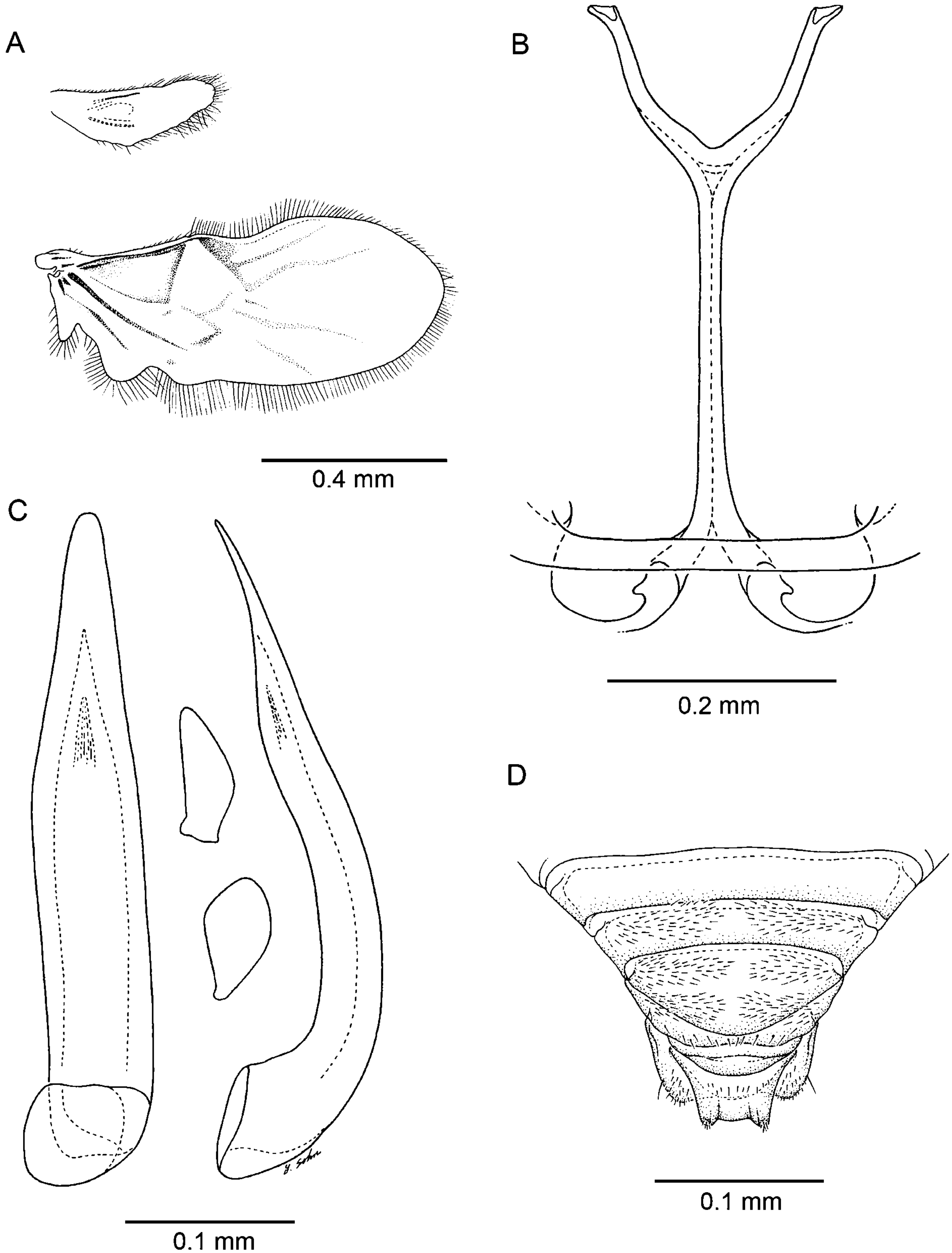

Fig. 3.2.6. *Meru phyllisae,* A, hind wing; B, metafurca; C, male genitalia; D, female genitalia. From: Spangler & Steiner 2005 (modified).

with sutures indistinct (positions marked by row of setae); first ventrite deeply and broadly divided medially for reception of metacoxal processes, internally with heavily sclerotized transverse septum along posterior margin. Posterior margins of ventrites 1–5 bearing a comb-like row of robust, flattened and grooved setae and fewer hair-like setae (Fig. 3.2.2 B, C). Ventrites 1 and 2 with punctures bearing robust wrinkled setae scattered over surface; flat pleated setae on ventrites 3–5 without associated punctures (unlike pleated setae on other body regions). Apical ventrite (sternite VII) wider than long, apical margin rounded; surface bearing irregular transverse band of flattened and grooved setae and fewer hair-like setae (Fig. 3.2.2 C). Male genitalia (Fig. 3.2.6 C) asymmetric; median lobe with curved, tubular base, becoming more straight, dorsoventrally flattened and tapering toward apex; parameres vestigial, scale-like; left paramere more rounded, laterally positioned at base of median lobe; right paramere smaller, more narrow, positioned on ventral side of base of median lobe; aedeagus with only slight torsion in repose; ring sclerite (sternum IX) complete. Female genitalia lacking sclerotized structures except for reduced short gonocoxostyli, each bearing a few small apical setae (Fig. 3.2.6 B).

Larvae, pupae and eggs. Larvae recently discovered (A. Short, pers. comm.), but not described yet. Other immature stages unknown.

Phylogeny and Taxonomy (Spangler & Steiner 2005; Beutel *et al.* 2006; Balke *et al.* 2008). The results of comprehensive cladistic analyses of morphological (Beutel *et al.* 2006) and molecular data (Balke *et al.* 2008) clearly demonstrate that Meruidae belong to Dytiscoidea. Autapomophic conditions of this lineage including *Meru* are the extensively fused metacoxae (large intercoxal septum), the origin of the metafurca from the intercoxal septum, and the loss of Mm furcacoxales anterior and posterior. The clade comprising Meruidae and Noteridae is suggested by the absence of the transverse ridge of the metaventrite, the fusion of abdominal sternites III and IV, the shape of the strongly asymmetric parameres, and the enlargement of antennomeres 5, 7, and 9. It is also supported by molecular data (Balke *et al.* 2008). The Meruidae + Noteridae clade is the sister group of the remaining Dytiscoidea.

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4. Elateroidea

Introduction, Phylogeny

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The constitution of Elateriformia has varied over time, as discussed in detail by Beutel & Leschen (2005) (see **1–14**). The series was first proposed by Crowson (1960) for his Dascilliformia (Crowson 1955) minus the family Dascillidae (which was combined with Scarabaeoidea to form the series Scarabaeiformia) and the families Eucinetidae, Clambidae and Scirtidae, which were placed in a superfamily Eucinetoidea. This classification was also used in Crowson (1981) except that a series Eucinetiformia was recognized and Rhipiceridae was added to Scarabaeiformia-Dascilloidea, based on Crowson (1971). In all of Crowson's classifications, the superfamily Elateroidea included Perothopidae, Eucnemidae, Throscidae, Cebrionidae, Elateridae, and Cerophytidae, although the last was omitted in error from the 1981 work.

Lawrence & Newton (1982) followed Crowson's classification in most respects. They did not define series as such, but considered all Eucinetiformia, Scarabaeiformia and Elateriformia as belonging to an "Elateriform lineage". Although Scarabaeoidea was tentatively included in this "lineage", some doubt was expressed about the relationship of the group to Dascilloidea. The families normally included in Elateroidea and Cantharoidea, plus the Artematopodidae and Brachypsectridae were considered to form a monophyletic group. In the first cladistic analysis of Elateriformia, Lawrence (1988) excluded Scarabaeoidea altogether, while Eucinetoidea were included as an outgroup in some analyses. The monophyly of Elateroidea + Cantharoidea + Artematopodidae + Brachypsectridae was confirmed in analyses based on both adult and larval characters, with the family Rhinorhipidae (known from adult characters only) at the base of this clade.

Elateroidea was restricted by Crowson (1955) to those taxa the adults of which have more or less rounded procoxae with concealed trochantins, no transverse metakatepisternal suture, contiguous metacoxae, hind wing with an apically truncate wedge cell, acutely projecting hind pronotal angles, head without a distinct frontoclypeal suture, trilobate aedeagus with freely articulated parameres, and 4 free Malpighian tubules, while larvae lack a free labrum or epicranial stem and have simple, non-channeled mandibles. Artematopodidae (then in Dryopoidea) were considered to be separable from elateroids on little more than exposed trochantins in the adult and a free labrum in the larva, and Brachypsectridae were considered to be even more difficult to separate on adult features. The superfamily Cantharoidea was considered to be the most likely group to be merged with Elateroidea.

Lawrence & Newton (1982) followed Crowson in considering Artematopodidae, Brachypsectridae, Elateroidea and Cantharoidea to form a monophylum, and Lawrence (1988) formally recognized an expanded Elateroidea to include all of these groups. The position of *Rhinorhipus* Lawrence at the base of the elateroid clade was considered to be tentative because of lack of information on the larva, combined with the fact that there are six free Malpighian tubules (instead of four as in all other members of the group). Furthermore, in cladograms produced by Lawrence *et al.* (1995), *Rhinorhipus* usually formed a clade with *Dascillus* Latreille (Dascillidae), *Sandalus* Knoch (Rhipiceridae) and *Dystaxia* LeConte (Buprestidae or Schizopodidae) and was never placed within the elateroid-cantharoid group.

In cladograms produced by Beutel (1995) and based on larval characters, Elateroidea (*sensu lato*) was always monophyletic, but this was true of neither Elateroidea (*sensu stricto*) nor Cantharoidea. Most cantharoid families plus Brachypsectridae formed a clade sister to Cerophytidae + Throscidae + Eucnemidae, while Cantharidae formed a clade with Artematopodidae and Elateridae. The non-monophyly of the Cantharoidea was also supported by Bocakova *et al.* (2007) in cladograms based on nuclear and mitochondrial gene sequences. While Elateroidea (*sensu lato*) was strongly supported in all cladograms, the soft-bodied groups usually placed in Cantharoidea never formed a monophyletic group. The major clusters were formed by 1) Lampyridae (including Ototretinae) + Cantharidae, 2) Elateridae (including Drilidae and usually Omalisidae) + Phengodidae (including Rhagophthalmidae), 3) Lycidae and 4) Eucnemidae. The positions of the genera *Drilonius* Kiegenwetter, *Telegeusis* Horn, *Trixagus* Kugelann and sometimes *Omalisus* Geoffroy varied with type of alignment and analysis: 1) *Drilonius*, *Telegeusis* and *Trixagus* formed a clade with Chelonariidae and outside Elateroidea; 2) *Drilonius* and *Telegeusis* formed a clade sister to Elateroidea and *Trixagus* was sister to Elateroidea minus *Drilonius* and *Telegeusis*; 3) *Drilonius* was in Eucnemidae, *Telegeusis* sister to Elateroidea minus Eucnemidae, and *Trixagus* sister to Lycidae; or 4) *Drilonius* and *Telegeusis* formed a clade sister to remaining elateroids, and *Trixagus* and *Omalisus* formed a clade within Eucnemidae. Similar results were published by Sagegami-Oba *et al.* (2007) and Bocak *et al.* (2008).

The Elateroidea, as here delimited, exhibit several major evolutionary trends which deserve further mention: 1) development of a type of defensive behavior known as "clicking" in adults of the families Cerophytidae, Eucnemidae, Throscidae and Elateridae, 2) reduction in sclerotization of the cuticle, often accompanied by chemical defense mechanisms and aposematic color patterns in adults of various families formerly included in Cantharoidea, and 3) retention of larval features (neoteny) in adults of at least some of these families; 4) the evolution of bioluminescence in both adults and larvae; 5) the occurrence of an elateroid type of ecdysis associated with biforous spiracles and the loss of the spiracular closing apparatus in larvae; and 6) consolidation of the larval maxillae and labium to form a maxillolabial complex.

The cuticular and muscular modifications which make the clicking maneuver possible have been discussed by Evans (1972, 1973) for Elateridae, but precursors of these conditions are exhibited by members of various families of Dascilloidea, Buprestoidea and Byrrhoidea. The evolution of a pro-mesothoracic interlocking device involving projections and concavities or crenulate edges at the posterior end of the prothorax, anterior ends of the elytra, scutellum and/or mesanepisterna, combined with a mesoventral cavity for reception of the prosternal process, allow these beetles to combine mobility with structural integrity, by the unlocking or locking of this device. The transformation of this condition to form the clicking mechanism involves the enlargement of the prothorax, increase in the mass of the M4 muscle (Larsén 1966), reduction of the size of the exposed portion of the procoxa, enclosure of the trochantin and (except in Cerophytidae) its fusion to the notum, enlargement and deepening of the mesoventral cavity combined with the formation of a prosternal rest and an oblique slide at the anterior end of the cavity. Based on the topology given by Bocakova *et al.* (2007), this condition could have arisen independently from three to five times in the Elateroidea. Vahtera *et al.* (2009), however, suggested that, given the complexity of the clicking mechanism, it could have evolved at the base of the elateroid clade and been subsequently lost on numerous occasions, usually in association with the development of soft-bodiedness (see below).

Cantharoidea were defined mainly on the shared morphological traits resulting from soft-bodiedness (generally reduced body sclerotisation and a soft, flexible abdomen with extensive intersegmental membranes reminiscent of those in the larvae). The molecular phylogenies mentioned above (Bocakova *et al.* 2007; Sagegami-Oba *et al.* 2007; Bocak *et al.* 2008) rejected monophyly of Cantharoidea and proposed multiple origin of both soft-bodiedness and probably closely related female neoteny of some groups within broadly defined Elateroidea. The hypothesis of frequent shifts to neotenic development opens a possibility that the morphological disparity suggesting establishment of families like Drilidae or some subfamilies like Leptolycinae (Lycidae) is not a result of the long evolutionary history, but a consequence of relatively recent modified function of the endocrine system. These events potentially led to homoplasious modifications of morphology. The resulting similarity of soft-bodied or neotenic lineages is therefore difficult to interpret in morphology based analyses.

Crowson (1972) postulated that some neotenous groups, specifically the Southeast Asian lycid genera *Duliticola* Mjöberg and *Lyropaeus* Waterhouse, are members of primitively neotenous lineages and that fully metamorphosed winged forms re-developed from neotenic ancestors. Similar scenarios of evolutionary 're-imaginalisation' were proposed for Lycidae by Kazantsev (2005), and equally for the closely related Lampyridae by Cicero (1988). Bocak *et al.* (2008) hypothesized that soft-bodiedness represents a first level of incomplete metamorphosis. Soft-bodied adults of both sexes are known in Telegeusidae, Omethidae, Cantharidae, Lycidae, Lampyridae, Phengodidae, Rhagophthalmidae, Drilidae, and Omalisidae. Some adult females within these families are neotenic, i. e., they maintain apparently juvenile features resulting in incomplete metamorphosis and, in extreme cases, the lack of adult stages. The neotenic development of females is obligatory in all Omalisidae, Drilidae, Phengodidae and Rhagophthalmidae, and in many lineages of Lampyridae and Lycidae. The modifications include females with vestigial wings, but adult-like thorax (Omalisidae, Lampyridae part), wingless females (Lampyridae part) or females with only mouthparts and head adult-like (Drilidae, Lampyridae part). Lineages affected by neoteny to the highest degree are found in Lycidae where females lack both pupal and adult stages and retain a larvae-like morphology after the last ecdysis (Wong 1996). Some neotenic lycids reach body sizes of five centimeters and more and are frequently referred to as 'trilobite larvae' due to their appearance (Gravely 1915; Mjöberg 1925). The corresponding males are regularly fully metamorphosed and only seldom brachelytrous (*Alyculus* Kazantsev in Lycidae and *Phosphaenus* Laporte in Lampyridae).

Several elateroid groups (Lampyridae, Phengodidae, Rhagophthalmidae and two independent groups of Elateridae (Agrypninae: Pyrophorini and Thylacosterninae: *Balgus* Fleutiaux) are known for their bioluminescence. Previous morphological studies (Crowson 1972, Beutel 1995) often suggested close relationships of cantharoid luminescent lineages (Lampyridae, Phengodidae). Latest molecular analyses (Bocakova *et al.* 2007; Sagegami-Oba *et al.* 2007) showed that bioluminescent groups have arisen at least four times in Elateroidea. Likewise, recent morphological analysis (Branham and Wenzel 2001, 2003) supported several independent originations of bioluminescence in Elateroidea. Although superficially similar, molecular conclusions differ substantially. While morphological study separates Rhagophthalmidae from Phengodidae, and *Drilaster* Kiesenwetter and *Stenocladius* Fairmaire from Lampyridae, neither of these conclusions were confirmed in the molecular studies, hence upholding the traditional view of the constitution of Phengodidae and Lampyridae (Crowson 1972; Lawrence *et al.* 1995). Conversely, latest molecular analyses found cantharoid luminescent groups Lampyridae and Phengodidae deeply separated which is also supported by the structural and biochemical differences of the luciferases in either group (Viviani 2002).

Vahtera *et al.* (2009) presented an hypothesis connecting the clicking mechanism with the evolution of bioluminescence. If the clicking mechanism evolved in ancestors of the entire elateroid complex, the bifunctional role of the pre-luciferase enzyme in combination with the high-energy demand of the pronotal muscle were the preadaptive features for the luminescence to evolve in the prothorax. Lineages evolving away from the compact elaterid-type body structure retained the predisposition for luminescence, once a suitable luciferin was available. The sources of luciferin type compounds in beetles, whether of symbiotic origin or not, facilitated the pronotal light spots at the muscular attachment points as well as the fat body region. This scenario predicts that the source for luciferin is most likely external and after becoming available for any elateroid clade could be picked up repeatedly. It also explains why this feature is restricted to this one group beetles – the clicking mechanism being unique within beetles.

Larval head structures of Elateroidea are quite characteristic, even though, as pointed out in Beutel (1995), several derived features are also found in larvae of all or most groups presently assigned to Byrrhoidea (see **1–2**). A tendency to concentrate or reduce the stemmata is found in both lineages. Well separated stemmata occur in so me groups of Byrrhoidea (e. g., Byrrhidae, Dryopidae, Heteroceridae) but in others (e. g., Psephenidae, Ptilodactylidae) they form tight clusters and in Eulichadidae there is a single large lens beneath which are two to five pigment spots. In Elateroidea there is never more than a single stemma on each side. As in all Byrrhoidea, elateroid larvae lack a basal mandibular mola, and as in Byrrhoidea (excluding Byrrhidae) the head is distinctly prognathous. Both conditions have evolved independently in different lineages of Coleoptera, notably in groups with predacious larvae (e. g., Adephaga, Hydrophiloidea, Cleroidea [see **1–7**, **1–10**, **2–9**]). A characteristic feature found in larvae of Elateroidea (and Byrrhoidea excluding Byrrhidae, some Ptilodactylidae and Eulichadidae) is a maxillolabial complex, with closely connected labium and maxillae (Beutel 1995). The ventral mouthparts are moved only as a structural unit vertically. The extrinsic tentoriomaxillary muscles are vertically arranged. Similar conditions have evolved independently in Cleroidea and in some supposedly related groups of Cucujoidea (Beutel & Ślipiński 2001). As in most byrrhoid groups (excluding Byrrhidae, Ptilodactylidae, Eulichadidae and Callirhipidae) the tentorium of elateroid larvae is strongly modified, with posterior arms very strongly developed, cranially directed and completely detached from the tentorial bridge. The dorsal and anterior parts of the tentorium are reduced. Interestingly, again a similar condition is found in cleroid larvae and in some groups of Cucujoidea (Beutel & Ślipiński 2001). Apparently this condition is linked with the formation of a maxillolabial complex. A set of features distinctly separating Elateroidea from Byrrhoidea is the presence of a strongly developed lateral tentoriohypopharyngeal muscle, a dense, preoral filter formed by long microtrichia, the immobilisation of the labrum, and the loss of the labral muscles. A labrum separated from the clypeal region is preserved only in Artematopodidae and Brachypsectridae. The preoral filter is apparently an adaptation to liquid feeding. A similar condition has evolved in Carabidae and Histeroidea (Beutel 1993, 1999). Unusual modifications of the mandibular apparatus are characteristic for larvae of most Eucnemidae and Throscidae, where mandibles may be fixed or exodont. Another specific modification is the presence of mandibular sucking channels occurring in Brachypsectridae, Lampyridae, and a few other groups. An unusual feature apparently linked with highly specialized liquid feeding habits is the origin of very strongly developed extrinsic maxillary muscles of the sclerotized ventral wall of the hypopharynx. A somewhat similar condition has evolved in Cleroidea and some cucujoid groups, where an anterior bundle of *M. tentoriostipitalis* originates from the ventral prepharyngeal wall or from the posteriormost hypopharynx (Beutel & Ślipiński 2001).

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4.1. Rhinorhipidae Lawrence, 1988

John F. Lawrence

Distribution. *Rhinorhipus tamborinensis* Lawrence has been collected in a few localities in southern Queensland, Australia, all at higher elevations in the vicinity of closed forest. It is likely that the species also occurs in montane regions in northern New South Wales.

Biology and Ecology. The largest series of adults were collected during the day on leaf surfaces of an introduced weed, *Ageratina adenophora* (Asteraceae), at the edge between rainforest and cleared areas. Unfortunately, this site has now become a suburb and recent collecting expeditions have failed to

Fig. 4.1.1. *Rhinorhipus tamborinensis* Lawrence, adult male, dorsal (from Lawrence 1988; © CSIRO Australia).

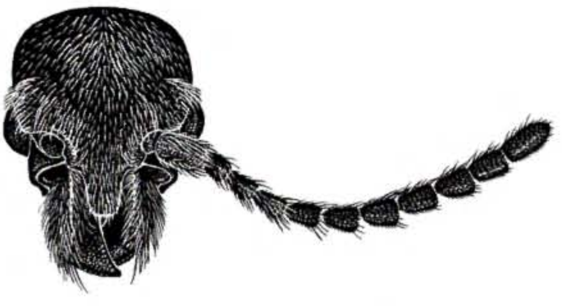

Fig. 4.1.2. *Rhinorhipus tamborinensis* Lawrence, adult female, dorsal (from Lawrence 1988; © CSIRO Australia).

produce more specimens. At another locality, a few beetles were found in an open area on low vegetation bordering a creek. When disturbed, the beetles exhibited a death-feigning reaction, dropping to the ground. Males greatly outnumbered females in this habitat. It is likely that these clearings were the sites of mating aggregations and that the beetles flew to them from within the rainforest. Red mud was present on a number of the specimens, which suggests that they either emerged from the soil after eclosion or sheltered there. The structure of the metacoxae and hind legs also suggests fossorial habits. The ovipositor is relatively unspecialized, so it is unlikely that the eggs are embedded in plant tissue or placed deep in soil. One female laid several eggs in the laboratory, but none of them hatched.

Morphology, Adults (Figs. 4.1.1–3). Length 5–8.5 mm. Body about 3 times as long as wide; slightly flattened above but moderately convex below. Heavily sclerotized and clothed with relatively stout and somewhat flattened, decumbent hairs.

Head longer than wide, strongly declined, abruptly constricted immediately behind eyes, so that no temples are present. With very short, median occipital endocarina but no transverse line. Eyes moderately large, protuberant, more or less circular, finely faceted, without interfacetal setae; ommatidium of exocone type with thick cornea and clear zone narrow or absent (Caveney 1986). Antennal insertions exposed, located in large, oblique, slightly raised circular fossae; subantennal grooves absent. Frontoclypeal region deflexed, strongly narrowed anteriorly, forming an elongate clypeal lobe which is apically rounded; frontoclypeal suture absent. Labrum elongate and slender, membranous, almost completely concealed by clypeus. Antennae 11-segmented, filiform to very slightly subserrate in both sexes, much longer in male than in female; sensory elements consisting of 2 types of trichoid sensilla evenly distributed along anterior edges of segments 4–11. Mandibles elongate, slightly and gradually curved mesally, unidentate, with simple, carinate incisor edge; deep, setose, dorsal cavity present at base (Fig. 4.1.3 B); mola absent; prostheca represented by short brush of hairs. Galea and lacinia reduced, membranous, densely setose; galea 1-segmented, truncate; lacinia subacute; apical palpomere slightly expanded near middle, apically truncate. Submentum very short and broad; mentum subtrapezoidal, biexcavate apically, with median tooth; ligula reduced, bilobed, setose; labial palps approximate; apical palpomere slightly expanded near middle, apically truncate. Hypopharyngeal and epipharyngeal surfaces clothed with distally inclined hairs. Subgenal ridges absent. Gular sutures moderately widely separated; pregular area subequal in length to gula, slightly concave. Corpotentorium and medially connected laminatentoria fused, forming single, broad bridge. Cervical sclerites small.

Pronotum about as long as wide, distinctly narrower than basal width of combined elytra, abruptly constricted at anterior third, with strongly produced and rounded anterior edge partly concealing head; lateral carinae absent; trisinuate posterior edge lacking margin or crenulations; promesothoracic interlocking device highly reduced, without lateral tubercles; sides of pronotum obliquely vertical, each with narrowly elongate, deep, oblique cavity at anterior fourth; posterior angles blunt and rounded, not produced, each one with smaller, deep cavity in front of it. Prosternum in front of coxae shorter than mid length of procoxal cavity, obliquely elevated, with strongly concave anterior edge; prosternal process long, narrow and slightly curved, narrowly rounded at apex, which fits into cavity on mesoventrite. Notosternal suture complete. Procoxae conical and projecting well below prosternum, without plates or concealed lateral extensions. Trochantin exposed, closely adpressed to sternum and only slightly movable (Fig. 4.1.3 A). Endopleuron free, with narrow basal stalk. Procoxal cavities widely open externally and internally; notal projections barely indicated. Scutellar shield relatively small, subtriangular, with base abruptly elevated and simple. Elytra about twice as long as combined width and 3 times as long as pronotum; more or less parallel-sided, with narrowly rounded apices; sutural flange deflected beyond apical fourth; each elytron with twelve more or less regular rows of deep, rounded, window punctures, in between which are rows of setiferous punctures; scutellary striole and apical interlocking tongue absent; epipleura narrow, weakly developed, not well marked but more or less complete. Mesoventrite about half as long as wide, narrowed and truncate anteriorly; on same plane as metaventrite, separated by complete sutures from mesanepisterna, which are separated from one another; discrimen absent; mesoventral cavity shallow, formed between paired, oblique carinae, which form mesal edges of procoxal rests, formed primarily by mesanepisterna. Mesanepisterna subtriangular, partly divided by oblique ridge anterior to which is major portion of concave procoxal rest. Mesepimeron smaller, partly fused to mesanepisternum, the pleural suture partly effaced at mesal end. Mesocoxa conical and projecting, without plate; with broadly exposed trochantin

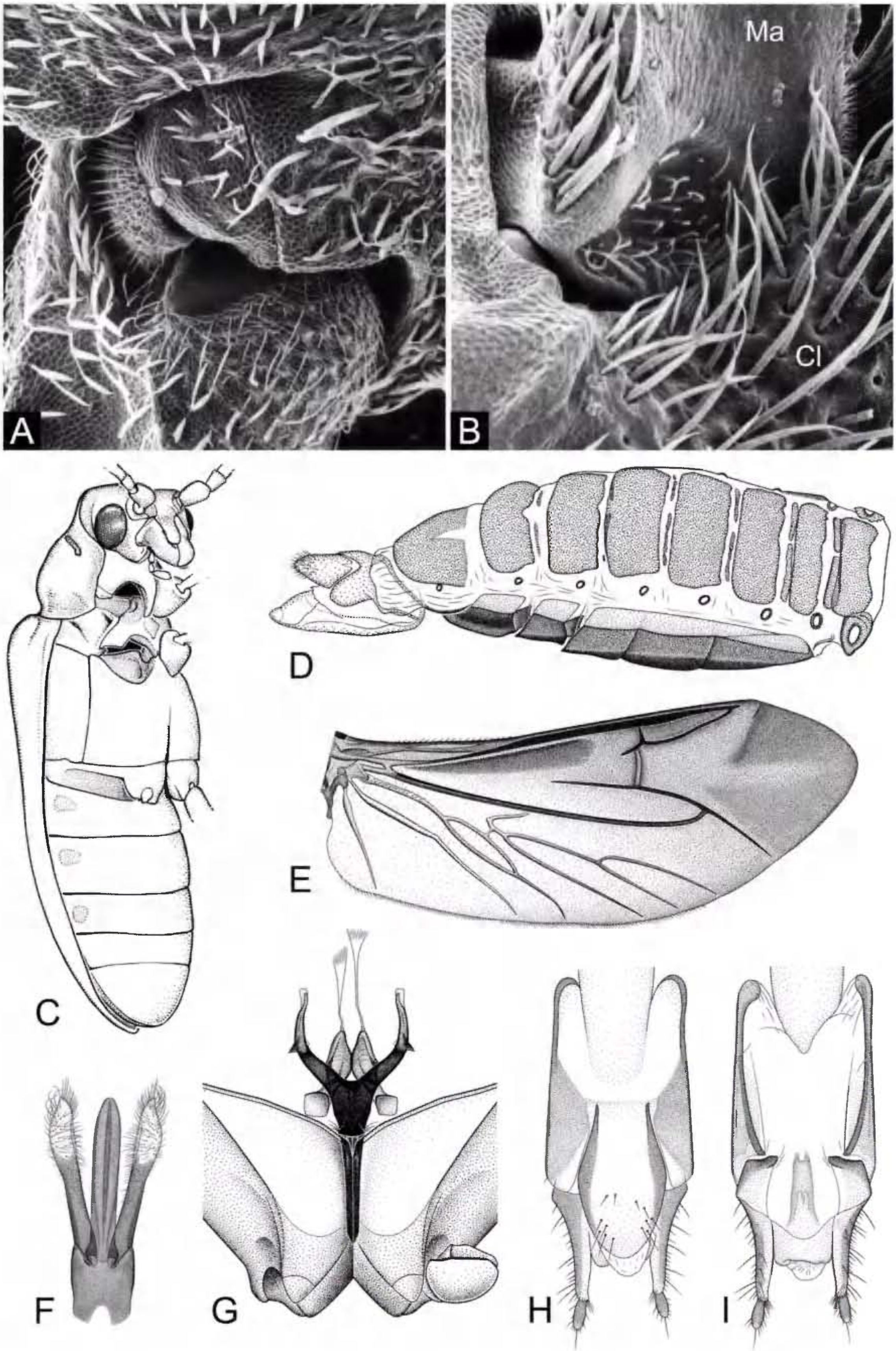

Fig. 4.1.3. *Rhinorhipus tamborinensis* Lawrence, adult features: A, prothorax, ventrolateral, showing coxal articular region and protrochantin abutting sternum; B, frontoclypeal region and base of left mandible, showing setose cavity; C, male, ventrolateral, with legs removed; D, male abdomen, dorsolateral, with pregenital sclerites extruded; E, male hind wing; F, aedeagus, ventral view; G, mesal portions of metacoxae and attached metendosternite, posterodorsal view; H–I, female abdominal apex: H, dorsal, I, ventral (all from Lawrence 1988; © CSIRO Australia).

and weakly developed secondary condyle (fitting into sides of metaventral process). Mesocoxal cavities narrowly separated, internally contiguous, about as long as wide, open laterally (partly closed by mesanepisternum and mesepimeron), with solid joint between meso- and metathoracic portions of coxal cavities. Mesometaventral junction with deeply notched mesoventral process overlapping narrowly rounded metaventral process. Metaventrite about 0.75 times as long as wide, strongly convex, with short discrimen, and no transverse (katepisternal) suture. Exposed portion of metanepisternum broad, about 2.5 times as long as wide, subquadrate with straight inner and outer edges and with outer carina and groove which fit against elytral epipleuron. Metepimeron fused to metanepisternum; pleural suture absent posteriorly. Metacoxae large and contiguous, extending laterally to meet elytral epipleura; coxal plates weakly developed. Metendosternite (Fig. 4.1.3 G) with long narrow stalk, most of which is attached to the mesal internal edges of the metacoxae, and moderately long, curved lateral arms; anterior process (which bears anterior tendons) with two halves separated basally so that a foramen is formed between them; ventrolateral processes expanded apically to form flat muscle attachments. Hind wing (Fig. 4.1.3 E) about 2.6 times as long as wide; apical field less than 0.2 times wing length; transverse folds meeting at point between anterior, oblique, linear sclerite and radial cell, which is well developed and more than 4 times as long as wide, with inner posterobasal angle right or slightly obtuse; cross-vein r3 short and slightly oblique, partly fused at base with r4; RP with basal section long, extending almost to mid wing, and apical section absent; R-M loop relatively narrow; medial spur more or less straight and extending to wing margin; medial field with five free veins, wedge cell well developed, apically acute; anal notch absent; AP undivided. Trochanterofemoral joints on fore and mid legs slightly oblique with base of femur well separated from coxa; that on hind leg strongly oblique, with trochanter produced along inner edge of tibia; femora and tibiae tuberculate; outer edges of tibiae denticulate; tibial apex slightly expanded, bearing two distinct spurs; metatibial apex more strongly expanded in female; tarsi 5-5-5; segments simple, without membranous lobes or setose pads beneath; claws pectinate; empodium well developed, bi- or trisetose.

Abdomen (Figs. 4.1.3 C, D) with five strongly convex ventrites, the first three of which are connate but separated by distinct sutures. Ventrite 1 (sternite III) deeply excavate for reception of metacoxae, with short triangular intercoxal process and distinct carina. Sternite VII (last ventrite) with narrow deep groove bordering free edge. Laterosternites well developed, those on segment VII delimited by distinct ridge; parasternites narrow, absent on posterior half of segment VII. Tergites all heavily pigmented, with microsetae sparsely and generally distributed around edges. Sternites V and VI each with paired sternomedian convergent and sternolateral divergent muscles; tergosternal muscles particularly well developed on sternites III–V, and represented externally by paired, glabrous elevations of the cuticle. Functional spiracles present on abdominal segments I–VIII, located in pleural membrane. Anterior edge of sternite VIII in male with short, triangular apodeme. Sternite IX broadly rounded anteriorly, without spiculum gastrale. Sternite VIII in female without median strut (spiculum ventrale) or anterolateral struts. Tergite IX in male emarginate. X well developed and free. Aedeagus (Fig. 4.1.3 F) trilobate, symmetrical, with short phallobase, long, narrow parameres, and longitudinally divided penis, with very short paired, basal struts and no ventral sclerotized lobe. Internal male reproductive system with large spermatophoral glands and closely associated seminal vesicles, large, thin-walled accessory glands, and testes consisting of ten pedicillate sperm tubes. Ovipositor (Fig. 4.1.3 H–I) short and broad, with divided coxites and spindle-shaped styli; paraprocts slightly longer than gonocoxites and styli combined, with ventral longitudinal baculi; coxites each with short basal section, transverse baculum, and elongate, narrow apex. Proctiger well developed; ventral sclerite present. Internal female reproductive system with vagina expanded to form weakly defined bursa copulatrix at point of entry of common oviduct bursa without spines or sclerotized plates; spermatheca consisting of long narrow lightly sclerotized tube continuous with anterior end of genital chamber; spermathecal gland attached by short duct to base of spermatheca. Alimentary canal consisting of long narrow oesophagus, large, thin-walled crop, simple proventricular area, without spines or plates, bilobed ventriculus without gastric caecae or regenerative crypts, short, bulbous pylorus bearing six free Malpighian tubules, moderately short ileum and somewhat enlarged rectum. Ventral nerve cord with metathoracic and first abdominal ganglia fused; ganglia VII and VIII completely fused, and ganglion VI partly fused to VII–VIII; connectives paired. [Caveney 1986; Lawrence 1988; Lawrence & Britton 1991, 1994; Lawrence & Newton 1995; Lawrence *et al.* 1995, 1999.]

Morphology, Larvae. Larvae unknown.

Phylogeny and Taxonomy. In cladograms produced by Lawrence (1988) (87 adult and 25 larval characters; all taxa of Elateriformia *sensu* Crowson 1973; Eucinetoidea outgroup), Rhinorhipidae was placed at the base of one of three clades: a) one consisting of all Elateroidea in the broad sense (including Artematopodidae, Brachypsectridae and the cantharoids), b) one consisting of Callirhipidae, Eulichadidae, Ptilodactylidae, Cneoglossidae, Psephenidae and Chelonariidae (Psephenoidea), or c) one consisting of both of the previous groups. Cladograms produced by Lawrence *et al.* (1995) (99 adult and 23 larval characters; all taxa of

Elateriformia *sensu* Crowson 1973 plus Scirtoidea; outgroups from Archostemata, Myxophaga and/or Staphylinoidea) produced different results. In all cladograms, Rhinorhipidae was included in Elateriformia and in most it formed a monophyletic group with Dascillidae, Rhipiceridae and Buprestidae. Based on these conflicting results, the family was considered to be Elateriformia *incertae sedis* by Lawrence & Newton (1995). Perhaps the discovery of the larva of *Rhinorhipus* and/or the collection of fresh specimens for DNA analysis will shed some light on the phylogenetic relationships of the group.

Acknowledgements

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4.2. Artematopodidae Lacordaire, 1857

John F. Lawrence

Distribution. The genus *Artematopus* Perty includes about 45 described species and many undescribed occurring from Nicaragua to Brazil. The closely related genus *Carcinognathus* Kirsch contains a single species from Peru, but probably occurs more widely in northern South America. *Electribius* Crowson contains two extant species from Mexico and El Salvador and four additional fossil species from Baltic amber. *Ctesibius eumolpoides* Champion is known from the Mexican states of Nuevo Leon and San Luis Potosí, while the related *Brevipogon confusus* (Fall) occurs throughout the southern half of California. *Allopogonia villosus* (Horn) is restricted to extreme southern California and northern Baja California. The genus *Macropogon* Motschulsky occurs throughout the northern part of North America and in eastern Asia, while species of *Eurypogon* Motschulsky are known from North and Central America, Italy, Japan and Taiwan. The two monotypic genera *Proartematopus* Crowson and *Electrapate* Iablokov-Khnzorian are known only from Baltic amber.

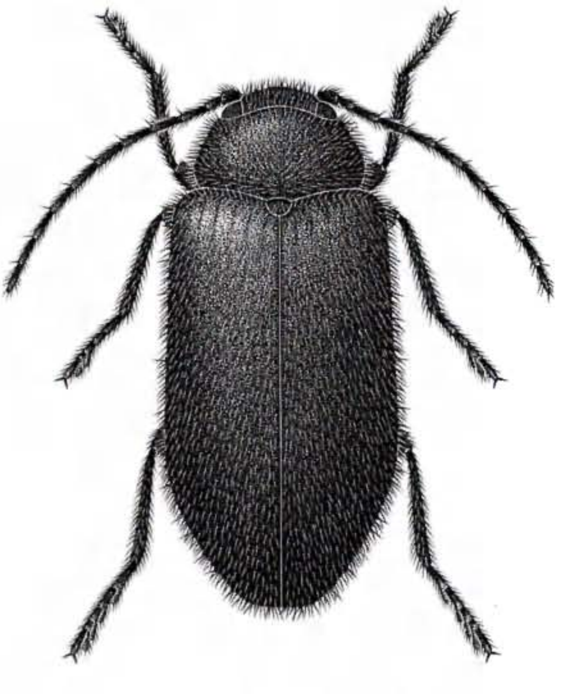

Fig. 4.2.1. *Brevipogon confusus* (Fall), adult, dorsal (from Lawrence 2005; © CSIRO Australia); length = 4 mm.

[Iablokoff-Khnzorian 1962; Crowson 1973, Lawrence 1995; Hörnschemeyer 1998; Lawrence 2005.]

Biology and Ecology. There seems little doubt that species of *Eurypogon* and *Macropogon* are closely associated with and probably feed on mosses growing on boulders. Cooper (1991) collected larvae and pupae of *Macropogon sequoiae* Hopping in mixed mats of moss, dominated by a species of *Grimmia* (Grimmiaceae) in the Sierra Nevada of California, while *Macropogon piceus* LeConte and *Eurypogon harrisi* (Westwood) are found in beds of a *Paraleucobryum* (Dicranaceae) on granitic boulders in New Hampshire. The latter were reared from early instars to adult on that moss alone. Gut contents are composed entirely of fine, unidentifiable particles, which appears to be due to the fact that the mouth cavity in these larvae are entirely blocked by dense patches of hairs, which filter out larger particles and create capillary forces. It is also likely that extra-oral digestion is involved. Crowson (1973) reported finding a teneral adult and full grown larva of *Eurypogon niger* (Melsheimer) under growths of a lichen (*Umbillicara* sp.) on granitic rocks in the Great Smoky Mountains of Tennessee. According to Champion (1897), adult *Artematopus*

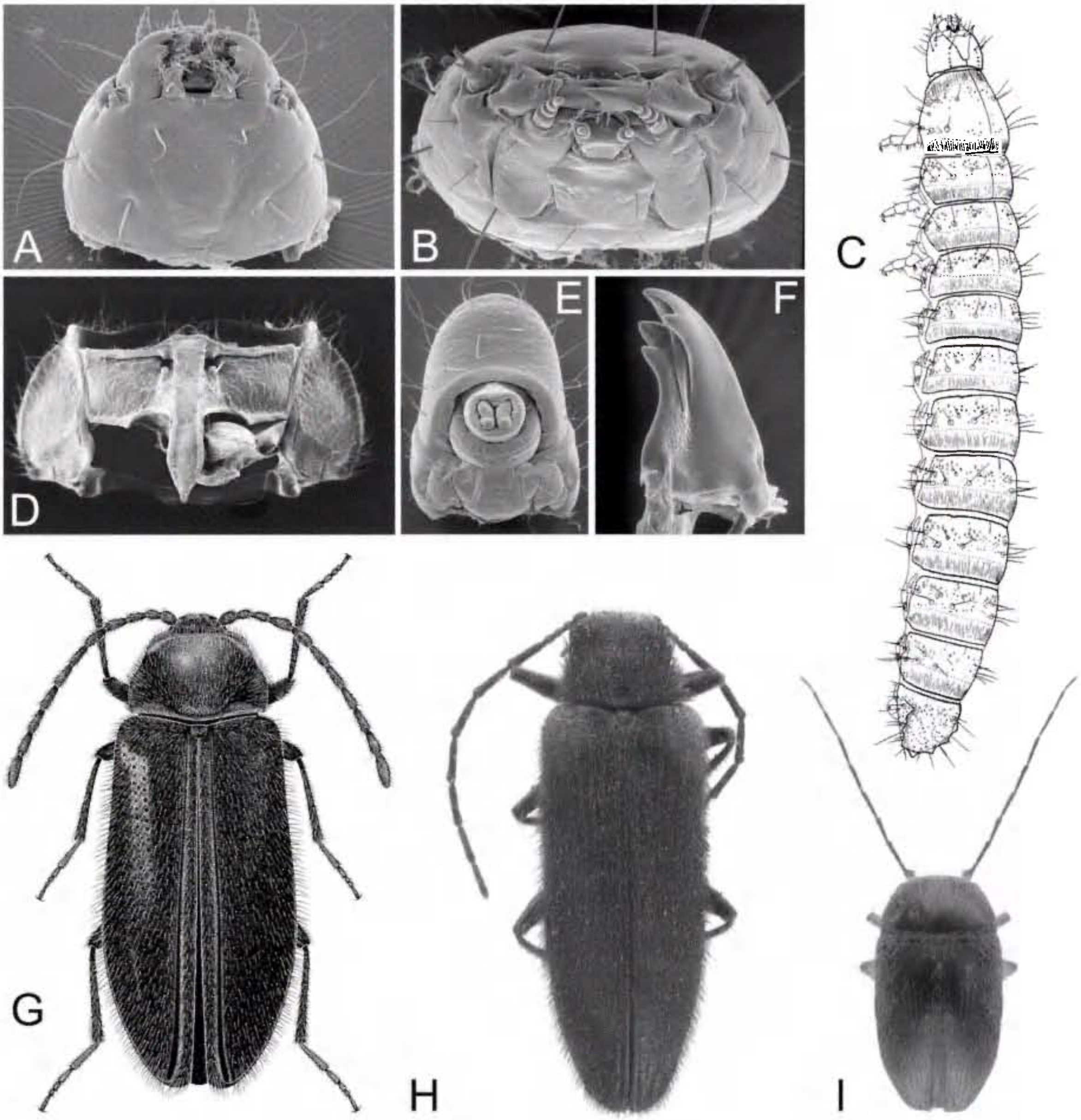

Fig. 4.2.2. A–B, E–F, *Eurypogon harrisi* Westwood, larva: A, head, dorsal; B, head, anterior; E, abdominal apex, ventral; F, left mandible, ventral (© J. F. Lawrence); C, *Macropogon sequoiae* Hopping, larva, dorsolateral (from Cooper 1991; © K. W. Cooper), length = 13 mm; D, *Artematopus* sp. (Ecuador), adult prothorax, ventral, with right coxa and trochantinopleuron removed (© CSIRO Australia); G, *Electribius crowsoni* Lawrence, adult, dorsal (from Lawrence 1995; © CSIRO Australia and Muzeum i Instytut Zoologii Polska Akademia Nauk, Warsaw), length = 2.82 mm; H, *Macropogon testaceipennis* Motschulsky, adult, dorsal (© CSIRO Australia), length = 8 mm; I, *Artematopus* sp. (Panama), adult, dorsal (© CSIRO Australia), length = 9 mm.

"are found upon bushes in dry places, chiefly on the savannas of the 'tierra caliente'". Larvae of *Artematopus discoidalis* Pic were collected in "the superficial layer of forest soil, just below litter" at Salesópolis, São Paulo, Brazil, and reared through to the adult stage (Costa *et al.* 1985). In the laboratory, live termites and tenebrionid larvae offered as food were not attacked, but cut up insect pieces were readily eaten. Although this indicates possible carnivorous or saprophagous habits, it does not eliminate the possibility that *Artematopus* larvae are also bryophagous.

Morphology, Adults (Figs. 4.2.1, 2 G, H, I). Length 2.5–10 mm. Body about 1.76–2.89 times as long as wide. Slightly flattened to moderately convex. Densely clothed with decumbent and erect or suberect hairs.

Head strongly declined, not abruptly constricted posteriorly. Posterior edge above occipital foramen distinctly bi-emarginate, forming pair of vertical impressions; without median endocarina. Transverse occipital ridge weakly developed or absent. Frontal region usually not or only slightly, gradually declined (moderately strongly declined in *Electribius*). Eyes well developed, slightly to strongly protuberant, entire, finely facetted, without or with very short, fine interfacetal setae; ommatidium of exocone type with reduced clear zone (Caveney 1986). Antennal insertions widely separated and exposed, located slightly in front of eyes, not raised. Subantennal groove usually absent or very weakly developed (well developed with deep, setose cavity in *Electribius*). Frontoclypeal suture absent; anterior clypeal margin emarginate or multidentate in some Neotropical species. Labrum free, well sclerotized and completely exposed, or sometimes lightly sclerotized, especially mesally, and partly concealed by clypeus; slightly to strongly transverse; anterior margin usually subtruncate, but sometimes cleft or emarginate. Antennae 11-segmented, filiform or serrate, moderately long, sometimes very long in male; antennomeres 2 and 3 or 2–4 sometimes much shorter than following ones; antennomeres 4–11 clothed with erect hairs in males of most species. Mandible unidentate and acute; incisor edge usually with one or two subapical teeth (absent in *Allopogonia* Cockerell); mola and prostheca absent. Maxilla with galea and lacinia short, broad, lightly sclerotized and pubescent; lacinia without uncus; apical maxillary palpomere fusiform to subtriangular or securiform. Labium with mentum subtrapezoidal; ligula short, broad, lightly sclerotized, undivided or cleft; apical labial palpomere fusiform or apically widened. Subgenal ridges absent. Gular sutures well separated; gula longer than wide. Corpotentorium absent. Cervical sclerites usually well-developed.

Pronotum about 0.45–0.7 times as long as wide; usually widest posteriorly; sides moderately straight, slightly sinuate or moderately to strongly curved anteriorly; base usually not to somewhat narrower than elytral bases; lateral carinae usually complete, sometimes vaguely indicated, simple, with or without raised margin; anterior angles right or rounded, not produced; posterior angles obtuse or right to acute, but not strongly produced; posterior edge usually bi- or trisinuate, simple, not margined; disc usually simple, sometimes with uneven glabrous elevations, with pair of basal cavities joined by transverse impression in *Electribius*. Promesothoracic interlocking mechanism weakly developed. Prosternum in front of coxae longer than mid length of procoxal cavity; slightly to strongly convex, with paired carinae (Fig. 4.2.2. D) (except in *Allopogonia*), with paired anterior cavities in *Artematopus* and *Carcinognathus*; anterior edge not produced, without mesal excavation. Prosternal process complete, parallel-sided, flat, overlapping mesoventrite; apex narrowly to broadly rounded; notosternal suture complete. Procoxae not or only slightly projecting, without concealed lateral extensions. Trochantins exposed, not closely adpressed to notum. Procoxal cavities strongly transverse, moderately narrowly separated, externally broadly open, without narrow lateral extensions, internally open. Scutellar shield well developed, anteriorly simple, abruptly elevated or not, posteriorly acute to broadly rounded. Elytra 1.36–2.47 times as long as combined width and 2.89–5.88 times as long as pronotum; punctation usually distinctly seriate (less so in *Ctesibius*), with eleven or twelve distinct puncture rows and no scutellary striole; sutural stria deeply impressed apically in *Electribius*; apices conjointly rounded, each with ventrally interlocking tongue; epipleura very narrow, sometimes incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are well separated from one another; anterior edge on same plane as metaventrite, with paired, slightly to strongly declined procoxal rests; discrimen present but incomplete; mesoventral cavity small and shallow to large and moderately deep. Mesocoxae not projecting. Trochantins exposed. Mesocoxal cavities moderately to widely separated, slightly transverse, open laterally (partly closed by mesepimeron, occasionally with mesanepisternum); with distinct joint between meso- and metathoracic portions of coxal cavities. Mesometaventral junction usually complex, monocondylic or dicondylic. Metaventrite moderately to strongly convex; discrimen moderately to very long; transverse (katepisternal) suture almost complete to short or absent, but usually located close to posterior edge of ventrite; postcoxal lines sometimes forming distinct axillary spaces; exposed portion of metanepisternum moderately elongate, three to four times as long as wide, broader anteriorly. Metacoxae contiguous, extending laterally to meet elytra, plates more or less complete but often weakly developed. Metendosternite with short lateral arms, no laminae, short to very long anterior process and approximate to well separated anterior tendons. Hind wing usually 2.2–2.5 times as long as wide, with apical field 0.18–0.24

times total wing length (0.37 times as long in *Electribius*); apical folds meeting apical wing margin separately; radial cell slightly to moderately elongate, with inner posterobasal angle right to acute; cross-vein r3 usually long, oblique, somewhat sinuate and meeting RP (although often incomplete in middle), sometimes shorter and more or less horizontal; basal portion of RP long to very long; apical portion absent; medial field with four or five free veins and no medial fleck; wedge cell usually well developed and apically truncate; anal lobe well developed, with AP undivided; anal embayment absent. Legs moderately long and slender, without tibial modifications; tibial spurs small, simple, equal; tarsi 5-5-5, tarsomeres 2–4 or 3–4 each with ventral, deeply bifid or occasionally emarginate lamella; basal pro- and mesotarsomeres with ctenidium in males of most *Macropogon*; pretarsal claws usually slightly expanded at base (with distinct basal tooth in *Carcinognathus*); empodium not prominent, usually concealed.

Abdomen with five connate ventrites, the sutures between them mesally obscured in *Electribius*. Ventrite 1 distinctly shorter than 2, without postcoxal lines; intercoxal process acute to broadly rounded or angulate. Patches of glandular hairs on ventrites 2–4 in male *Allopogonia*. Ventrite 5 longer than preceding ones, often bearing glandular hairs near the apex, much longer in males of *Brevipogon* and *Ctesibius*, where it is completely, densely clothed with glandular hairs. Abdominal tergites moderately to heavily sclerotized. Spiracles located in pleural membrane, those on segment VIII functional. Anterior edge of sternite VIII in male without median strut (except in *Electribius*). Tergite IX in male usually slightly to moderately emarginate and X well developed and free or partly fused to IX (IX and X completely fused in *Electribius*); sternite IX usually broadly rounded at base, without spiculum gastrale. Aedeagus of trilobate type, symmetrical; parameres usually individually articulated, basally fused in *Allopogonia*, fused to form complete tube in *Electribius*. Penis undivided with short anterior struts. Sternite VIII in female with long spiculum ventrale. Ovipositor long and moderately slender, lightly sclerotized; paraprocts much longer than gonocoxites, which are subdivided, with apical styli. Internal female tract usually greatly enlarged in vicinity of gonopore to form uterine bursa bearing patches of asperities or window-like sclerites; anteriorly-attached spermatheca usually complex and multichambered, with gland attached near its apex; *Electribius* with large anterior bursa, with spermatheca and spermathecal gland attached by a long duct near its base. [Forbes 1926; Crowson 1955, 1973, 1975; Lawrence 1982, 1988, 1995, 2005; Caveney 1986; Kukalová-Peck & Lawrence 1993, 2004; Lawrence *et al.* 1995, 1999 b; Young 2002.]

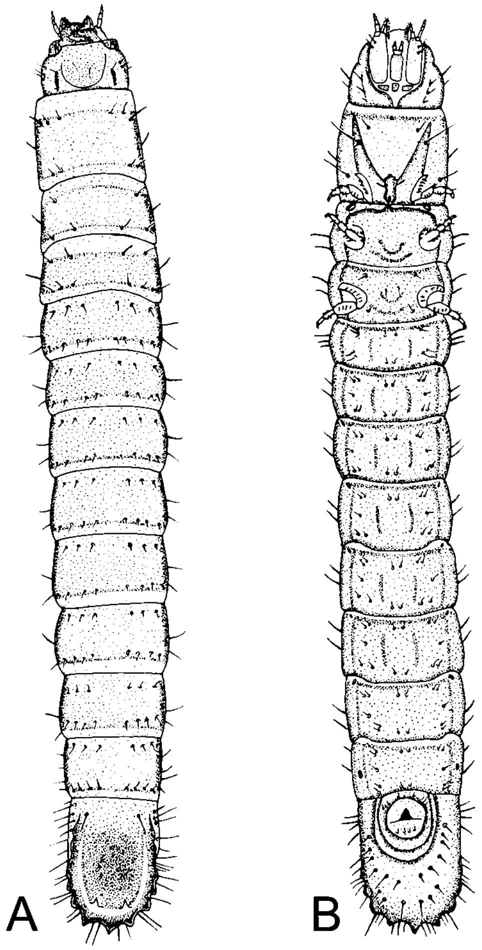

Fig. 4.2.3. *Artematopus discoidalis* Pic, larva: A, dorsal; B, ventral (from Costa *et al.* 1985; © Museu de Zoologia, Universidade de São Paulo); length = 15 mm.

Morphology, Larvae (Figs. 4.2.2 A–C, E, F, 3 A, B). Body relatively straight, elongate, more or less parallel-sided, subcylindrical to somewhat flattened. Dorsal surfaces usually moderately heavily pigmented, ventral surfaces lightly so. Vestiture consisting of fine hairs or setae only.

Head protracted and prognathous, somewhat flattened, with rounded sides. Posterior edge distinctly emarginate. Epicranial stem absent or very short; frontal arms V-shaped or U-shaped, with bases usually well separated (apparently contiguous in *Artematopus*); endocarina absent. One stemma present on each side, with well developed lens. Frontoclypeal suture absent or only vaguely indicated; clypeus broadly emarginate anteriorly. Labrum separated from clypeus by suture but more or less immobile, strongly transverse, broadly, deeply emarginate anteriorly (in *Artematopus* slightly concave with median tooth and triangular epipharyngeal sclerome). Antennae short, 3-segmented, with sensorium on antennomere 2 usually half as long as 3 (as long as 3 in *Artematopus*), conical or palpiform. Mandibles symmetrical, moderately stout; apex obliquely bidentate with two dorsal retinacula, or unidentate with a single large retinaculum (*Artematopus*); accessory ventral process absent; mola and prostheca absent; mandibular base with brush of hairs in *Artematopus*. Ventral mouthparts strongly retracted, forming maxillolabial complex; maxillary articulating area highly reduced or absent. Cardines undivided, transverse, well separated; stipes elongate; galea and lacinia short and subequal, the former 2-segmented and palpiform, the latter densely setose; palp 4-segmented. Labium consisting of prementum, mentum and submentum, the last sometimes unpigmented and not clearly separated from mentum, but distinctly separated from gula; ligula absent or shorter than labial palps, which are 2-segmented and separated by more than width of first palpomere. Hypopharyngeal sclerome present. Hypostomal rods absent; ventral epicranial ridges weakly developed. Gular sutures separate; gula longer than wide. Short and stout posterior tentorial arms arise immediately posterad of maxillolabial complex; other parts of tentorium reduced (*Macropogon*). Extrinsic and intrinsic labral muscles absent. Tentoriocardinal and tentoriostipital muscles strongly developed, almost vertical. Median premental retractor absent; *M. tentoriopraementalis* inferior bipartite, longer part originating from hind margin of head capsule like *M. tentoriopraementalis* superior. Closed prepharyngeal tube present, strongly flattened; posterior precerebral pharyngeal dilator strongly developed; ventral dilators and dorsal postcerebral dilators absent. Brain and suboesophageal ganglion shifted to prothorax (Beutel 1995).

Prothorax longer than meso- or metathorax but not as long as the two combined. Thoracic terga without special armature. Prothoracic presternum divided into anterior and posterior sclerites, the latter diamond-shaped with a longitudinal endocarina. Biforous mesothoracic spiracle located on spiracular sclerite (anterior laterotergite); atrophied metathoracic spiracle present;. Legs short, stout, 5-segmented, armed with short spines and setae; pretarsus claw-like, with two setae lying side by side; coxae large and narrowly separated.

Abdominal terga I–VIII simple and subequal. Tergum IX distinctly longer than VIII, extending onto ventral surface; posterior three-fourths of dorsal surface slightly concave and lined laterally and posteriorly by a continuous ridge, which is often crenate or lined with slightly upturned teeth; sternum IX strongly transverse and apically emarginate. Segment X forming a short, cylindrical, ventrally projecting pygopod. Spiracles biforous, located on tergal plates above laterotergites. [Böving & Craighead 1931; Costa *et al.* 1985, 1988; Cooper 1991; Lawrence *et al.* 1999 a.]

Phylogeny and Taxonomy. Artematopodidae were included in Dascillidae in older works (Champion 1897; Pic 1914; Arnett 1963), moved (as Eurypogonidae) to the superfamily Dryopoidea by Crowson (1955), and later combined with Callirhipidae and Brachypsectridae in a separate elateriform superfamily Artematopoidea (Crowson 1973). Lawrence & Newton (1982) suggested that both Artematopodidae and Brachypsectridae (but not Callirhipidae) were part of a monophyletic group containing those families usually placed in Elateroidea and Cantharoidea. In cladograms produced by Lawrence (1988) and Lawrence *et al.* (1995), based on adult and larval characters, and Beutel (1995), based on larval features only, artematopodids were usually placed within Elateroidea in this broad sense. There are currently three subfamilies recognized: Electribiinae, Allopogoninae and Artematopodinae. Lawrence (1995) redescribed the fossil subfamily Electribiinae Crowson based on recent species, and Hörnschemeyer (1998) described additional fossil forms. Ctesibiinae, proposed by Crowson (1973), was combined with Macropogoninae and Artematopodinae into a single subfamily by Lawrence (1995) and in a later study (Lawrence 2005) he elevated the tribe Allopogoniini Crowson (1973) to subfamily rank.

Acknowledgements

CSIRO Australia is acknowledged for support of research and CSIRO Australia, Muzeum I Instytut Zoologici, PAN, Warsaw, Museu de Zoologia, Universidade de São Paulo and Prof. K. W. Cooper are gratefully acknowledged for allowing me to use copyrighted figures. The following artists are acknowledged: S. P. Kim (Figs. 4.2.1, 2G) and S. Ide (Figs. 4.2.3 A, B). I am grateful to S. A. Ślipiński and A. Seago for assistance in obtaining and scanning published illustrations, Rolf Beutel for calling my attention to internal structures of the larval head, F. Dolambi for assistance with digital photography, and Anne Hastings for preparation of the plates. Portions of this Chapter benefited from research carried out with the support of a National Science Foundation grant "Assembling the Beetle Tree of Life" (DEB-0531768).

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4.3. Brachypsectridae Horn, 1881

Cleide Costa, Sergio A. Vanin, John F. Lawrence, Sergio Ide and Marc A. Branham

Distribution. The family contains the single genus *Brachypsectra* LeConte with four described extant species: *B. fulva* LeConte occurring in the more arid parts of the southwestern United States and northern Mexico, *B. vivafosile* Woodruff from the Dominican Republic, *B. lampyroides* Blair from southern India and *B. fuscula* Blair from Singapore. In addition, an undescribed species from northern Australia is known from larvae only, and an adult and larvae of *B. moronei* Branham were described from Miocene amber in the Dominican Republic. [Lawrence & Newton 1995; Wu 1996; Woodruff 2004; Costa *et al.* 2006.]

Biology and Ecology. Adult males of *Brachypsectra* are usually attracted to lights at night, but are probably short-lived. Most known females have been reared from larvae in the laboratory. *Brachypsectra* larvae are usually collected beneath loose bark, in cracks in rock, in leaf bases of monocolyledonous plants or under leaves or other debris on the ground. The larvae appear to be non-specific ambush predators, remaining inactive until approached by prey. Some of the prey items recorded for *B. fulva* are small spiders, an ant, an immature solpugid (Solifugae) and a larva of a tenebrionid beetle. When approached by a spider or other invertebrate of appropriate size, the larva was observed to arch its back, so that the prey is wedged between the articulated, spine-like tergum IX and the perforated sucking mandibles. It has been

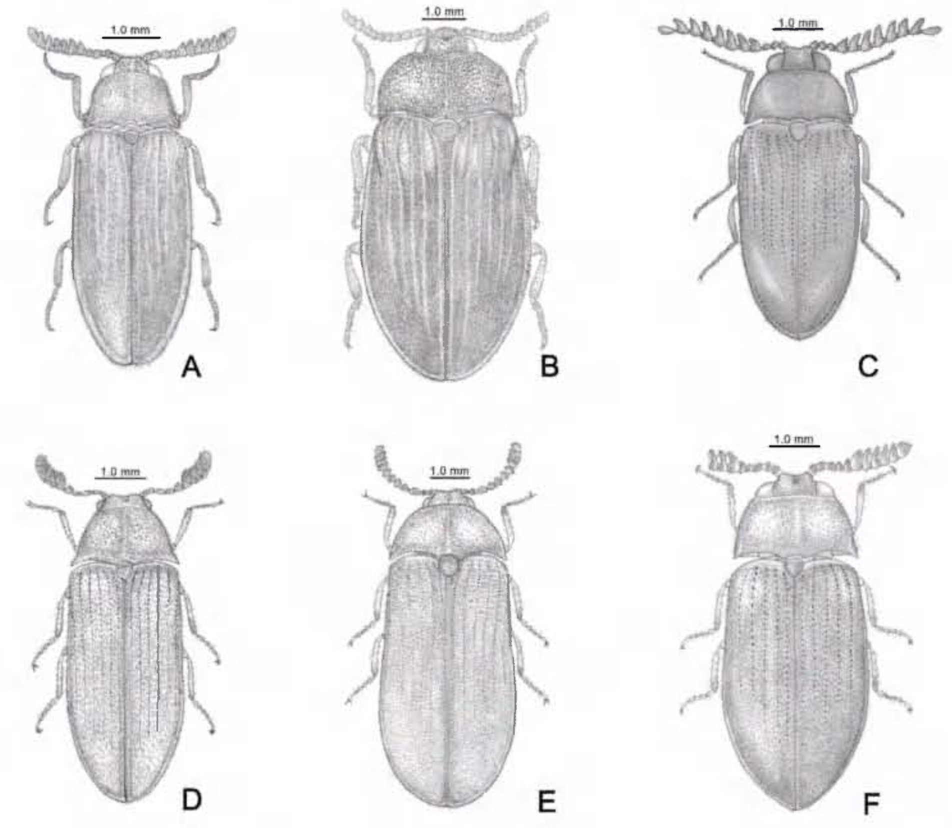

Fig. 4.3.1. A–F, Adult habitus. A, *Brachypsectra fulva* (male); B, *B. fulva* (female) C, *B. vivafosile* (male); D, *B. lampyroides* (male); E, *B. lampyroides* (female); F, *B. fuscula* (male) (after Costa *et al.* 2006).

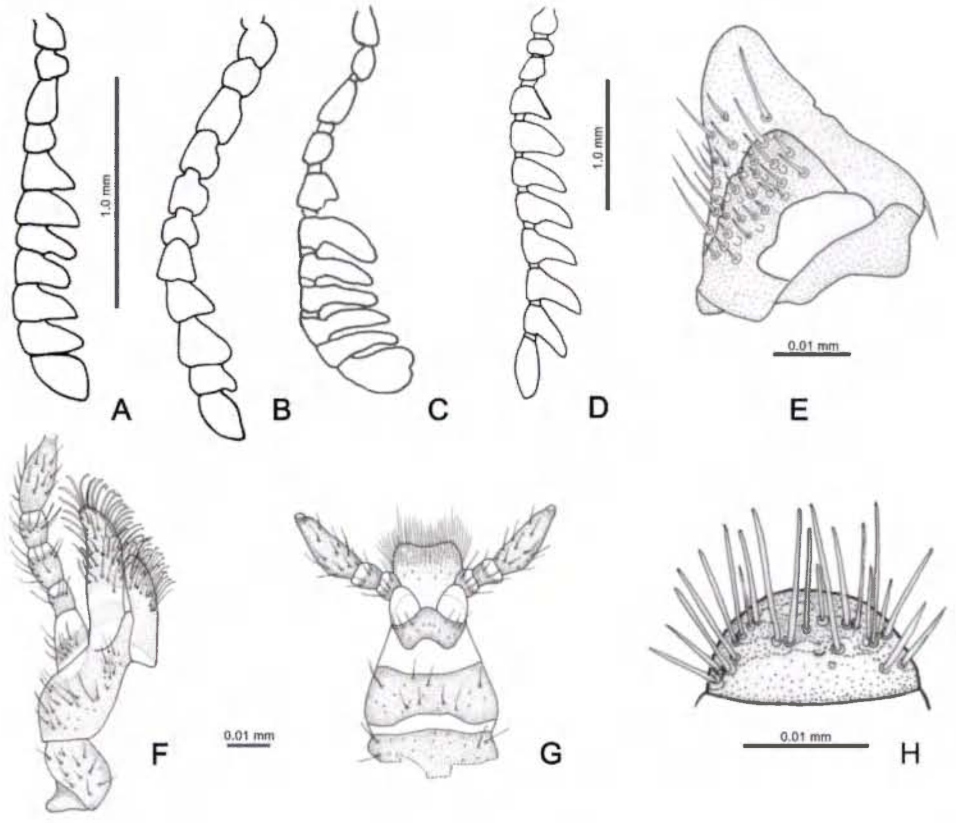

Fig. 4.3.2. A–H, Adult structures. A–D, antennae: A, *Brachypsectra fulva* (male); B, *B. fulva* (female); C, *B. lampyroides* (male); D, *B. vivafosile* (male). E–H, mouthparts of *B. fulva* (male): E, mandible, dorsal; F, right maxilla (ventral); G, labium; H, labrum (after Costa *et al.* 2006).

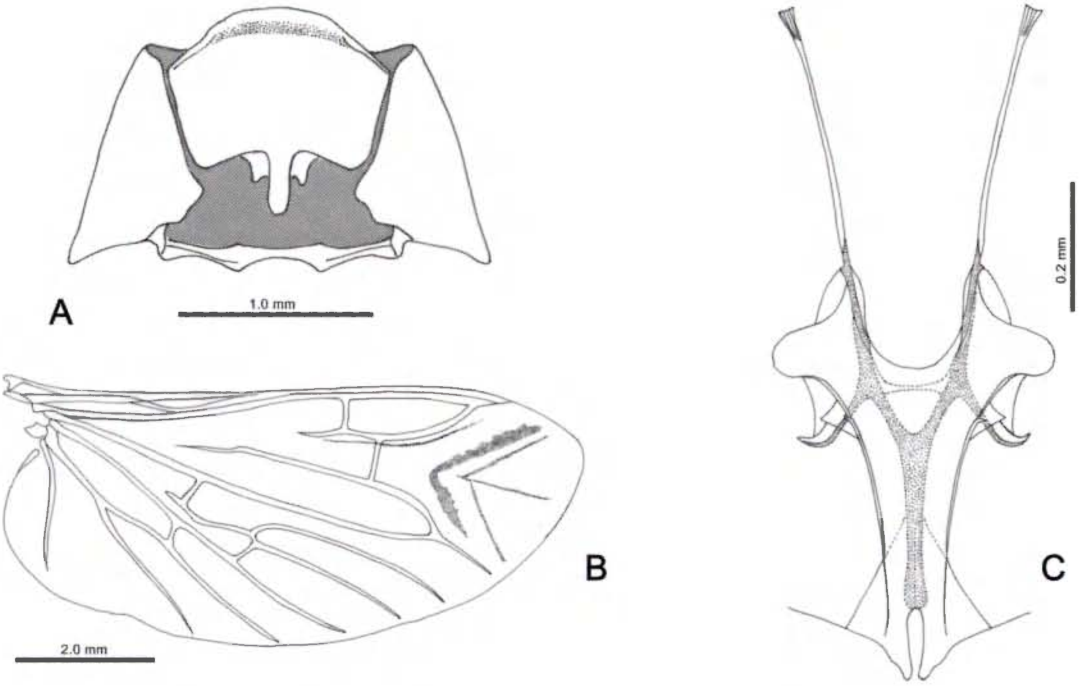

Fig. 4.3.3. A–C, Adult structures, *Brachypsectra fulva* (male). A, prothorax (ventral); B, hind wing; C, metendosternite (dorsal) (after Costa *et al.* 2006).

hypothesized that the small papillae on the dorsum of the larva may produce an allomone for attracting prey. Pupation occurs in a very wide-laced silken cocoon. [Ferris 1927; Neck 1993; Fleenor & Taber 1999; Costa *et al.* 2006.]

Morphology, Adults (Fig. 4.3.1 A–F). Length about 4 to 8 mm. Body oblong to somewhat elongate, about 1.9–2.7 times as long as wide, more or less flattened and finely pubescent.

Head slightly shorter than wide, slightly declined, deeply inserted into prothorax. Strongly constricted behind eyes forming very short neck consisting of little more than an expanded rim on either side of occipital foramen; dorsal rim of foramen slightly biemarginate. Occipital region without carina. Eyes large, more or less globular, strongly protruding and finely facetted, with exocone ommatidia (Caveney 1986) and no interfacetal hairs. Frontoclypeal region strongly declined anteriorly, so that mouthparts directed ventrally; transverse or longitudinal carinae absent. Antennal insertions slightly visible from above, placed within saucer-like fossae which are separated by flat area about two-thirds the width of one fossa; each continuing ventrally and laterally to form a short, oblique subantennal groove. Frontoclypeal suture absent; anterior edge of frontoclypeus broadly emarginate. Labrum (Fig. 4.3.2 H) relatively small; free, well sclerotized, slightly transverse and strongly rounded apically, with tormae straight, simple, and apically acute. Antennae (Figs. 4.3.2 A–D) 11-segmented, with antennomeres 4, 5 or 6 to 10 expanded apically on one side to form a pectinate club with the terminal antennomere; scape slightly longer than wide and slightly longer than pedicel, which is subquadrate; antennomere 3 distinctly elongate, the following one or two slightly so. Mandible (Fig. 4.3.2. E) small, subtriangular, unidentate, without mola or prostheca. Maxilla (Fig. 4.3.2 F) with galea and lacinia subequal in length; galea more or less hyaline and lined with setae; lacinia lightly pigmented and densely setose, without hook or spine; apical palpomere fusiform. Labium (Fig. 4.3.2. G) with mentum transverse and trapezoidal; ligula short, slightly emarginate apically and setose; apical palpomere fusiform. Subgenal ridges absent. Gular sutures well separated posteriorly and strongly converging anteriorly. Corpotentorium absent. Cervical sclerites moderately well developed; anterior ones straight, slender and lightly sclerotized; posterior ones slightly longer, thicker and slightly curved.

Pronotum about 0.5–0.6 times as long as wide; widest posteriorly, with distinct lateral carinae the anterior third of which are concealed from above; anterior angles more or less oblique, not produced forward; posterior angles acute, produced laterally and posteriorly, embracing elytral bases, bearing carinae which extend anteriorly and end at posterior third of disc, which is slightly convex in male but somewhat inflated anteriorly in female; posterior edge trisinuate with moderately developed interlocking device. Prosternum in front of coxae (Fig. 4.3.3 A) at least twice as long as shortest diameter of procoxal cavity, slightly convex, with short chin piece, slightly curved ventrally and anteriorly truncate; head rest strongly transverse and slightly declined. Prosternal process moderately narrow, parallel-sided, slightly curved dorsally; apex broadly rounded, extending posteriorly to fit into mesoventral cavity. Notosternal sutures complete and more or less open (with exposed membrane). Procoxae not projecting below prosternum, with well-developed articulating area and slender trochantin more or less concealed by expansion of prosternal cowling; endopleuron free, not fused to notum. Procoxal cavities strongly transverse, externally broadly open, with narrow lateral extensions; internally open. Scutellar shield abruptly elevated, with straight, carinate basal edge, slightly rounded lateral edges and rounded to subtruncate or slightly emarginate apex. Elytra about 1.5–2 times as long as greatest combined width and 3.75–5 times as long as pronotum; sides subparallel or slightly wider at posterior third; apices conjointly, broadly rounded; disc flattened, with nine very weakly impressed punctate striae; sutural stria slightly more deeply impressed than others and scutellary striole absent; humeri moderately well developed; carinate anteriorly, the carinae continuing mesally and continuous with the scutellar carina; epipleura narrowed from base to about level of anterior third of metanepisternum, more or less uniform in width beyond that point and complete to apex. Mesoventrite separated by complete sutures from mesanepisterna, which are well separated from one another; anterior edge on same plane as metaventrite, with pair of large, shallow procoxal rests, which flank a raised median boss and are contiguous laterally with similar rests on mesanepisterna; posteriorly with a relatively large, deep mesoventral cavity, which extends well beyond anterior edges of coxal cavities; discrimen absent. Mesocoxae transverse, not projecting, with exposed trochantins. Mesocoxal cavities separated by a little more than one-third shortest diameter of one of them; laterally open (partly closed by mesanepisternum and mesepimeron); without distinct joint between meso- and metathoracic portions of coxal cavities. Mesometaventral junction complex with metaventral knob fitting into notch on mesoventral process. Metaventrite relatively long and flat; discrimen well developed, vaguely indicated anteriorly but extending beyond base of metaventral process; transverse (katepisternal) suture absent; visible portion of metanepisternum moderately narrow, more or less parallel-sided and distant from mesocoxal cavity; metepimeron concealed beneath elytra. Metacoxae strongly transverse, extending laterally to meet epipleura; coxal plates narrow but more or less complete. Metendosternite (Fig. 4.3.3 C) with long stalk, short, broad arms, weakly developed ventrolateral processes and well developed, bilobed anterior process, with tendon at apex of each lobe and deep excavation between lobes. Hind wing (Fig. 4.3.3 B) about 1.85–1.9 times as long as wide, with very short apical field with a pair of strongly oblique, apically diverging sclerotizations; radial cell moderately large, elongate, its base complete, forming right inner posterobasal angle; cross-vein r3 short and slightly oblique; RP extending to basal third of wing, without apical extension; medial field with five free veins; MP_{3+4} with basal cross-vein and spur, apically forked; CuA_1 meeting MP_4 just beyond fork; wedge cell absent; anal lobe well developed, with undivided AP; anal embayment absent. Legs slender and simple; trochanters moderately elongate; trochanterofemoral joints on fore and mid legs slightly oblique, those on hind legs strongly so; tibial spurs absent; tarsi 5-5-5; tarsomeres 1–4 combined more than twice as long as 5; tarsomere 4 slightly reduced with weak ventral lobe; pretarsal claws simple; empodium visible, bisetose.

Abdomen with five free ventrites. Ventrite 1 not much longer than 2, without postcoxal lines; intercoxal process acute. Ventrites 1–4 subequal in length, 5 broadly rounded at apex. Abdominal spiracles on segments I to VIII, located in pleural membrane. Sternite VIII in male anteriorly bisinuate, forming pair of short lateral struts and short, broad, rounded median plate. Sternite IX broadly rounded anteriorly, subtruncate posteriorly. Tergite IX in male distinctly emarginate and separated from tergite X, which is subtruncate. Sternite VIII in female trapezoidal, posterior edge sinuous and setose; spiculum ventrale well developed. Aedeagus (Figs. 4.3.4 A–B) of trilobate type, symmetrical; phallobase about as long as wide, slightly emarginate at base; parameres with apical, laterally curved hooks; penis undivided, with short basal struts. Ovipositor moderately elongate, lightly sclerotized; paraprocts slightly longer than coxites, which are transversely divided into two lobes; proximal lobe with obliquely transverse baculum; distal lobe narrowed and palp-like; stylus well developed, terminal. Internal tract with long anterior bursa and spermathecal duct entering between gonopore and base of bursa; spermatheca lightly pigmented. Malpighian tubules four, free. Midgut with regenerative crypts. [Hlavac 1975; Kasap & Crowson 1975; Lawrence & Britton 1991, 1994; Lawrence *et al.* 1999 b; Young 2002; Woodruff 2004; Costa *et al.* 2006.]

Morphology, Larvae (Figs. 4.3.5 A–B; 5 A–B; 7 A–B). Length up to 15 mm. Body broadly ovate, strongly flattened and disc-like, with moderately long, branched projections on all thoracic segments and abdominal segments I–VIIII; head and tergite IX darkly pigmented, upper surfaces unevenly pigmented, varying from white to yellow or brown, covered with small setiferous tubercles, flattened pigmented areas of varying size and shape, and a median row of subconical projections lined with setiferous tubercles; lower surfaces very lightly pigmented, except for presternal area, thoracic spiracular sclerites, and apical portions of legs. Vestiture consisting mainly of expanded, modified setae, which on most of the dorsal surface form an irregularly multisided, flattened scales with a median stalk and spiculate upper surface.

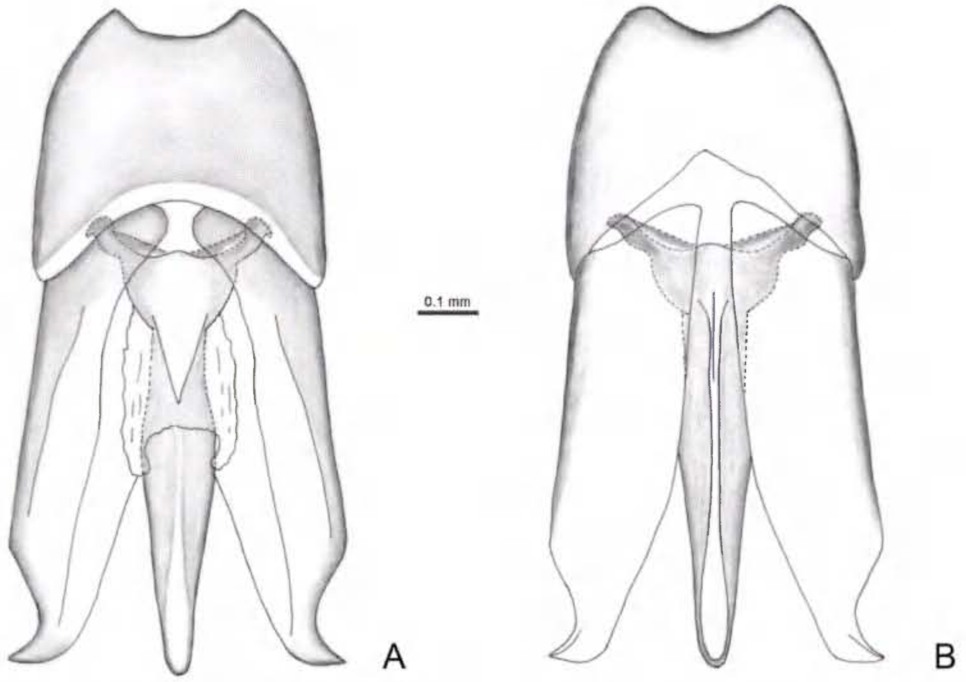

Fig. 4.3.4. A–B, Aedeagus, *Brachypsectra fulva*, A, ventral; B, dorsal (after Costa *et al.* 2006).

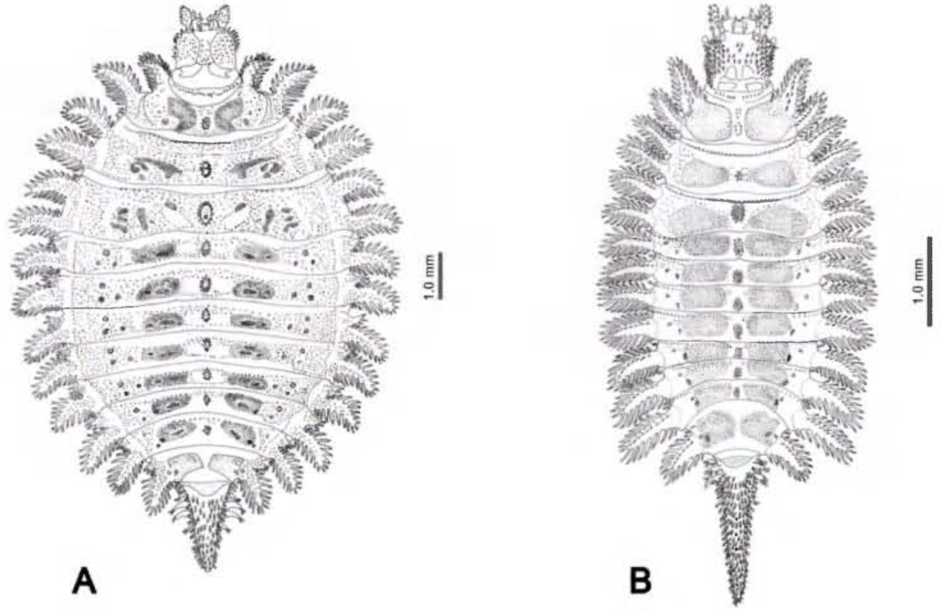

Fig. 4.3.5. A–B, Larval habitus. A, *Brachypsectra lampyroides*; B, *Brachypsectra* sp. (after Costa *et al.* 2006).

Head (Figs. 4.3.6 A–B, 7 A–B) prognathous and protracted, elongate and more or less parallel-sided, much narrower than prothorax; usually slightly elevated and capable of being strongly elevated. Posterior edge as seen from above broadly emarginate. Epicranial stem very short; frontal arms slightly lyriform, sometimes vaguely indicated. Endocarinae absent. One large stemma on each side, with well-developed lens. Frontoclypeal suture present or absent. Labrum free, slightly transverse, expanded apically with biemarginate apex bearing four stout setae. Antennae well developed, about two-thirds as long as greatest head width, 3-segmented; antennomere 1 about as long as wide, and 2 about 8 times as long and irregularly club-shaped, heavily pigmented and clothed with modified setae; antennomere 3 and palpiform sensorium highly reduced and lying side by side at outer edge of oblique apex of antennomere 2. Mandibles symmetrical, narrow and falcate, strongly curved mesally, perforate with completely enclosed internal channel; widely separated at base, without mola or prostheca. Ventral

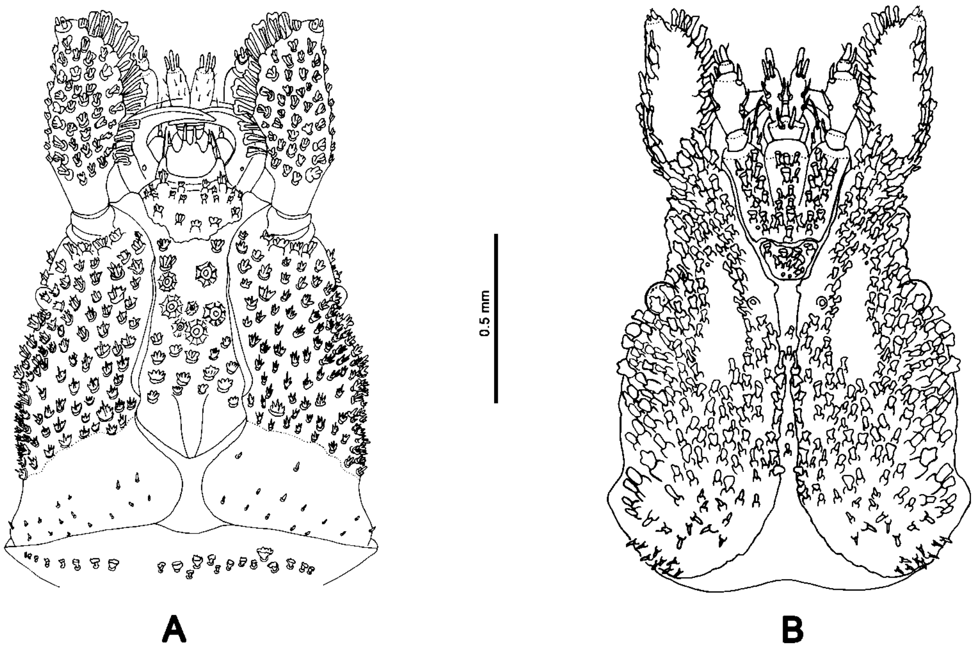

Fig. 4.3.6. A–B, Larval head, *Brachypsectra fulva*. A, dorsal; B, ventral (after Costa *et al.* 2006).

mouthparts moderately retracted, forming maxillolabial complex without articulatory area; maxillae with cardines fused together forming single median, trapezoidal plate; stipes elongate; galea small, palpiform and articulated, with single seta at apex; lacinia fixed, slender, curved and falcate; palp 4-segmented, with palpomere 2 as long as 1, 3 and 4 combined. Labium with mentum and submentum fused; postmentum completely fused to stipes on each side, separated by slight impression only; palps 2-segmented, approximate, with palpomere 1 much longer than 2; ligula absent. Hypopharynx without sclerome. Hypostomal region (ventral head closure) longer than maxillolabial complex; gular sutures fused. Hypostomal rods and ventral epicranial ridges absent.

Thoracic terga and abdominal terga I–VIII moderately to strongly transverse; the former each with a pair of narrow subacute, slightly posteriorly curved, branched processes on each side; the latter each with a single similar process in front of which is a reduced process without branches. Protergum slightly longer than either meso- or metathoracic terga; preceded by membranous cervical region bearing transverse row of setiferous tubercles; body of protergum with single median oval projection and pair of moderately large, irregular pigment patches, which may be broken up or accompanied by smaller patches laterally; centers of patches or entire small patches with smooth surfaces, in contrast to other areas, which are more or less uniformly covered with setiferous tubercles. Meso- and metaterga similar, but with main pigment patches smaller and more broken up, and with median projections larger than that on protergum. Prothoracic sternum unpigmented, except for pair of patches on cervicosternum; clothed mainly with short, simple stout setae, except in front of procoxae and on cervicosternum, where most setae arise from tubercles; procoxae separated by slightly more than greatest coxal diameter; meso- and metacoxae separated by about two coxal diameters. Legs well developed, with tibiotarsus slightly longer than femur and pretarsus forming distinct claw bearing a pair of setae.

Abdominal segments I–VIII about 1.5 times as long as thorax; terga I–VII all with median projection, smaller paramedian patches, and one or two small, rounded pigment patches just behind spiracular opening; paramedian patches often small and transverse on anterior segments but larger on posterior ones. Tergum VIII without median projection and with paramedian patches occupying most of dorsum. Tergum IX forming long, narrow, heavily sclerotized, articulated plate, which has several lateral branches at base, narrows towards subacute apex, and is covered with setiferous tubercles. Anterior abdominal sterna without or with one pair of small lateral pigment spots, these increasing in size and number on sterna V to VII. Sternum VIII with single pair of larger pigment patches. Sternum IX membranous and segment X not distinguishable. Spiracles biforous but reduced in size, borne on short spiracular tubes; mesothoracic spiracles located ventrally on anterolateral transverse spiracular sclerites; abdominal spiracles located dorsally on lateral portion of tergite; all spiracles with closing apparatus. [Barber 1905; Blair 1930; Böving & Craighead 1931; Lawrence 1991; Lawrence & Britton 1991, 1994; Lawrence *et al.* 1999 a; Young 2002; Costa *et al.* 2006.]

Phylogeny and Taxonomy. LeConte (1874) placed his genus *Brachypsectra* in Rhipiceridae, based on its

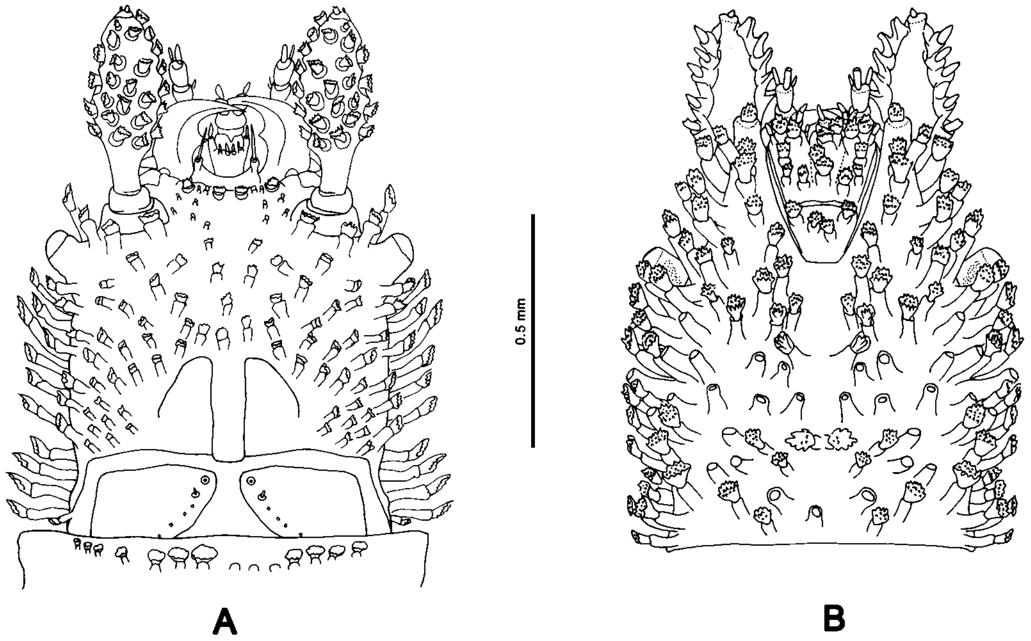

Fig. 4.3.7. A–B, Larval head, *Brachypsectra* sp. (Australia). A, dorsal; B, ventral (after Costa *et al.* 2006).

resemblance to *Zenoa* Say (now placed in Callirhipidae), and Horn (1881) proposed the tribe Brachypsectrini within Dascillidae. Forbes (1926) found that the type of wing folding in *Brachypsectra* was similar to that found in Lampyridae and Elateridae, but not in Dascillidae, and Blair (1930) concluded that the tribe should be raised to family rank, allied more closely to Elateridae than Dascillidae. Crowson vacillated between placing the family in Cantharoidea (1955) or in a group also containing the families Artematopodidae and Callirhipidae (1973). Kasap & Crowson (1975) returned the family to Cantharoidea based mainly on the free abdominal ventrites (with more or less complete longitudinal musculature), a condition considered to be derived through neoteny in Elateriformia and unlikely to have evolved independently in the two groups. In cladograms produced by Lawrence (1988) and Lawrence *et al.* (1995) based on both adult and larval characters, Brachypsectridae was placed at or near the base of a clade containing Cerophytidae, Eucnemidae, Throscidae and Elateridae (Elateroidea *sensu stricto*) or a clade including these families plus the Cantharoidea (Elateroidea *sensu lato*). In Beutel's (1995) analysis of elateriform larvae, the family always clustered with Cantharoidea based mainly on the channeled mandibles. [Lawrence & Newton 1982, 1995.]

Acknowledgements

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4.4. Cerophytidae Latreille, 1834

Cleide Costa, Sergio A. Vanin, John F. Lawrence and Sergio Ide

Distribution. The family includes three genera: the Holarctic *Cerophytum* Latreille and the Neo-tropical *Brachycerophytum* Costa *et al.* and *Phytocerum* Costa *et al.* The distributions of the 21 known species are as follows: Nearctic Region: *C. convexicolle* LeConte (western U. S. A.) and *C. pulsator* (Haldeman) (eastern U. S. A.); Palaearctic Region: *C. elateroides* (Latreille) (southern and central Europe) and *C. japonicum* Sasaji (Japan); Neotropical Region: *B. fuscicorne* (de Bonvouloir) (Mexico to Colombia), *B. sinchona* Costa *et al.* (Peru and Bolivia), *P. alleni* Costa *et al.* (Costa Rica and Nicaragua), *P. belloi* Costa *et al.* (Brazil), *P. birai* Costa *et al.* (Brazil), *P. boliviense* (Golbach) (Bolivia), *P. burakowskii* Costa *et al.* (Trinidad), *P. cayennense* (de Bonvouloir) (Mexico, French Guiana, and Brazil),

Fig. 4.4.1. *Phytocerum minutum*, male (from Costa *et al.* 2003), Length = 5.1 mm.

P. distinguendum (Soares & Peracchi) (Brazil, Paraguay, and Argentina), *P. golbachi* Costa *et al.* (Argentina), *P. ingens* Costa *et al.* (Brazil), *P. inpa* Costa *et al.* (Brazil), *P. minutum* (Golbach) (Argentina), *P. simonkai* Costa *et al.* (Trinidad), *P. serraticorne* Costa *et al.* (Guatemala), *P. trinidadense* (Golbach) (Trinidad), and *P. zikani* (Soares & Peracchi) (Brazil). [Costa *et al.* 2003].

Biology and Ecology. Adult cerophytids have been collected at light traps or Malaise traps, by beating vegetation, or in association with rotten wood or bark. *Cerophytum elateroides* has been reported from a number of deciduous tree genera, including *Ulmus* (Ulmaceae), *Fagus* and *Quercus* (Fagaceae), *Salix* and *Populus* (Salicaceae), *Acer* (Aceraceae), *Tilia* (Tiliaceae), *Betula* (Betulaceae), and *Juglans* (Juglandaceae). Adults are capable of "clicking" in the same manner as Elateridae (by the sudden release of the prothorax, which is held under tension by a small projection at the anterior edge of the mesoventral cavity), but it is also possible that the enlarged and modified profemora and the lack of metacoxal plates in Cerophytidae are both connected in some way with escape behavior. The larva of *C. elateroides* was first described by Rey (1887) based on specimens collected with an adult in the rotten trunk of *Sambucus* (Caprifoliaceae). Mamaev (1978) redescribed and illustrated the *Cerophytum* larva based on a series of specimens found in the dark fungus–infested wood (brown rot) of a dead standing *Ulmus* in association with larvae of Oedemeridae. It is likely that these larvae feed in old brown–rotten wood belonging to a variety of hardwoods. [Buysson 1910; Horion 1953; Lawrence 1991; Steiner 2000; Johnson 2002; Costa *et al.* 2003.]

Morphology, Adults (Fig. 4.4.1). Length 4.3–9.2 mm. Body about 2.2–2.6 times as long as wide, slightly flattened above, strongly convex below, usually black or yellowish-brown in color and clothed with recumbent and/or suberect hairs.

Head about as long as wide, deeply inserted into prothorax and only slightly declined, not abruptly constricted posteriorly. Occipital region with weak transverse carina continuing behind and below eyes to form short subgenal ridges. Median endocarina

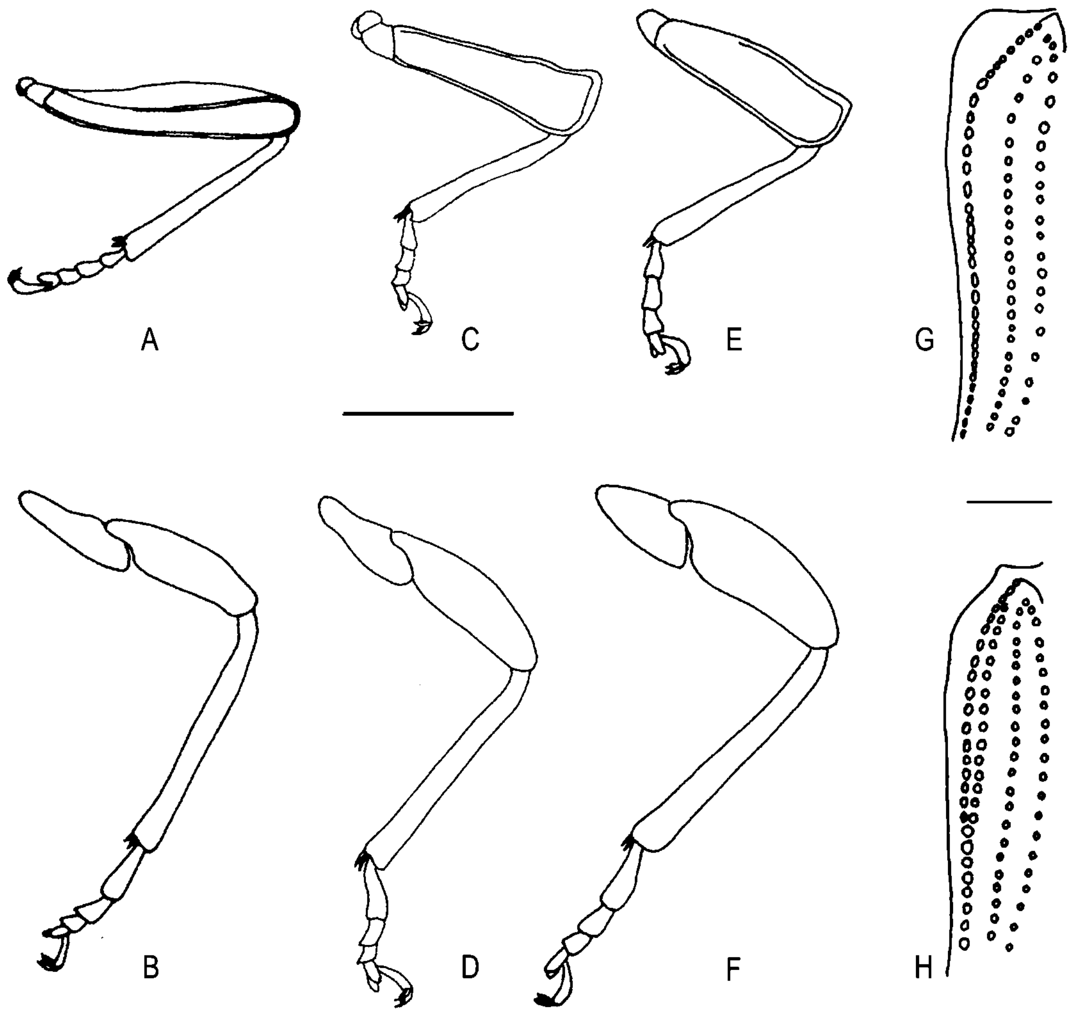

Fig. 4.4.2. *Cerophytum elateroides*, A, fore leg; B, hind leg. *Brachycerophytum fuscicorne*; C, fore leg; D, hind leg; G, basolateral portion of left elytron. *Phytocerum distinguendum*; E, fore leg; F, hind leg. *Phytocerum boliviense*; H, basolateral portion of left elytron. Scale lines = 1.0 mm (A–F, G, H). (from Costa *et al.* 2003).
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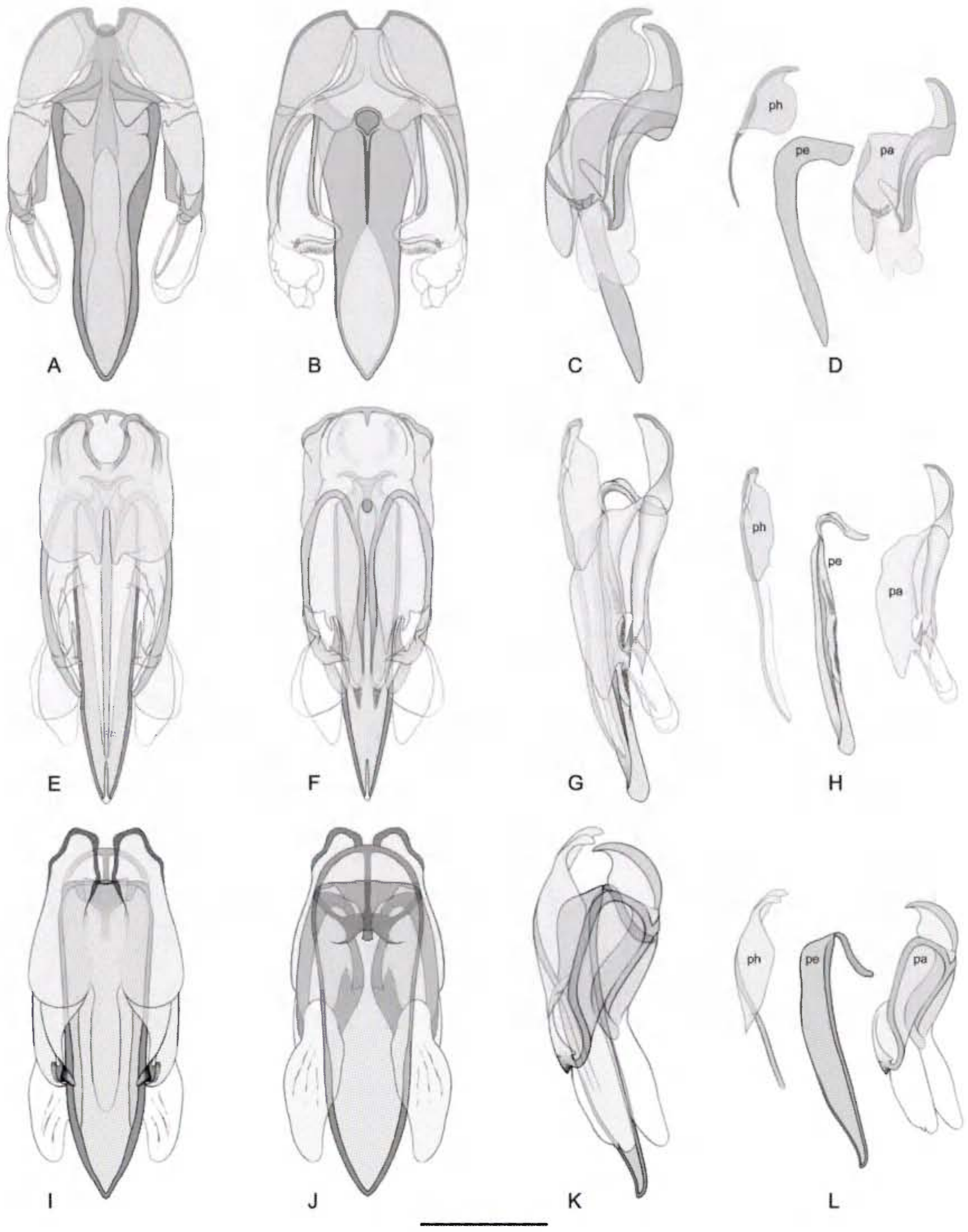

Fig. 4.4.3. Aedeagus, ventral, dorsal, lateral, and lateral with parts separated. A–D, *Cerophytum pulsator*; E–H, *Brachycerophytum sinchona*; I–L, *Phytocerum cayennense*; pa = parameres; pe = penis; ph = phallobase. Scale lines = 1.0 mm (A–C, E–G, I–K, D, H, L). (from Costa *et al.* 2003).

absent. Frons produced in front of eyes forming median prominence bearing antennal insertions, with or without median carina, strongly declined anteriorly, so that frontoclypeal region is more or less vertical and mouthparts are ventrally oriented; frontoclypeal suture absent. Eyes large, more or less globular, strongly protruding and finely facetted, with exocone ommatidia and no interfacetal setae. Antennal insertions moderately close together, concealed by frontal ridges or partly exposed from above; subantennal grooves absent. Labrum free, well sclerotized, strongly transverse and truncate. Antennae 11-segmented, serrate to pectinate from antennomere 3 to 10, with rami arising from base of each; 11 simple and narrowly rounded or notched; scape more than 3 times as long as pedicel, which is attached subapically, so that antennae are more or less geniculate. Mandibles narrow, strongly curved, unidentate and acute; without mola but with membranous prostheca. Maxillae with both galea and lacinia densely setose at apex; apical palpomere more or less expanded and truncate, usually securiform or elongate oval. Ligula membranous, rounded apically; palps approximate; apical palpomere subtriangular. Gular sutures widely separated. Corpotentorium absent. Cervical sclerites well developed.

Prothorax about 0.55–0.7 times as long as wide. Pronotum usually widest anteriorly, without lateral carinae; anterior angles not produced; posterior angles acute and slightly produced laterally or obtuse; posterior edge more or less straight or slightly sinuate; disc moderately convex; interlocking device weakly developed. Notal hypomera extensive, obliquely vertical; notosternal sutures complete. Prosternum in front of coxae at least twice as long as shortest diameter of procoxal cavity, strongly convex; anterior edge truncate or with ventrally directed chin piece; head rest (upper surface of anterior edge of sternum) strongly oblique (from lateral perspective) and hemispherical to strongly transverse; prosternal process moderately broad and curved dorsally, laterally expanded at middle to form secondary condyle on each side, then narrowed to form acute apex which fits into mesoventral cavity. Procoxae not projecting ventrally, each with long, narrow internal extension, articulating with long, concealed trochantin and its attached endopleuron, the latter not fused to hypomeron. Procoxal cavities circular to slightly transverse, open internally and externally. Scutellar shield abruptly elevated, with straight basal edge; lateral edges slightly rounded and apex subacute to rounded. Elytra about 1.7–2 times as long as combined width and 3.4–4.4 times as long as pronotum; with nine distinct rows of deep window punctures, sometimes with an additional subhumeral row (Fig. 4.4.2 G–H); scutellary striole absent; epipleuron wide anteriorly, abruptly narrowed just behind humeri and extending almost to apex, narrow posterior portion weakly delimited and almost vertical (completely visible in lateral view). Mesoventrite on same plane as metaventrite, with large, deep mesal cavity, preceded by sclerotized lip, flanked anteriorly by a pair of concave areas and posteriorly by mesocoxal cavities, and extending posteriorly almost to edge of ventrite. Mesoventrite separated by complete sutures from mesanepisterna, which are widely separated at midline, each posteriorly fused to mesepimera (a vague internal ridge probably indicating position of reduced pleural apophysis) and with a narrow, oblique housing into which the pronotal hypomeron fits; anterior edge of mesoventrite on same plane as metaventrite, with large, deep mesal cavity, preceded by a convex lip (sometimes with pair of small, slightly declined procoxal rests), flanked anteriorly by pair of concave areas and posteriorly by mesocoxal cavities, and extending posteriorly almost to edge of ventrite. Mesocoxal cavities oblique, separated by more than shortest diameter of one of them; open laterally (partly closed by mesepimeron), with solid joint between meso- and metathoracic portions of cavity; meso-metaventral junction a straight line. Metaventrite strongly convex, without discrimen or transverse (katepisternal) suture; visible portion of metanepisternum very narrow and distant from mesocoxal cavity; metacoxae large, somewhat oblique, strongly developed internally, and extending laterally to meet elytral epipleura; coxal plates absent. Metendosternite with long stalk, short, broad arms, and well developed anterior process bearing approximate tendons. Hind wing about 2.25 times as long as wide, with very short apical field bearing two parallel, oblique, anterior sclerotizations and sometimes an additional oblique posterior one; radial cell elongate, its base complete, forming a right or very slightly acute angle; cross-vein r3 moderately long and slightly oblique, extending almost to RP, which extends to basal third of wing; medial field with four free veins (MP_3, MP_4+CuA_1, CuA_2 and AA_3); wedge cell and anal notch absent, AP_{3+4} undivided. Legs (Fig. 4.4.2 A–F) moderately long and slender. Protrochanter less than one-fifth length of femur with trochanterofemoral joint truncate or slightly oblique; profemur subequal in length to protibia, with ventral longitudinal carina and slight concavity into which the protibia fits, sometimes with additional longitudinal carina on posterior surface. Meso- and metatrochanters more than half as long as corresponding femora with trochantofemoral joints strongly oblique; meso- and metafemora without longitudinal carina and only 0.75 to 0.85 times as long as corresponding tibiae. Tibial spurs paired and subequal on all tibiae; tarsi 5-5-5; tarsomeres 1 and 5 about equal in length, 2 shorter than 1, 3 and 4 subequal, the latter with a ventral lobe; pretarsal claws pectinate; empodium not visible.

Abdomen strongly convex. Basal four ventrites connate, 1 slightly shorter than 2, with narrow, acute intercoxal process. Ventrites 2, 3 and 4 subequal; 5 broadly rounded at apex. Abdominal spiracles present on segments I to VIII, located in pleural membrane. Sternite VIII in male broadly rounded anteriorly, without median strut. Sternite IX similarly rounded at base, produced apically to form elongate, narrow, apically rounded, lightly sclerotized process. Tergite IX in male narrowly emarginate almost to base, distinctly separated from tergite X, which is long and narrow with rounded apex. Aedeagus (Fig. 4.4.3 A–L) of trilobate type, symmetrical; phallobase, parameres and penis with extensive weakly sclerotized areas; phallobase ventrally less sclerotized in the center and more sclerotized at the proximal edge, with shallow to deep anterior emargination and long, narrow posterior process which is closely associated with ventral surface of the penis; parameres ventrally, loosely articulated to phallobase fused dorsally at base forming a more or less developed convex anterior projection which is divided into two parts, the proximal one

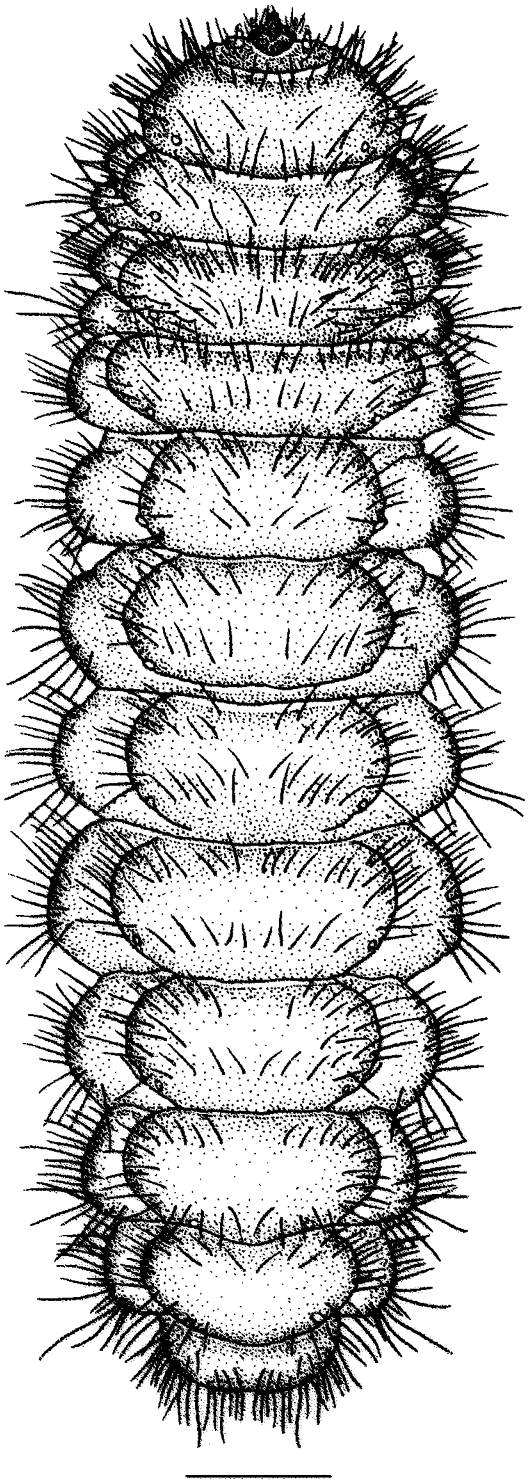

Fig. 4.4.4. *Cerophytum elateroides*, larva, dorsal. Scale line = 1.0 mm. (from Costa *et al.* 2003).

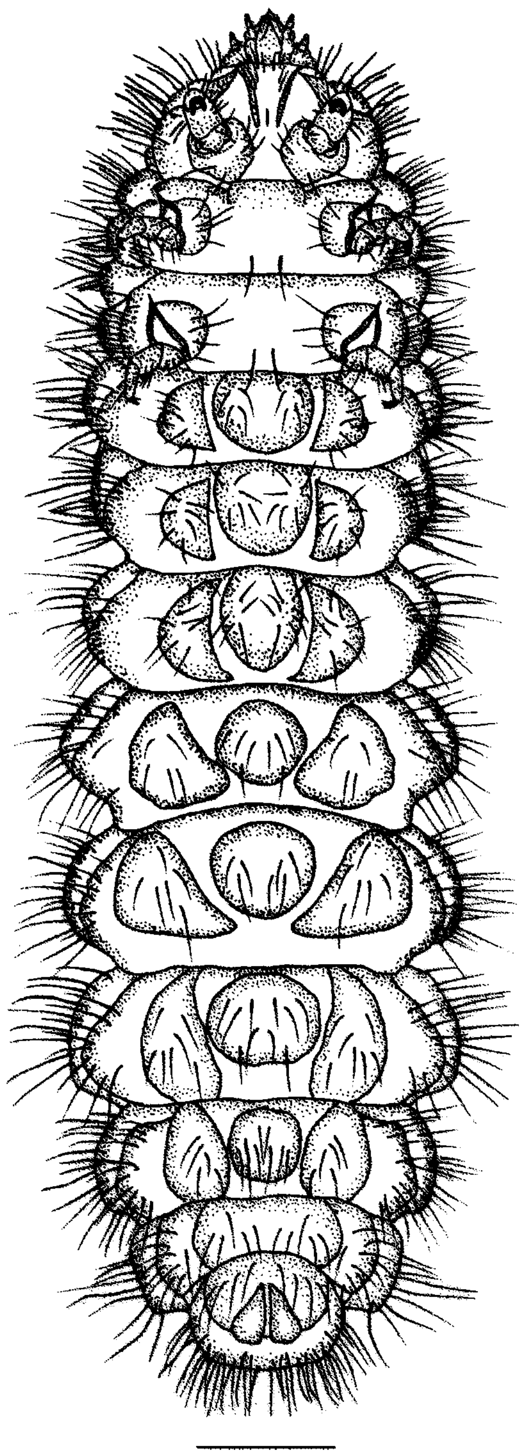

Fig. 4.4.5. *Cerophytum elateroides*, larva, ventral. Scale line = 1.0 mm. (from Costa *et al.* 2003).

sclerotized and with variable hook-like structures and the distal one membranous, unilobate, bilobate or trilobate; penis more or less flattened; base with median, dorsally curved strut which joins parameres dorsally at their point of fusion. Sternite VIII in female forming long spiculum ventrale. Ovipositor long and narrow; coxites not divided, styli short and terminal, baculi elongate. Internal female tract consisting of elongate vagina, large terminal bursa with one or two pairs of basal embedded sclerites; spermatheca present or absent. [Caveney 1986; Costa *et al.* 2003.]

Morphology, Larvae. Length 3.0–15.0 mm. Body (Figs. 4.4.4–5) elongate, robust but more or less parallel-sided, slightly curved ventrally. White in color, except for legs, anterior part of protergum and head capsule, which are yellow, and pretarsus,

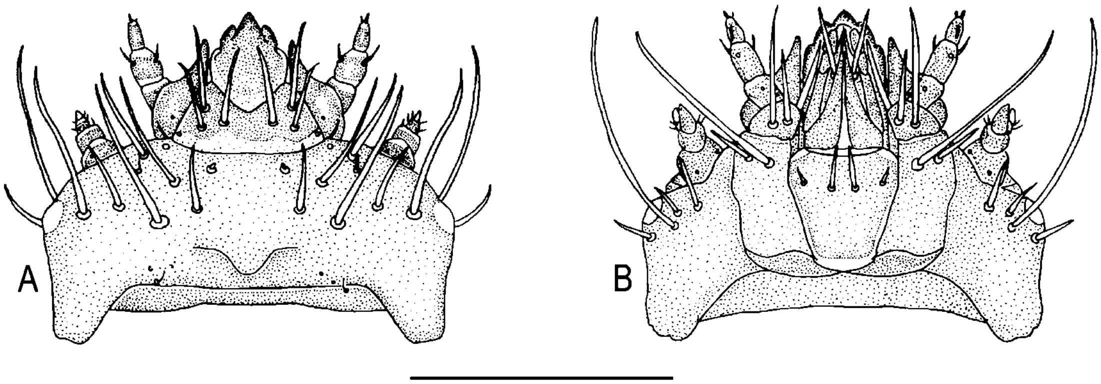

Fig. 4.4.6. *Cerophytum elateroides,* larval head, A, dorsal; B, ventral. Scale line = 1.0 mm. (from Costa *et al.* 2003).

internal prothoracic skeleton and labial plate, which are dark brown; vestiture consisting of fine setae only.

Head (Fig. 4.4.6 A–B) prognathous and protracted or slightly retracted, much narrower than thorax, strongly transverse and flattened above. Posterior edge not emarginate. Frontal arms and dorsal endocarinae absent. One stemma with well developed lens present on each side of head. Frontoclypeal suture vaguely indicated. Labrum fused to head capsule, strongly transverse, deeply emarginate and lightly pigmented. Antennae short, 3-segmented; subconical sensorium on preapical antennomere longer than apical antennomere, which bears a second conical sensorium. Mandibles flattened, symmetrical and non-opposable, more or less parallel to one another and fitting into lateral channels on the labial plate; each mandible with basolateral, rounded expansion, narrow, blade-like, sharply acute apex, and internal channel extending from near base to apex; mola, prostheca and accessory ventral process absent. Ventral mouthparts strongly retracted forming maxillolabial complex; maxillary articulating area absent. Maxillae well separated from one another by labium; cardines not clearly delimited; stipes elongate; galea and lacinia forming slender, blade-like, channelled mala, which is narrowly acute at apex; maxillary palpomeres three, but palpiger enlarged and partly articulated at base, so that palps appear 4-segmented. Prementum and hypopharynx forming 5-dentate sclerome; postmentum subquadrate and strongly convex; labial palps 2-segmented with subacute apical palpomere, closely adpressed to side of sclerome and scarcely visible except in side view. Ventral longitudinal endocarinae present along lateral edges of maxillae and between maxillae and labium. Hypostomal region, hypostomal rods, ventral epicranial ridges and gula absent.

Prothorax almost as long as meso- and metathorax combined. Thoracic terga simple, without sclerotization, asperities, rugosities or carinae. Venter with two pairs of anterior sclerotizations: lateral, subtrapezoidal and slightly curved pleurites, which extend from the neck region to the anterior articulations of procoxae, and oblique, slender, sternal rods, which converge posteriorly and define a subtriangular area, which is lightly sclerotized and has a short endocarina near the posterior end. Legs relatively short. Procoxae large, oval, strongly oblique and moderately heavily pigmented, separated by about 0.25 times the shortest diameter of one of them; protrochanters short and lightly pigmented; femora stout, only slightly longer than wide, subcylindrical; tibiotarsus short and broad, about one-third as long as femur; pretarsus slightly shorter than tibiotarsus, heavily pigmented, deeply emarginate forming a pair of claw-like processes, one slightly shorter than the other; pretarsal setae two, lying side by side. Mesocoxae and metacoxae smaller than procoxae and separated by about 3 times the shortest diameter of one of them; trochanter similar to that on fore leg; femur more slender, about twice as long as wide; tibiotarsus about two-thirds as long as femur and slender; pretarsus slender, claw-like, with two setae.

Abdomen about 3 times as long as thorax. Segments I–VIII each with three clearly defined lateral lobes on each side (laterotergites, pleurites and laterosternites). Terga densely clothed with long hairs but without sclerotizations, carinae or asperities. Paired gland openings present on all thoracic terga and abdominal terga I–VIII. Segment IX about half as long as VIII, tergum dorsal, simple, without urogomphi; X about one third as long as IX, cylindrical and terminal, without pygopods. Thoracic and abdominal spiracles biforous; closing apparatus present. [Mamaev 1978; Lawrence 1991; Lawrence *et al.* 1999 a; Costa *et al.* 2003.]

Phylogeny and Taxonomy. Latreille (1825) placed his genus *Cerophytum* in the group Sternoxi of the Famille Serricornia, along with Buprestidae and most elateroid genera known at the time. In 1834, he proposed a family group based on *Cerophytum*, and this was recognized by Lacordaire (1857) who suggested a relationship with Eucnemidae. Crowson (1955) considered the family to be part of the

Elateroidea (*sensu stricto*), and this has been followed by most workers. The unusual, apparently plesiomorphic nature of the cerophytid propleurocoxal mechanism prompted Hlavac (1975) to remove the group from Elateroidea and place it together with two other elateriform families of doubtful affinities, Artematopodidae and Brachypsectridae. In cladograms produced by Lawrence (1988) Cerophytidae formed a clade with Eucnemidae and Throscidae (*sensu stricto*) or was basal to a clade containing these two families plus Elateridae. A similar association was found in analyses conducted by Calder *et al.* (1993), Beutel (1995), and Lawrence *et al.* (1995). In Muona's (1993) revision of Eucnemidae, Cerophytidae were considered basal to the elateroid complex (Elateroidea *sensu* Crowson 1955) and in a later cladistic analysis (Muona 1995) Cerophytidae and Eucnemidae formed one clade whereas Throscidae (*sensu* Crowson 1955) represented a derived group within Elateridae. The larva of *Cerophytum* is highly unusual and differs from those of all other Elateroidea in having unique mouthparts involving paired sucking grooves, styliform mandibles and maxillae, paired thoracic and abdominal glands and bifurcate pretarsi.

The genus *Anischia* Fleutiaux (1896) was considered by its author to be related to *Cerophytum*, mainly because of the lack of metacoxal plates, and is often placed in Cerophytidae (Schenkling 1928; Crowson 1955). The genus has also been placed in Elateridae (Fleutiaux 1936; Lawrence & Newton 1995) or considered as a separate family (Lawrence *et al.* 1999 b), but a recent cladistic analysis of larval and adult characters combined with DNA sequence data strongly supports its inclusion in Eucnemidae (Lawrence *et al.* 2007). The extinct genus *Aphytocerus* Zherichin (1977) has also been included in this family based on two species in fossil resin (retinite) from the Upper Cretaceous of Siberia. Its inclusion in the family must remain tentative based on the limited information available on the structure of the fossil specimens.

Costa *et al.* (2003) carried out a phylogenetic analysis of the 21 known species in the family, with outgroups from Elateridae, Throscidae and Eucnemidae. Three main clades were recognized: (*Cerophytum* (*Brachycerophytum*, *Phytocerum*)). Synapomorphies for the family include: 1) chin piece ventrally directed; 2) posterior pronotal angles produced laterally; 3) metatrochanters more than half as long as metafemora; 4) base of tergite IX and sternite X fused; 5) parameres divided into proximal sclerotized and distal membranous regions; 6) phallobase Y-shaped; 7) parameres projecting anteriorly, beneath phallobase. Possible larval synapomorphies are: sucking mouthparts formed by styliform mandibles and maxillae enclosed in separate lateral channels; anterior pretarsi bifurcate; and labium forming a five-toothed plate. The Holarctic genus *Cerophytum* is characterized by having the profemur with a longitudinal carina and the dorsal region of the parameres fringed. Synapomorphies for the Neotropical clade include: posterior angles of pronotum reduced; upper distal angle of profemur acute and produced; and lateroposterior margin of phallobase protruding over the bases of parameres. *Brachycerophytum* is distinguished by the ninth elytral stria strongly convex, basal portion of penis strongly constricted and bursa copulatrix without smooth and elongate sclerites. Autapomorphies of *Phytocerum* include the lack of a chin piece, presence of an additional row of punctures between stria 8 and 9, and the absence of a sclerotized spermatheca.

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4.5. Eucnemidae Eschscholtz, 1829

Jyrki Muona

Distribution. Eucnemidae are cosmopolitan in distribution but most abundant and diverse in the tropics. Slightly less than 200 genera and about 1500 species are included in the family. Many monotypic genera, especially in the subfamily Macraulacinae, are based on autapomorphic forms and may turn out to be superfluous. The species-rich world-wide genera *Microrhagus* Dejean, *Fornax* Laporte, and *Dromaeolus* Kiesenwetter appear to be based on plesiomorphic characters. Much of the diversity in tropical regions remains undescribed and the true number of species is likely to exceed 3000. *Anelastes* Kirby, *Melasis* Olivier, *Isoriphis* Boisduval & Lacordaire, *Hylochares* Laporte and

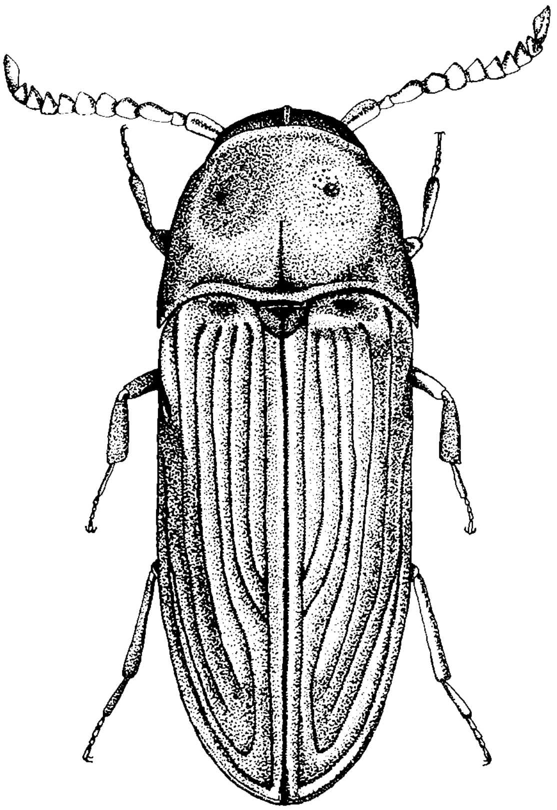

Fig. 4.5.1. *Eucnemis americana* (Horn), adult, dorsal (from Muona 2000; © Finnish Museum of Natural History), length = 6 mm.

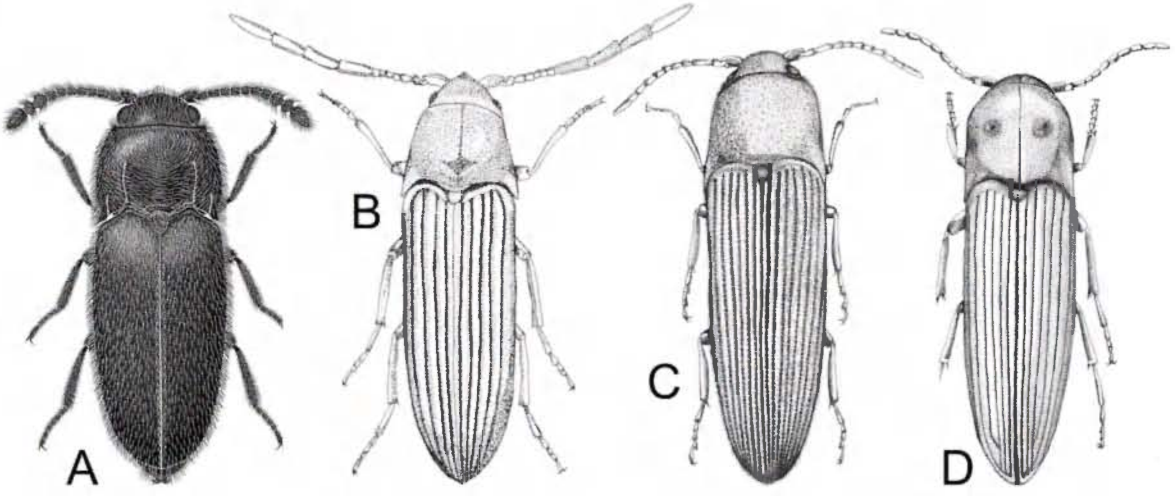

Fig. 4.5.2. Eucnemidae adults, dorsal: A, *Anischia stupenda* Fleutiaux (© CSIRO Australia), length = 3 mm; B, *Epiphanis cornutus* Eschscholtz, length, = 5 mm; C, *Schizophilus subrufus* (Randall), length = 8 mm; D, *Nematodes humphreyi* Muona, length = 10 mm; (B–D from Muona 2000; © Finnish Museum of Natural History).

Hylis de Gozis are typical Holarctic genera. *Perothops* Laporte, *Schizophilus* Bonvouloir, *Onichodon* Newman and *Palaeoxenus* Horn are Nearctic and *Anelastidius* DuVal is restricted to the Palaearctic. *Anischia* Fleutiaux, *Dendrocharis* Guerin-Méneville and *Vitellius* Bonvouloir represent Pantropical elements. Many clades suggest Gondwanan distributions and *Arrhipis* Bonvouloir, *Entomosatopus* Bonvouloir, *Dyscharachthis* Blackburn and *Phaenocerus* Bonvouloir have species on all Southern continents, whereas other putative Gondwanan clades have been split to two or three genera, and do not occur in south temperate regions (e. g., *Poecilochrus* Bonvouloir (Asia) + *Idiotarsus* Bonvouloir (Americas)). The Ethiopian fauna is characterized by many endemic species of *Phyllocerus* Lepeletier & Audinet-Serville. The Indomalayan region is very rich in species. The tribe Galbitini comprises 4 genera and about 50 species. The Australian fauna is phylogenetically diverse and rich with about 90 described species and about 90 undescribed species. Typical predominantly Australian genera include *Hemiopsida* MacLeay, *Dyscharachthis* Blackburn, and *Euryptychus* LeConte. The New Zealand fauna is phylogenetically poor with few species and include the dominant endemic genera *Talerax* Sharp and *Neocharis* Sharp. [Schenkling 1928 a, b; Muona 1991 b, 1993 a, b; Alaruikka & Muona 2007; Muona & Brüstle 2008.]

Biology and Ecology. Adult Eucnemidae are rarely encountered although they can be regionally abundant, especially in the tropics. Most species develop in rotten wood and adults are usually encountered running on trunks and stumps, especially on broken surfaces. Many species are nocturnal and are attracted to light-traps and most are excellent fliers and often caught in Malaise traps. Most species of Eucnemidae click well although not as readily as most Elateridae. However, *Anischia* species and some Melasini do not seem to click at all. Most species have sexually dimorphic antennae with several different types of receptors on the antennomeres and conspicuous excretory pits on the head, prosternum and hypomera (Fig. 4.5.3A). Chemical communication certainly plays an important role in their behavior. The well described swarming of *Melasis buprestoides* (Linnaeus) (Palmqvist 1952) is probably not typical of the family as a whole as observations of the mating in other species differ (*Hylochares, Hylis, Dromaeoloides* Fleutiaux, *Microrhagus*; J. Muona pers. obs.). Adult Eucnemidae are short-lived and it is unclear whether they feed. The few studied forms of *Hylis* and *Xylophilus* Mannerheim may lack a functional gut altogether (Dodelin *et al.* 2005). Most Eucnemidae require forests with a good supply of dead wood and many are listed as endangered in heavily populated regions. Most eucnemid larvae are legless and lignicolous and the great majority do not construct galleries. Instead they move slowly with the help of their wedge-shaped head, internal hydrostatic pressure, and small densely spinose plates on their body. The spinose dorsal and ventral plates of the abdomen are pressed against the wood and at the same time the head is forced forward through the soft wood. Solid particles have not been found in the gut and the larvae appear to obtain all their nutrition by sucking liquid from the moist wood. Presumably this is a form of extra-oral digestion – the larvae vomit digestive juices in the wood in order to break down the fungal hyphae or possibly myxomycete plasmodium. Eucnemidae larvae have roundish smooth plates both dorsally and ventrally on most abdominal segments in addition to the spinose ones. These plates (usually referred to as areoles) function as organs for removing extra liquid from the body. A few basal groups of Eucnemidae (e. g., *Phyllocerus*, *Perothops*) develop in soil. [Lucht 1981; Hammond 1990;

Penny & Arias 1992; Muona 1993 b, 2000; Muona & Brüstle 2008; Muona & Teräväinen 2008.]

Morphology adults (Figs. 4.5.1–3). Length 1.5 mm (*Anischia, Microrhagus*) to 40 mm (*Phlegon*). Body moderately elongate to very elongate, 2–6 times as long as wide, narrowing caudally or parallel-sided; elytra slightly expanded basally and tapered apically; prothorax often curved laterally so that narrowest point is at pronoto-elytral junction (as in most Elateridae); moderately to strongly convex dorsally; ventrally either moderately convex or flat. Color frequently yellowish-brown to black and uniform (*Fornax, Dromaeolus, Microrhagus*), sometimes brightly bicoloured (*Scython* Laporte, *Palaeoxenus, Spinifornax* Fleutiaux), or even metallic (*Nodema* Fleutiaux). Vestiture rarely absent (*Gastraulacus* Guérin-Méneville), often consisting of fine decumbent, posteriorly oriented hairs (e. g., *Fornax, Microrhagus*); setae sometimes bicoloured (*Dromaeolus*) or flat and scale-like forming striking dorsal patterns (Galbitini, *Poecilochrus*).

Head strongly transverse, slightly to strongly declined, deeply inserted into prothorax, not abruptly narrowed posteriorly to form neck. Posterior edge bi-emarginate, forming median tooth, with or without median carina. Fine transverse occipital ridge usually present, often continuing below eyes as weak subgenal ridges. Median endocarina absent. Eyes highly variable, small to large, entire or almost so, flat to protruding, finely facetted. Antennal insertions exposed and usually separated by less than length of antennomere 1 but sometimes much more so (Dendrocharini, Gastraulacini); subantennal grooves variable, from absent to short and shallow to wide and deep with either group of pores or deep pits. Frontoclypeal area gradually declined, with mouthparts anteroventrally or ventrally oriented; frontoclypeal suture absent; anterior edge of clypeus mostly broadly rounded concave or bisinuate, rarely truncate. Labrum attached beneath edge of clypeus, membranous (many species) or partly visible, slightly sclerotized and densely covered with hairs (Melasini), or partly visible, strongly transverse, rounded anteriorly and with distinct median emargination (*Anischia*). Antennae usually 11-segmented (12-segmented in *Phyllocerus* males); variable in length, not extending to base of prothorax (many Melasinae) to longer than body (*Plesiofornax* Coquerel); antennomeres moniliform (many Macraulacini) to strongly flabellate (e. g., *Galbites* Fleutiaux), sometimes gradually expanded apically, incrassate or clavate, or more abruptly expanded to form weak 2- to 5-segmented club (*Anischia, Anelastes*, and many Melasinae); scape always inflated; pedicel often tiny, attached subapically with sharp tooth just laterad of attachment; antennomere 3 usually distinctly elongate; sensory elements either evenly distributed (*Anelastes*) or present only on apical antennomere and at or around apex on others. Mandibles variable, either evenly curved and elongate or short and broad, only slightly longer than wide at base, unidentate or bidentate; mola absent or reduced; if present sub-basal, consisting of group of asperities several of which form a transverse, comb-like structure; distinct hyaline area present at base of mesal edge; prostheca absent. Maxilla usually with unequal lobes; galea articulated; lacinia narrowed apically; terminal maxillary palpomere variable, often slightly widened at middle, narrowed apically and obliquely truncate at apex; frequently more strongly developed in males than in females. Labium with truncate ligula; terminal palpomere similar to that of maxillary palp but not sexually dimorphic. Rarely ventral mouthparts grotesquely developed, divided into dozens of branch-like structures (*Cladus* Bonvouloir, *Hyperpalpus* Lucht). Gular sutures variable, often widely separated. Corpotentorium very narrow, slightly arched; anterior tentorial arms expanded mesally and sometimes fused at midline to form broad anterior bridge (laminatentorium). Cervical sclerites well developed, each divided into two or three parts. Proventriculus variable from weakly developed (*Perothops*) to consisting of setose pads alternating with elongate hyaline processes lined with saw-like teeth.

Pronotum variable, wider than long to more than twice as long as wide, usually widest at about middle; sides parallel to strongly rounded. Lateral carinae absent (*Langurioscthton* Heller), very fine (*Anelastes*), divided (most Dirhagini), or strongly developed and entire (most species), sometimes not visible for their entire lengths from above; anterior angles absent to right. Anterior edge simple or minutely serrate (Dirhagini). Posterior angles acute and mostly produced. Hind edge with well-developed interlocking device, sometimes including pair of deep sublateral cavities for receiving paired processes on anterior edges of elytra (*Anischia*). Disc usually convex or flattened and slightly grooved in front of scutellum; sometimes with large gibbosities (e. g., *Galbites*), rarely with two pairs of longitudinal carinae extending anteriorly from hind edge (*Anischia*). Hypomeron without antennal grooves or cavities in *Phyllocerus, Perothops, Anelastes*, Pseudomeninae and many Melasinae, with deep antennal grooves running along lateral edge in Eucneminae and Macraulacini (rarely wider than rest of hypomeron in some Macraulacini), with variably-shaped antennal grooves running across notosternal suture in Dirhagini (Fig. 4.5.3 A). Posterior surface of hypomeron usually with crural impression (often separated by carina from rest of hypomeron) for reception of profemora. Notosternal suture complete or partly to almost entirely obliterated (some Dirhagini). Prosternum well developed in front of coxae, moderately convex and produced anteriorly to form broad chin-piece; prosternal process variable, short and poorly developed (e. g., *Hemiopsida*) to moderately long and straight or parallel-sided except posteriorly, where sides taper to form subacute apex; about as wide as coxal cavity (many species) to long and knife-like; surface either smooth or with median and/or lateral carinae. Procoxae globular, with very short internal extension. Trochantinopleuron reduced, concealed and fused to wall of hypomeron. Procoxal cavities moderately broadly open; notal projections short and subacute. Well developed scutellar shield either flat or abruptly elevated basally, with straight basal edge and parallel sides or with rounded lateral edges and subacute apex. Elytra 1.2 to 4 times as long as wide, subparallel to tapering posteriorly; anterior edge of each more or less carinate and produced at middle to form carinate lobe fitting into cavity at base of pronotum; fine sutural stria usually present and extending almost to apex; scutellary striole absent; other striae absent to well-developed and deep (*Vitellius* and other taxa), with interstices flat to convex and odd ones sometimes keeled and/or wider than even ones (*Galbites* and other taxa); punctation absent to present and doubled, confused or seriate; epipleura moderately to strongly developed, anteriorly sometimes grooved (some Macraulacini and Eucneminae); usually tapering posteriorly and reaching elytral apex, sometimes with apical portion vertical. Mesoventrite longer than wide to distinctly wider than long; anterior edge at middle with deep notch bordered by a raised lip that is sometimes flanked by a pair of large, shallow, horizontal procoxal rests. Anterior lip contiguous posteriorly with diagonal slide leading into a deep mesoventral cavity extending well beyond the anterior edges of the mesocoxae. Mesocoxae globular, separated by a distance from about half the longest diameter of one (*Perothops*) to slightly more than one diameter. Mesocoxal cavity laterally open (partly closed by mesopleuron and not by meeting of meso- and metaventrites). Mesanepisternum separated from mesepimeron by complete pleural suture (*Perothops*) or solidly joined to mesanepimeron with no trace of pleural suture or pleural ridge. Meso-metaventral junction distinctly sinuate to straight, with metaventral knob fitting into cavity on mesoventrite. Metaventrite higly variable, from strongly transverse to more than twice as long as wide; without discrimen. Postcoxal lines usually absent (*Anischia* with two postcoxal lines arising from posterior edge of each mesocoxal cavity: one beginning at posteromesal edge of cavity and extending posterolaterally and the other beginning just behind mesepimero-metanepisternal junction, extending mesally and then abruptly posteriorly near lateral edge of cavity); sometimes with distinct grooves for reception of tibiae (many Eucneminae) and tarsi (*Gastraulacus* etc.). Visible portion of metanepisternum variable; usually very narrow and more or less parallel-sided, sometimes wide and short or strongly widening caudad; anterior edge distant from mesocoxal cavity. Metacoxae slightly oblique, usually contiguous and extending laterally to meet epipleura (in Anischia well separated, extending laterally almost to epipleura but separated from them by posterior portions of metanepisternum and metepimeron; coxal plates usually well developed and complete but narrowed laterally, sometimes parallel-sided (e. g., *Rhagomicrus* Fleutiaux, *Dendrocharis*), rarely completely absent (*Anischia*). Metendosternite usually with moderately to very long, slender stalk and short lateral arms, each bearing a long tendon; anterior process usually long and narrow, with more or less approximate anterior tendons; sometimes short, broad and bilobed, with moderately widely separated tendons (e. g., *Perothops* and *Phyllocerus*); in *Anischia*, stalk short and broad; anterior process absent and arms long and anteriorly oblique with tendons located near apices. Hind-wing short, about 2 times as long as wide (*Farsus* Jacquelin DuVal, *Temnus* Fleutiaux) or as much as 3 times as long as wide (*Hylotastes* Bonvouloir); apical field well developed, about 0.4 times total wing length (*Anischia*, *Porraulacus* Fleutiaux, *Proxylobius* Fleutiaux, etc.) or reduced, about 0.15 times total wing length; with one to five oblique sclerites, (usually with an anterior, posterior, and median one); radial cell 1.5–5 times as long as wide with posterobasal angle more or less right or rounded; cross-vein r3 usually very slightly oblique and almost longitudinal, sometimes absent; cross-vein r4 arising towards apex of cell, long and slightly sinuate; basal portion of RP variable. Medial field usually with five free veins all reaching wing margin, sometimes with three or four veins not reaching wing margin, without veins in *Porraulacus*; MP_{3+4} with well developed basal cross-vein and usually with CuA_1 joining it before MP_3-MP_4 fork; base of MP_3 incomplete; wedge cell either absent or present and often longer than medial spur, 1.5 to 4 times as long as wide, with apex oblique; CuA_{1+2} arising near apical third of cell and often slightly longer than CuA_1; AA_3 meeting CuP near base of wedge cell or absent; anal notch present or absent. Legs stout to long and slender; hind legs somewhat longer than anterior pairs; trochanter rarely very long, almost half as long as femur in *Anischia*, usually much shorter (especially protrochanter); trochanterofemoral joint oblique; tibiae variable, often relatively slender, only slightly enlarged apically, rarely strongly flattened (*Melasis*) or flattened and with tarsal grooves (Dendrocharini); protibial apex usually with one spur, occasionally with two spurs of equal length (e. g., *Perothops*, *Phyllocerus*, *Anischia*); tarsomeres variable: either simple with 1–4 decreasing in length and 5 usually as long as previous two or three combined (many Dirhagini), or tarsomeres 1–4 densely pubescent and 5 as long as 1–4 (many Eucnemini), or tarsomeres 1–4 with distinct lobes (Galbitini, Dendrocharini); pretarsal claws often simple or basally dentate (many Macraulacini) or serrate (*Perothops*), rarely with basal setae (*Pseudomenes* Fleutiaux); empodium weakly developed but usually not visible beyond apex of tarsomere 5; protarsus often sexually dimorphic: male protarsomere 1 with complete or basal sex-comb (Macraulacini; Fig. 4.5.3 B) or with apical sex-comb (Dirhagini).

Abdomen slightly to very elongate, with five ventrites. Ventrites 1–4 often subequal in length; 5 distinctly longer; all ventrites usually connate; in *Anischia*, ventrites 1–3 connate, 4 and 5 movable, and ventrite 1 with two postcoxal lines on each side of intercoxal process; in *Perothops*, ventrite 1 somewhat longer than 2 with acute intercoxal process, 2–4 slightly decreasing in length, 5 somewhat longer than 4, ventrites 1 and 2 distinctly connate, 3–5 at least slightly movable and posterolateral corners of 2–4 produced and acute. Abdomen rarely with grooves for reception of tarsi (*Gastraulacus*, *Temnus*, *Temnillus* Bonvouloir). Spiracles on segments I to VIII located in pleural membrane. Tergites often membranous but sometimes all tergites well sclerotized (*Dromaeolus*, *Asiocnemis* Mamaev, etc.) or VIII–X lightly sclerotized (*Anischia*). Sternite VIII in male with paired lateral struts. Sternite IX in male with paired lateral struts only (*Anischia*, *Temnillus*, etc.) or with broadly rounded anterior lobe and usually with sclerotized border; tergites IX and X in male clearly separate (*Perothops*, *Phyllocerus*, etc.) or more or less fused together. Sternite and tergite VIII in female variable, often lightly sclerotized; spiculum ventrale absent (*Perothops*, *Phyllocerus*, etc.) or well developed and long, either basally articulated (*Pseudomenes*, *Schizophilus*, *Anischia*) or solidly fused (most taxa). Aedeagus of the trilobate type but quite variable. Several different types may be distinguished: 1) phallobase subquadrate, slightly flattened and dorsally open (sclerotized ventrally), symmetrical, between one-third and two-thirds as long as parameres which are broadly fused dorsally and narrowly so ventrally, ventrally each paramere tapering anteriorly, to form acute, dorsally or laterally curved strut (many Melasinae and Macraulacinae), divided penis with short or long basal struts (many Melasinae, all Macraulacinae); 2) phallobase slightly flattened anteriorly, with paired ventral struts and a dorsal process which is fused to parameres (Perothopinae and Phyllocerini); 3) phallobase divided in two lateral sclerites; parameres and penis strongly dorsoventrally flattened (Anelastini); 4) phallobase reduced, elongated, rod-shaped, resembling letter Y, parameres and penis slender, parameres soft, densely hairy mediad (*Pseudomenes* Bonvouloir); 5) phallobase short, asymmetrical, laterally compressed, about a third the length of parameres which are fused together at basal half to form a tube; apex of parameres narrowly rounded truncate or slightly expanded to form lateral tooth; penis relatively short, with body about half as long as parameres but with paired anterior struts which may extend almost to base of parameral tube; penis attached to parameres at point where parameral tube ends and free parameres begin (*Anischia*); 6) parameres and penis fused together forming a tube, phallobase well developed (Dirhagini), or strongly reduced (Dendrocharini); 7) penis shield-like and parameres apparently very small (most Eucneminae), rarely also phallobase reduced and membranous (*Temnillus* etc.) or penis divided in dorsal and ventral lobes (*Entomosatopus* Bonvouloir). Ovipositor of three major types: 1) short and sclerotized and lacking distinct segments (e.g., *Sarpedon* Bonvouloir); 2) short and sclerotized and divided in two parts with styli absent (*Hylochares*, etc.) or present, 3) ovipositor moderately long and slender (most

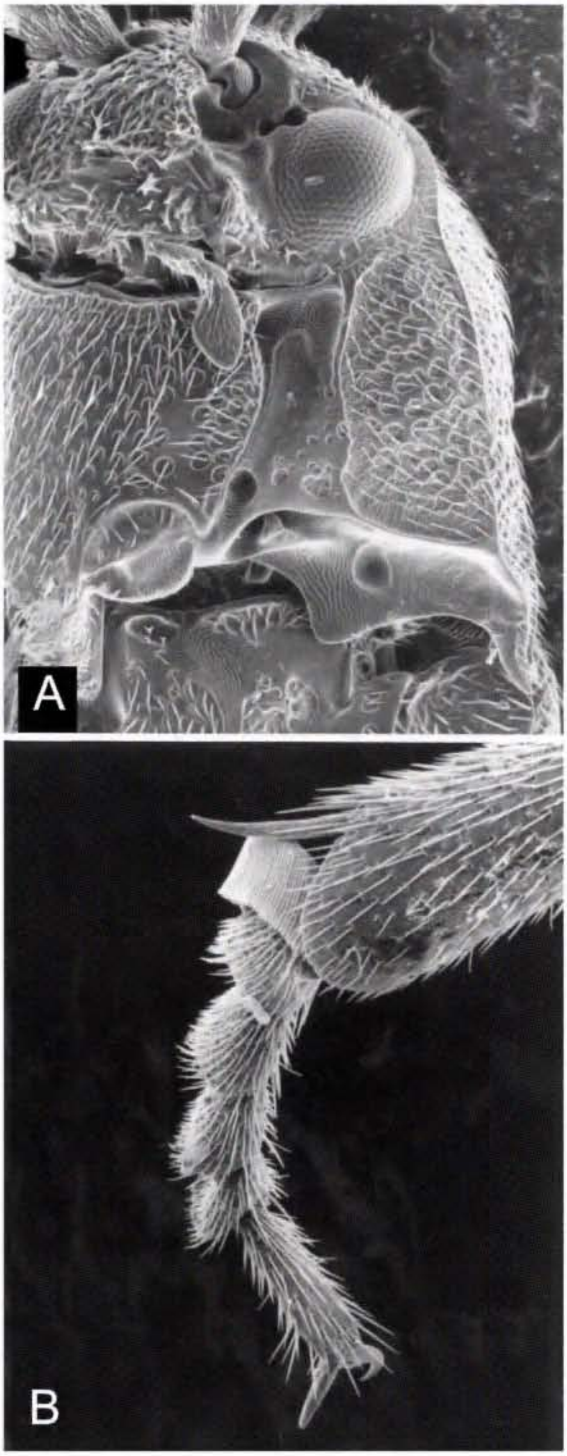

Fig. 4.5.3. Eucnemidae adults: A, *Microrhagus pygmaeus* (Fabricius), ventral view of head and prothorax showing notosternal antennal grooves and excretory pits close to eye and on hypomere; B, *Dicaptothorax koebeli* (Blackburn), male protarsus showing complex sex-comb on base of tarsomere 1.

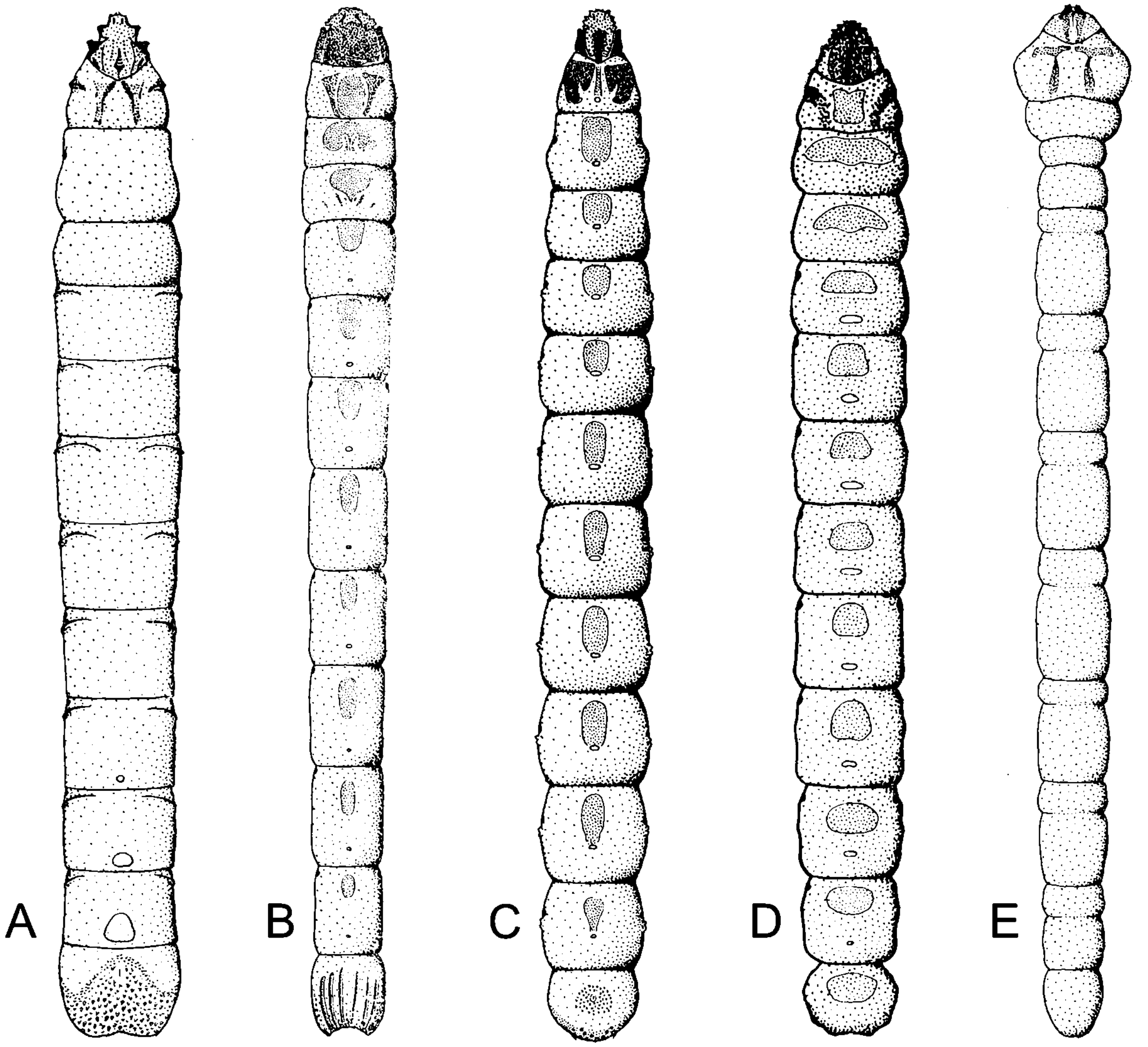

Fig. 4.5.4. Eucnemidae larvae: A, *Asiocnemis morawitzi* Semenov, ventral; B, *Euryptychus lewisi* Fleutiaux, dorsal; C, *Thambus friwaldskyi* Bonvouloir, ventral; D, *Eucnemis zaitzevi* Mamaev, dorsal; E, *Isorhipis melasoides* (Laporte), dorsal. (A–E from Mamaev 1976).

taxa) to longer than body and very slender (e. g., Nematodini, *Hylis*); paraprocts with longitudinal bacula 1.5 to 8 times as long as coxites which are membranous to sclerotized, narrowed apically and either undivided or divided into two parts; styli well developed apically (Perothopinae and Phyllocerinae) or laterally attached and often minute. Female genital tract variable, with three major types: 1) with large bilobed bursa with weakly sclerotized and elongate spermatheca attached by short duct between bases of two bursal lobes, and spermathecal gland attached by long narrow duct to base of spermatheca (Perothopinae, Phyllocerinae, Pseudomeninae, Phelgoninae); 2) bursa undivided with spermatheca well sclerotized and ribbed, undivided or divided into 2–3 parts (Melasinae, Eucneminae, Macraulacinae); 3) genital tract enlarged anteriorly to form an elongate to almost spherical uterus to which the common oviduct and spermathecal duct are separately attached; bursa copulatrix absent; spermatheca elongate and cylindrical, finely transversely ribbed with a basal collar and apical invaginated pocket; spermathecal gland attached basally just beyond the collar. [Burakowski 1991; Lawrence *et al.* 2007; Muona 1991 b, 1993 b.]

Description Larvae (Figs. 4.5.4–6). Body elongate, usually parallel-sided, sometimes widest at metathorax (*Perothops*, Melasini, *Hylochares*); moderately to strongly flattened (most) or subcylindrical (*Perothops*, Melasini, some Dirrhagini), rarely hypermetamorphic, swollen and maggot-like (some Eucnemini). Evenly soft or well sclerotized, rarely with dorsal surfaces more heavily sclerotized than ventral ones (*Anischia*, *Phyllocerus*). Color of head and apex of last tergum often darkened, rest of body white to yellowish, rarely very dark brown. All segments nearly equal in size or abdominal segments transversely subdivided forming pseudosegments (Melasini), or thoracic segments and abdominal segments I–VI more or less inflated at middle and strongly narrowed at either