A Phylogenetic Review of *Charis* and *Calephelis* (Lepidoptera: Riodinidae)

JASON P. W. HALL[1] AND DONALD J. HARVEY

Department of Systematic Biology-Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560–0127

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ABSTRACT A phylogenetic analysis of the Neotropical riodinid butterfly genera *Charis* Hübner and *Calephelis* Grote & Robinson is presented. Cladistic analyses using 31 characters of male and female genitalia and external facies generated cladograms indicating that *Charis* is paraphyletic with respect to *Calephelis.* The analyses highlight the existence of four major clades, the *ocellata* Hewitson, *cleonus* Stoll, *anius* Cramer, and *virginiensis* Guérin-Méneville groups, which we treat as genera. The generic names *Charis* and *Calephelis* are applicable to the last two groups, but new genera are described for the first two: *Seco* n. gen. for the *ocellata* group and *Detritivora* n. gen. for the *cleonus* group. Each genus is diagnosed and provided with illustrations of representative adults and male and female genitalia, a synonymic checklist and list of all known foodplants. The following taxa are misplaced in the analyzed clade: *aerigera* Stichel and *xanthosa* Stichel are transferred from *Charis* to *Emesis* F. (n. combs.), and *myrtis* H. Druce is transferred from *Charis* to *Exoplisia* Godman & Salvin (n. combs.). *Charis irina* Stichel is synonymized with *Charis iris* Staudinger (n. syn.) and *Charis cadytis acroxantha* Stichel is synonymized with nominate *C. cadytis* Hewitson (n. syn.). The taxon *candiope* H. Druce is transferred from *Charis* to *Calephelis* for the first time (n. comb.) and *iris* and *velutina* Godman and Salvin are returned to *Calephelis* from *Charis* (rev. combs.).

KEY WORDS *Calephelis*, *Charis*, cladistics, foodplants, Neotropics

THE NEOTROPICAL RIODINID genus *Charis* Hübner, [1819] has long been overlooked in systematic studies of the family, probably because of the small size, often relatively drab coloration and apparent abundance of most species. *Charis* has never been unambiguously defined and has often been confounded with *Calephelis* Grote & Robinson, 1869, and *Chalodeta* Stichel 1910 (d'Abrera 1994). Recent revisions of large monophyletic groups within *Charis* (Hall and Harvey 2001, Harvey and Hall 2002) have fully elucidated the previously grossly underestimated species diversity of the genus and highlighted the evolutionary importance of these insects in furthering our knowledge of Neotropical biogeography, particularly that of Amazonia (Hall and Harvey 2001, 2002).

During the course of revisionary work, the external and internal heterogeneity of *Charis* became fully apparent and suspicions arose concerning its monophyly with respect to *Calephelis*, a large genus of externally similar-looking butterflies, many of which occur throughout the United States. The purpose of this study was to test the monophyly of *Charis* through a set of comprehensive species-level cladistic analyses and clearly define the monophyletic subunits generated.

[1] E-mail: jpwhall@hotmail.com.

Materials and Methods

Museum Acronyms. Specimens were studied from the following collections, whose acronyms are used throughout the text: (AME) Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, USA; (BMNH) The Natural History Museum, London, England; (CMNH) Carnegie Museum of Natural History, Pittsburgh, PA, USA; (CJC) Collection of C. Callaghan, Bogotá, Colombia; (JHKW) Collection of J. Hall and K. Willmott, Washington, DC, USA; (MC) Collection of Matthew Cock, Ascot, UK; (USNM) National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; (ZMHU) Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany; (ZSM) Zoologische Staatssammlung, Munich, Germany.

Taxa Studied. The monophyly of the rather homogeneous *Calephelis*, which has been defined by its members possessing bare instead of hairy eyes, a yellow brown ventral surface and two jagged submarginal silver lines on both wing surfaces (McAlpine 1971, Austin 1997), has never been in doubt. Therefore, we included only two species of *Calephelis* in the phylogenetic analyses to represent the genus, including the type species, *virginiensis* Guérin-Méneville, [1832]. To test the monophyly of *Charis*, all species apparently

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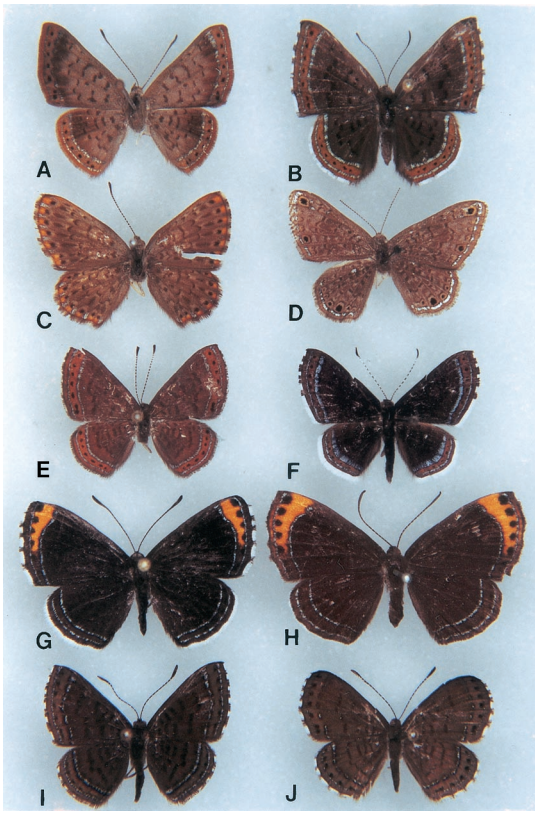

Fig. 1.

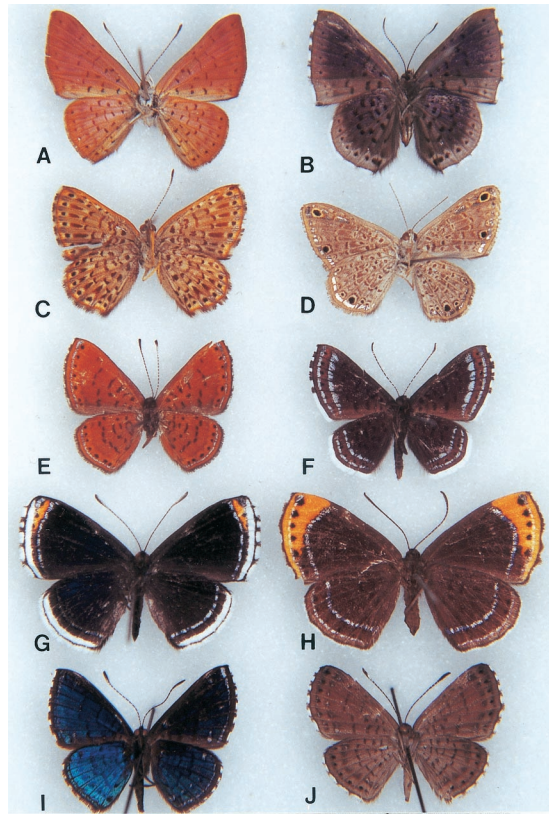

Fig. 2.

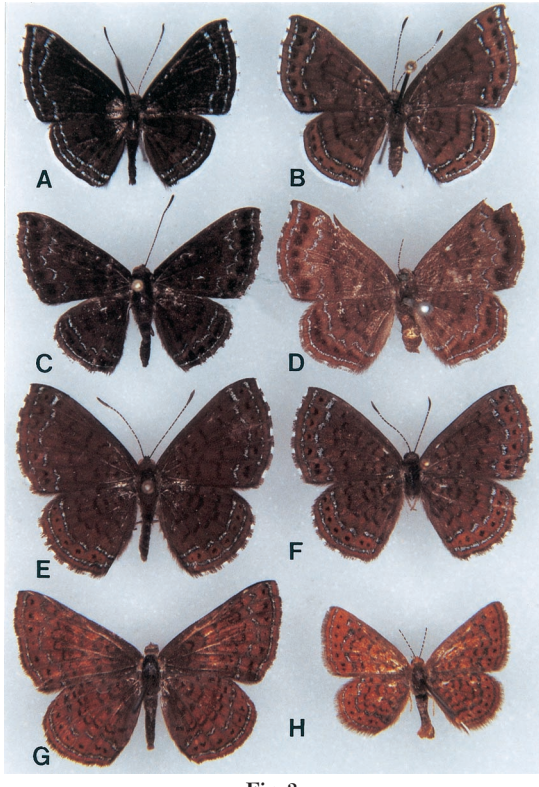

Fig. 3.

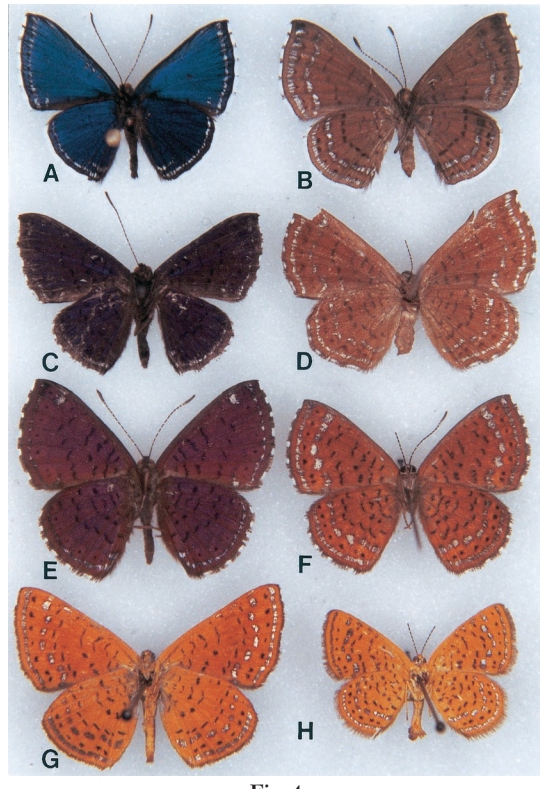

Fig. 4.

Fig. 1. Dorsal surface of adults. Males unless otherwise stated. (A) *Dachetola azora*, João Pessoa, Paraíba, Brazil; (B) *Chalodeta chitinosa*, Pakitza, Madre de Dios, Peru; (C) *Seco aphanis*, Iguaçu, Misiones, Argentina; (D) *Seco ocellata*, Puerto Colombia, Atlantico, Colombia; (E) *Detritivora gynaea*, Linhares, Espírito Santo, Brazil; (F) *Detritivora cleonus*, Mana River, Saint Laurent du Maroni, French Guiana; (G) *Charis cadytis*, Itamonte, Minas Gerais, Brazil; (H) *Charis cadytis*, female, Castro, Parana, Brazil; (I) *Charis anius*, Río Negro, Meta, Colombia; (J) *Charis anius*, female, Salto Napac, Pichincha, Ecuador.

Fig. 2. Ventral surface of same adults in Fig. 1.

Fig. 3. Dorsal surface of adults. (A) *Calephelis iris*, male, San Vito, Puntarenas, Costa Rica; (B) *Calephelis iris*, female, Alluriquín, Pichincha, Ecuador; (C) *Calephelis velutina*, male, Jacatepec, Oaxaca, Mexico; (D) *Calephelis velutina*, female, Coatepec, Veracruz, Mexico; (E) *Calephelis candiope*, male, Victoria, Caldas, Colombia; (F) *Calephelis candiope*, female, Victoria, Caldas, Colombia; (G) *Calephelis laverna*, male, Macará, Loja, Ecuador; (H) *Calephelis virginiensis*, male, Vicksburg, MS, USA.

Fig. 4. Ventral surface of same adults in Fig. 3.

belonging to that genus needed to be represented in the analyses. Since phylogenetic hypotheses had already been proposed for the monophyletic *Charis gynaea* (Hall and Harvey 2001) and *cleonus* groups (Harvey and Hall 2002), only two species from each of these clades were included in the analyses. Having examined the external facies and genital morphology of all species listed by Callaghan and Lamas (2001) as belonging to *Charis*, it became apparent that three species, *aerigera* Stichel, 1910, *xanthosa* Stichel, 1910, and *myrtis* H. Druce, 1904, were unrelated to the remainder and that one species, *irina* Stichel, 1928, was a synonym (see below). The remaining nine *Charis* species (*sensu* Callaghan and Lamas 2001) were all included in the analyses. A representative sample of adult phenotypes used in the analyses is illustrated in Figs. 1–4.

The widespread but very rare *aerigera* superficially resembles *Charis* species because of its small size and double row of dorsal submarginal silverish lines. However, the male genitalia lack a deep notch in the anterior portion of the tegumen, thus placing it outside the tribe Riodinini (*sensu* Harvey 1987). Because of similarities in the external facies, particularly the extensive metallic markings, and male genitalia, we place *aerigera* in the *cereus* group of *Emesis* F., 1807 (*incertae sedis* section, four forewing radial veins (FRV), of Harvey 1987) (n. comb.). The male genitalia of the equally rare *xanthosa*, described from females only without a type locality, also lack the synapomorphy for the Riodinini and those for all other tribes, but do not closely match the genitalia of any genus currently placed in the *incertae sedis* section (4 FRV). Based on great similarities in the male genitalia, "*Charis*" *xanthosa* appears to be most closely related to "*Audre*" *guttata* (Stichel 1910), and the two species probably together require a new genus. In the interim, we transfer *xanthosa* to *Emesis*, whose species it most closely resembles externally (n. comb.). The southern Andean *myrtis* is very similar externally and in its genital morphology to the Amazonian *Exoplisia cadmeis* (Hewitson, 1866), its probable sister species. Since the morphology of *cadmeis* typifies *Exoplisia* Godman and Salvin, 1886, we transfer *myrtis* to that genus (n. comb.).

The taxon *irina* was described by Stichel (1928) as a full species from a single Costa Rican male that was subsequently destroyed while on loan to W. McAlpine. Examination of the morphology slide in the ZMHU prepared by McAlpine from the holotype revealed genitalia indistinguishable from those of *Charis iris*. Since the original description of *irina* also does not differ significantly from that species, we synonymize *irina* with *iris* (n. syn.). The only other synonymy made here is that of *acroxantha* Stichel, 1910, with nominate *Charis cadytis* Hewitson, 1866 (n. syn.). *Charis acroxantha*, described from the southeastern Brazilian states of Rio de Janeiro and São Paulo, does not differ significantly from the nominate, described from Rio Grande do Sul, and discrete subspecies are not discernible.

Morphology. Dissections were made by means of standard techniques, after abdomens were soaked in hot 10% potassium hydroxide (KOH) solution for approximately five minutes, and subsequently stored in glycerol. Locality data for dissected specimens of *gynaea* and *cleonus* group species are given by Hall and Harvey (2001) and Harvey and Hall (2002), respectively, and data for the remaining specimens used in the phylogenetic analyses are given in Table 1. Light microscopy examination was done with an Olympus SZH. Scanning electron microscopy was conducted using a Leica Stereoscan 440 with material mounted on aluminum stubs using carbon tape and sputter coated with gold/palladium. Morphological terms for genitalia follow Klots (1956) and Eliot (1973), and the terminology for wing venation follows Comstock and Needham (1918).

Characters. A total of 31 characters was identified from the eyes (two), wing shape and pattern (18), abdomen (one), male genitalia (eight) and female genitalia (two) (Figs. 5–8). Phylogenetically uninformative autapomorphies were excluded. The character matrix is presented in Table 2.

Head. 1. *Eyes:* bare (0) (Fig. 5A); hairy (1) (e.g., Fig. 5C). CI = 0.5, RI = 0.67.

The presence of bare eyes was used by McAlpine (1971) and Austin (1997) to define *Calephelis* exclusive of *Charis*. Hairy eyes are uncommon in the Riodinini.

2. *If eyes hairy (1:1), hairs:* short [2.87–5.39 U] (1) (Fig. 5B); long [6.09–7.91 U] (2) (Fig. 5C). CI = 0.5, RI = 0.75.

Numbers were calculated by dividing hair length in ocular units by forewing length in cm.

Wing Shape. 3. *Forewing apex:* round (0) (e.g., Fig. 1G); falcate (1) (e.g., Fig. 3C). CI = 0.33, RI = 0.33.

Dorsal Wing Pattern. 4. *Ground color of male:* brown or black (0) (e.g., Fig. 1G); orange-brown (1) (e.g., Fig. 3G); dark iridescent blue (2) (Fig. 1F). CI = 1, RI = 1.

Table 1. All dissections examined for phylogenetic analyses except for *gynaea* and *cleonus* group species (see Hall and Harvey 2001, Harvey and Hall 2001)

Taxon	Dissections examined
azora Godart, [1824] (outgroup)	1 ♂, Brazil, Paraíba, João Pessoa (USNM); 1 ♂, Brazil, Minas Gerais, Paracatu (USNM); 1 ♀, Brazil, Minas Gerais, Itamonte (USNM); 1 ♂, Brazil, Rio de Janeiro, Teresópolis (USNM)
chitinosa Hall, 2002 (outgroup)	1 ♂, Ecuador, Sucumbíos, Limoncocha (JHKW); 1 ♂, Peru, Huánuco, Tingo Maria (USNM); 1 ♂, 1 ♀, Peru, Madre de Dios, Pakitza (USNM); 1 ♂, "Peru" [=Bolivia] (USNM); 1 ♂, Brazil, Rondônia, Cacaulândia (USNM)
aphanis Stichel, 1910	1 ♂, Argentina, Entre Ríos, La Soledad (BMNH); 1 ♂, Argentina, Misiones, Iguaçu (BMNH)
ocellata Hewitson, 1867	1 ♂, Colombia, Atlantico, Puerto Colombia (CMNH)
calagutis Hewitson, 1871	2 ♂, Ecuador, Loja, Macará (JHKW); 1 ♀, Ecuador, Pichincha, Salto Napac (USNM)
argyrea Bates, 1868	2 ♂, Ecuador, Napo, Pimpilala (JHKW); 1 ♂, Peru, San Martín, Juanjui (CJC); 1 ♂, Peru, Madre de Dios, Pakitza (USNM); 1 ♂, Brazil, Pará, Belém, (ZMHU); 1 ♀, Brazil, Rondônia, vicinity of Cacaulândia (USNM); 1 ♀, Trinidad (MC)
cadytis Hewitson, 1866	1 ♂, Brazil, Minas Gerais, Barbarena (USNM); 1 ♀, Brazil, Minas Gerais, Itamonte (USNM); 1 ♀, Brazil, Espírito Santo, Loureiro (USNM); 1 ♂, Brazil, Paraná, Morretes (USNM)
anius Cramer, 1776	1 ♂, Nicaragua, Zelaya, Nueva Guinea (AME); 1 ♂, Costa Rica, Cartago, Juan Viñas (USNM); 1 ♀, Costa Rica, Heredia, Finca La Selva (UNSM); 1 ♂, Panama, Chiriquí, Chirquicto (USNM); 1 ♂, Panama, Panamá, Cerro Campana (USNM); 1 ♂, Panama, Canal Zone, Cocolí (USNM); 1 ♂, Venezuela, Mérida, Santa Clara (AME); 1 ♂, Venezuela, Amazonas, Yavita (AME); 1 ♂, 1 ♀, Colombia, Valle de Cauca, Río Anchicayá (AME); 1 ♂, Colombia, Tolima, Río Chili (AME); 1 ♀, Colombia, Tolima, Payande (AME); 1 ♂, Colombia, Meta, Río Negro (USNM); 1 ♂, Ecuador, Carchi, Río Baboso (JHKW); 1 ♂, Ecuador, Los Ríos, Río Palenque (USNM); 1 ♂, Ecuador, Sucumbíos, Lumbaquí (USNM); 1 ♂, Ecuador, Sucumbíos, Limoncocha (USNM); 1 ♂, Ecuador, Napo, Tena (USNM); 1 ♂, Ecuador, Pastaza, Shell (JHKW); 1 ♂, Ecuador, Zamora-Chinchipe, Bombuscara (JHKW) 1 ♂, Brazil, Amazonas, Tefé (AME); 1 ♂, Brazil, Pará, Taperinha (AME); 1 ♂, French Guiana, Cayenne, Matoury (USNM); 1 ♂, Trinidad, Saint Anne's (AME)
iris Staudinger, 1876	1 ♂, "Costa Rica" (ZMHU); 1 ♂, Costa Rica, Alajuela, Bijagua (USNM); 1 ♂, Costa Rica, Puntarenas, Palmar Norte (AME); 1 ♂, Panama, Panamá, Cerro Campana (USNM); 1 ♂, 1 ♀, Ecuador, Pichincha, Alluriquín (USNM): 1 ♂, Ecuador, Bolívar, Balzapamba (ZSM)
velutina Godman & Salvin, 1878	1 ♂, Mexico, Veracruz, Motzorongo (USNM); 1 ♂, Mexico, Veracruz, Santa Rosa (USNM); 1 ♂, Mexico, Veracruz, Presidio (AME); 1 ♀, Belize, Cayo, Camp Sibun (USNM); 1 ♂, Honduras, Cortés, San Pedro Sula (USNM); 1 ♂, 1 ♀, Honduras, Panamá, El Zapotal (USNM)
candiope H. Druce, 1904	3 ♂, 1 ♀, Colombia, Caldas, Victoria (USNM)
laverna Godman & Salvin, 1886	1 ♂, 1 ♀, Ecuador, Loja, Macará (JHKW)
virginiensis Guérin-Méneville, [1832]	1 ♂, USA, Texas, Houston (USNM); 1 ♂, 1 ♀, USA, Alabama, Daphene (AME) 1 ♀, USA, Mississippi, Clinton (USNM)

5. *Inner silver submarginal line:* present (0) (e.g., Fig. 1G); reduced to faint apical fleck or absent (1) (e.g., Fig. 1D). CI = 1, RI = 1.

6. *If number of silver submarginal lines two (5:0), inner line:* straight (0) (e.g., Fig. 1F); jagged (1) (e.g., Fig. 3E). CI = 1, RI = 1.

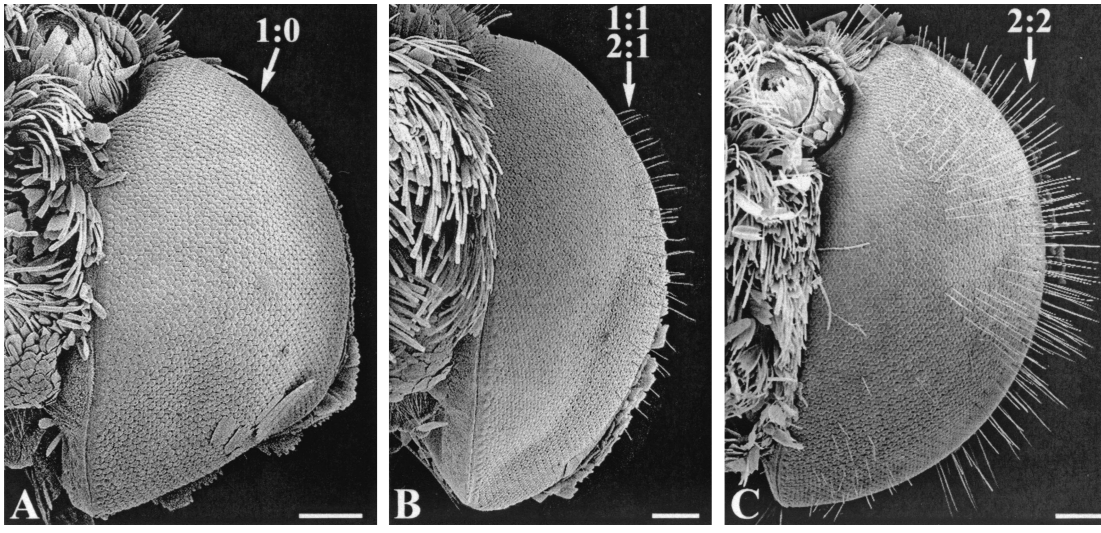

Fig. 5. Scanning Electron Micrographs of left male eye. Character numbers and states refer to the character list in *Materials and Methods.* Scale bars = 100 μm. (A) *Calephelis virginiensis;* (B) *Charis cadytis;* (C) *Detritivora matic.*

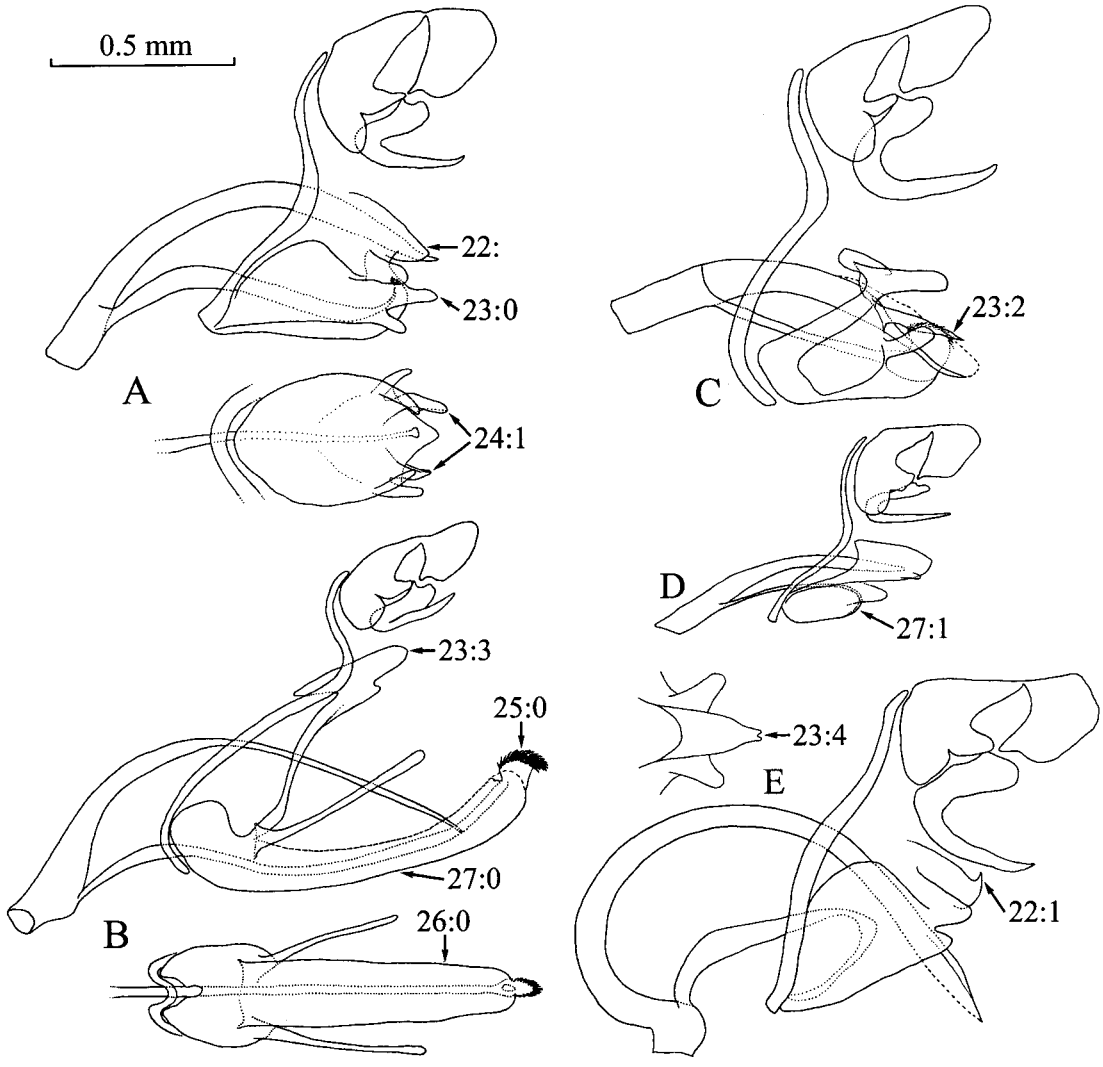

Fig. 6. Male genitalia of *Seco*, *Detritivora*, and *Charis* in lateral view unless otherwise stated. Character numbers and states refer to the character list in *Materials and Methods.* (A) *Seco calagutis*, Macará, Loja, Ecuador, also pedicel and valve complex in ventral view; (B) *Detritivora matic*, Puerto Napo, Napo, Ecuador, also pedicel and lower valve processes in ventral view; (C) *Detritivora nicolayi*, Potrerillos, Chiriquí, Panama; (D) *Charis anius*, Yavita, Amazonas, Venezuela; (E) *Charis cadytis*, Barbacena, Minas Gerais, Brazil, also transtilla tip in ventral view.

In all species with a straight inner silver line except *cadytis*, it also parallels the outer line.

7. *If number of silver submarginal lines two* (5:0), *area between lines on hindwing:* orange-brown (0) (e.g., Fig. 1E); brown (1) (e.g., Fig. 1I). CI = 0.5, RI = 0.67.

8. *If number of silver submarginal lines two (5:0), submarginal black spots:* approximately equidistant between silver lines (0) (e.g., Fig. 1E); immediately proximal to outer silver line (1) (e.g., Fig. 1I). CI = 0.5, RI = 0.5.

9. *Forewing fringe:* brown with variable numbers of spaced white elements (0) (e.g., Fig. 1I); entirely brown (1) (e.g., Fig. 3C); half white (in anal region) and half brown (2) (Fig. 1F). CI = 1, RI = 1.

10. *Hindwing fringe:* brown with variable numbers of spaced white elements (0) (e.g., Fig. 1I); entirely white (1) (Fig. 1F); entirely brown (2) (e.g., Fig. 3G). CI = 0.33, RI = 0.5.

Ventral Wing Pattern. 11. *Ground color of male:* blue or purple (0) (e.g., Fig. 4A); brown (1) (e.g., Fig. 2D); orange-brown (2) (e.g., Fig. 4G). CI = 0.5, RI = 0.67.

12. *Ground color of female:* brown (0) (e.g., Fig. 2J); orange-brown (1) (e.g., Fig. 4F). CI = 0.33, RI = 0.6.

13. *Ground color:* approximately uniform shade (0) (e.g., Fig. 4E); mixture of lighter and darker shades (1) (e.g., Fig. 2D). CI = 1, RI = 1.

14. Outer forewing silver submarginal line in male: absent (0) (e.g., Fig. 2B); present (1) (e.g., Fig. 2F). CI = 0.5, RI = 0.

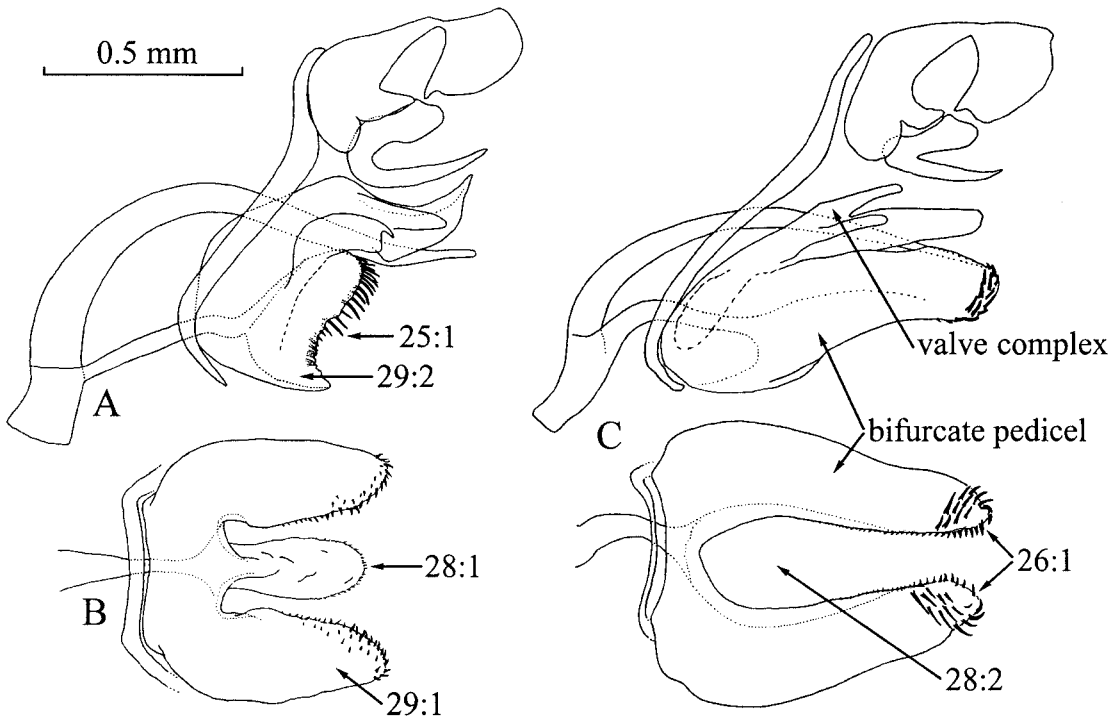

Fig. 7. Male genitalia of *Calephelis* in lateral view unless otherwise stated. Character numbers and states refer to the character list in *Materials and Methods.* A, *Calephelis candiope*, Victoria, Caldas, Colombia; B, *Calephelis iris*, Bijuaga, Alajuela, Costa Rica, only ventral view of pedicel; C, *Calephelis virginiensis*, Houston, TX, USA, also pedicel in ventral view.

15. *Inner forewing silver submarginal line in male:* absent (0) (e.g., Fig. 2E); restricted to elongate apical fleck (1) (Fig. 2D); restricted to small flecks in apex and/or tornus (2) (e.g., Fig. 2I); present and continuous (3) (e.g., Fig. 2F); present and broken (4) (e.g., Fig. 4G). CI = 0.8, RI = 0.88.

16. *Inner forewing silver submarginal line in female:* absent (0); restricted to elongate apical fleck (1); present and continuous (2) (Fig. 2H); present and broken (3) (e.g., Fig. 4F). CI = 0.75, RI = 0.83.

17. *Individual postdiscal spots:* straight (0) (e.g., Fig. 2E); outwardly curved (1) (e.g., Fig. 2D). CI = 0.5, RI = 0.67.

18. *Postdiscal spot in forewing cell Cu1:* proximal to spot in cell Cu2 (0) (e.g., Fig. 2B); distal to spot in cell Cu2 (1) (e.g., Fig. 4G). CI = 0.5, RI = 0.5.

The taxon *cadytis* is coded with a "?" as no black forewing markings are visible.

19. *Silver spot in forewing cell R3:* absent (0) (e.g., Fig. 2E); present (1) (e.g., Fig. 4G). CI = 0.5, RI = 0.5.

Because this silver marking is an extension of the inner postdiscal line, all taxa lacking this line (15:0) are coded with a "?."

20. *Black spots in each of forewing cells R4+5 to R2:* present (0) (e.g., Fig. 4G); absent (1) (e.g., Fig. 2E). CI = 1, RI = 1.

The taxon *cadytis* is coded with a "?" as no black forewing markings are visible.

Male Abdomen. 21. *Ventral color:* brown (0) (e.g., Fig. 2G); orange-brown (1) (e.g., Fig. 4G). CI = 1, RI = 1.

Male Genitalia. 22. *Transtilla:* straight (0) (e.g., Fig. 6A); up-turned at tip (1) (e.g., Fig. 6E). CI = 0.5, RI = 0.67.

23. *Transtilla tip:* modified into two long posteriorly and upwardly curved projections (0) (Fig. 6A); modified into two elongate downwardly pointing projections (1) (see illustrations in Hall 2001, for *Dachetola*); modified into two short straight and pointed posterior projections (2) (Fig. 6C); an unmodified "hood" (3) (e.g., Fig. 6B); bifurcate (4) (Fig. 6E). CI = 0.75, RI = 0.83.

24. *If transtilla tip modified into two long posteriorly and upwardly curved projections (23:0), projections:* approximately symmetrical (0); asymmetrical (1) (Fig. 6A). CI = 1, RI = 1.

25. *Large, well sclerotized acanthae on pedicel:* restricted to tip (0) (e.g., Fig. 6B); not restricted to tip (1) (e.g., Fig. 7A). CI = 1, RI = 1.

The taxa *azora*, *cadytis*, and *anius* are coded with a "?" as their pedicels possess no acanthae. A separate absent state is not coded for these three taxa as the presence of acanthae is not independent from the possession of a posteriorly elongate pedicel, a character already coded in character 27.

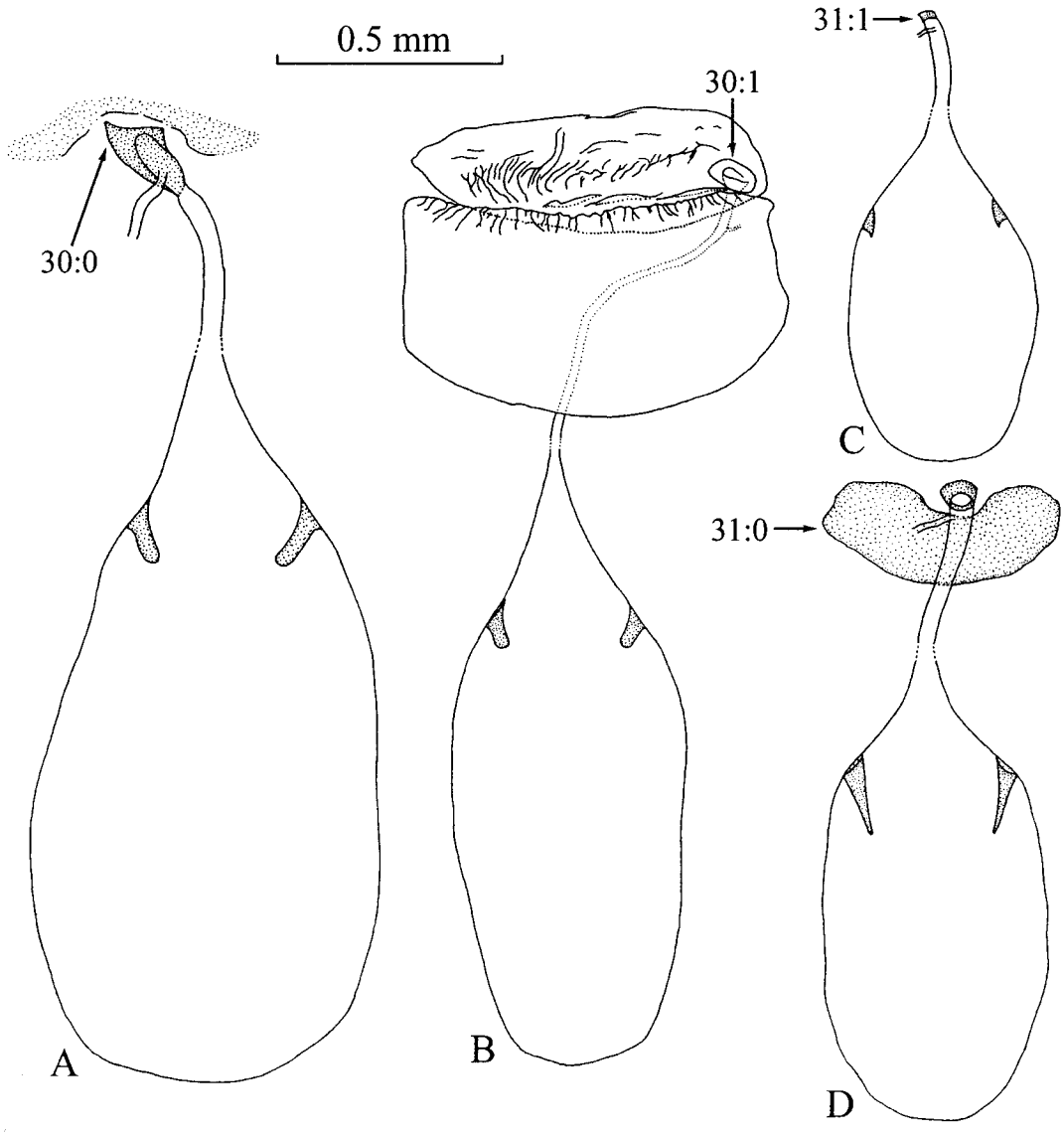

Fig. 8. Female genitalia in dorsal view. Character numbers and states refer to the character list in *Materials and Methods.* (A) *Seco calagutis;* (B) *Detritivora matic;* (C) *Charis anius;* D, *Calephelis virginiensis.*

26. *Pedicel:* not bifurcate (0) (e.g., Fig. 6B); bifurcate (1) (e.g., Fig. 7C). CI = 1, RI = 1.

McAlpine (1971) and Austin (1997) treated the posteriorly elongate spiny male genital processes of *Calephelis* as valvae. However, these processes actually form part of a highly modified bifurcate pedicel, and the considerably smaller components of the valve complex are positioned dorsally and anteriorly.

27. *Pedicel:* modified into a posteriorly elongate structure (0) (e.g., Fig. 6B); simple and strap-like (1) (e.g., Fig. 6D). CI = 1, RI = 1.

28. *If pedicel bifurcate (26:1), a posteriorly elongate central portion:* present (1) (Fig. 7B); absent (2) (Fig. 7C). CI = 1, RI = 1.

29. *If pedicel bifurcate (26:1), projections:* posteriorly elongate and tubular (1) (e.g., Fig. 7B); short and "blade"-like (2) (Fig. 7A). CI = 1, RI = 1.

Female Genitalia. 30. *Ostium bursae:* approximately central (0) (e.g., Fig. 8A); asymmetrically displaced to left or right (1) (Fig. 8B). CI = 1, RI = 1.

Within state (1) only *argyrea* possesses a left displacement of the ostium.

31. *Sclerotization on eighth abdominal sternite:* present (0) (e.g., Fig. 8D); absent (1) (Fig. 8C). CI = 1, RI = 1.

Phylogenetic Analyses. The phylogenetic analyses presented here are based on 31 morphological characters for fifteen *Charis* and *Calephelis* species. Each

Table 2. Character matrix for phylogenetic analysis

					5				10				15				20				25				30			
Dachetola azora	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	?	0	0	0	1	?	?	0	1	0	0	0	0
Chalodeta chitinosa	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Seco aphanis	1	1	0	0	1	?	?	?	0	0	1	0	1	1	0	0	1	0	?	0	0	0	0	1	0	0	0	0	0	?	?
Seco calagutis	0	0	0	0	1	?	?	?	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Seco ocellata	0	0	0	0	1	?	?	?	0	0	1	0	1	1	1	?	1	0	0	0	0	0	0	1	0	0	0	0	0	?	?
Detritivora nicolayi	1	2	0	0	0	0	0	0	0	2	2	1	0	0	0	0	0	1	?	1	0	0	2	?	0	0	0	0	0	1	0
Detritivora gynaea	1	2	0	0	0	0	0	0	0	2	2	1	0	1	0	0	0	1	?	1	0	0	3	?	0	0	0	0	0	1	0
Detritivora argyrea	1	2	1	0	0	0	0	0	0	2	1	0	0	1	3	2	0	1	0	1	0	0	3	?	0	0	0	0	0	1	0
Detritivora matic	1	2	1	2	0	0	0	0	2	1	0	0	0	1	3	2	0	1	0	1	0	0	3	?	0	0	0	0	0	1	0
Detritivora cleonus	1	2	0	2	0	0	0	0	2	1	0	0	0	1	3	2	0	1	0	1	0	0	3	?	0	0	0	0	0	1	0
Charis cadytis	1	1	0	0	0	0	1	1	0	1	0	0	0	1	3	2	0	?	0	?	0	1	4	?	?	0	1	0	0	0	1
Charis anius	1	1	0	0	0	0	1	1	0	0	0	0	0	1	2	3	0	1	0	0	0	0	3	?	?	0	1	0	0	0	1
Calephelis iris	1	1	1	0	0	1	1	1	0	1	0	0	0	1	2	3	0	1	0	0	0	1	4	?	1	1	0	1	1	0	0
Calephelis velutina	1	1	1	0	0	1	1	0	0	0	0	1	0	1	2	3	0	1	0	0	0	1	4	?	1		0	1	1	0	0
Calephelis candiope	1	1	0	0	0	1	0	0	0	0	0	1	0	1	2	3	1	1	1	0	0	1	4	?	1	1	0	2	2	0	0
Calephelis laverna	0	0	0	1	0	1	0	0	1	2	2	1	0	1	4	3	0	1	1	0	1	0	3	?	1	1	0	2	1	0	0
Calephelis virginiensis	0	0	0	1	0	1	0	0	1	2	2	1	0	1	4	3	0	1	1	0	1	0	3	?	1	1	0	2	1	0	0

initial analysis was performed using a heuristic search with 1,000 random addition sequence TBR replicates in PAUP 4.0b4a (Swofford 2000), with all characters equally weighted and unordered. If more than a single most parsimonious cladogram (MPC) was generated, *a posteriori* reweighting was implemented in the form of successive approximations character weighting (SACW) (Farris 1969), using the rescaled consistency index of each character. Analyses were conducted with both of the following outgroups together and with each individually: *Chalodeta chitinosa* Hall (2002) and *Dachetola azora* (Godart, [1824]). The sister taxon to the ingroup is currently unknown, but these genera were used as outgroup taxa because they were hypothesized to be closely related to the ingroup. Analyses were also conducted using characters 26 and 27 as distinct binary characters (as presented in the character list and matrix) and as a single multistate character with the same outgroup combinations as above. The strength of branch support was estimated by means of 1000 bootstrap replicates in PAUP (Felsenstein 1985), and by calculating decay indices (Bremer 1988, 1994) with the program AUTODECAY 4.0 (Eriksson 1998) in combination with PAUP. Character distributions were studied using MacClade 3.05 (Maddison and Maddison 1995) and mapped onto the cladogram in Fig. 9B. Instances of ambiguous character optimization were resolved by adopting the most plausible evolutionary scenario.

Results and Discussion

Phylogenetic Analyses. With *chitinosa* only as an outgroup, the unweighted heuristic search generated a single MPC (length 68, CI = 0.66, RI = 0.78) indicating the relationships of the ingroup to be *ocellata* group + (*cleonus* group + (*anius* group + *virginiensis* group)). With *azora* only as an outgroup, the unweighted heuristic search generated four MPCs (length 73, CI = 0.62, RI = 0.74), which varied in the relative placement of the four aforementioned groups. After two iterations of SACW, a single MPC was generated (length 34.45, CI = 0.79, RI = 0.88) identical to that produced using *chitinosa* as the outgroup. Using both *chitinosa* and *azora* as outgroups, the unweighted heuristic search generated two MPCs (length 75, CI = 0.61, RI = 0.75) which placed *chitinosa* either basal to the four aforementioned groups or as sister to the *cleonus*, *anius* and *virginiensis* groups. After two iterations of SACW, a single MPC was generated (length 36.02, CI = 0.79, RI = 0.88) identical to the second unweighted MPC. In conclusion, all outgroup and weighting combinations except the unweighted analysis with *azora* as outgroup produced the same ingroup cladogram. Because *Chalodeta* appears to share more characters in common with the ingroup than *Dachetola* Hall, 2001, the cladogram with *C. chitinosa* only as outgroup is illustrated as the best estimate of relationships in the ingroup (Fig. 9).

Figure 9 indicates that *Charis*, even as preliminarily conceived here with the exclusion of *aerigera*, *xanthosa* and *myrtis*, is paraphyletic with respect to *Calephelis.* Because there is no convincing character support uniting all four species groups or the *cleonus*, *virginiensis* and *anius* groups (see below), it seems most prudent to divide *Charis* into several genera. The *ocellata*, *cleonus* and *virginiensis* groups are reasonably well supported by decay indices of three or above and regarding each as a genus is not problematic. The *anius* group is relatively weakly supported and consistently groups with *Calephelis*, so we debated whether to combine the two groups. However, because doing so would mean synonymizing the very well known North American genus *Calephelis* with the older generic name *Charis*, we decided against it. Thus, to maximize stability, we restrict *Charis* to its type species, *anius* Cramer, 1776, and its apparent sister species *cadytis* Hewitson, 1866, and maintain an expanded *Calephelis* that additionally includes *iris* Staudinger, 1876, *velutina* Godman and Salvin, 1878 (rev. combs.) and *candiope* H. Druce, 1904 (n. comb.). The new genera *Seco* and *Detritivora* are described below for the *ocellata* and *cleonus* groups, respectively.

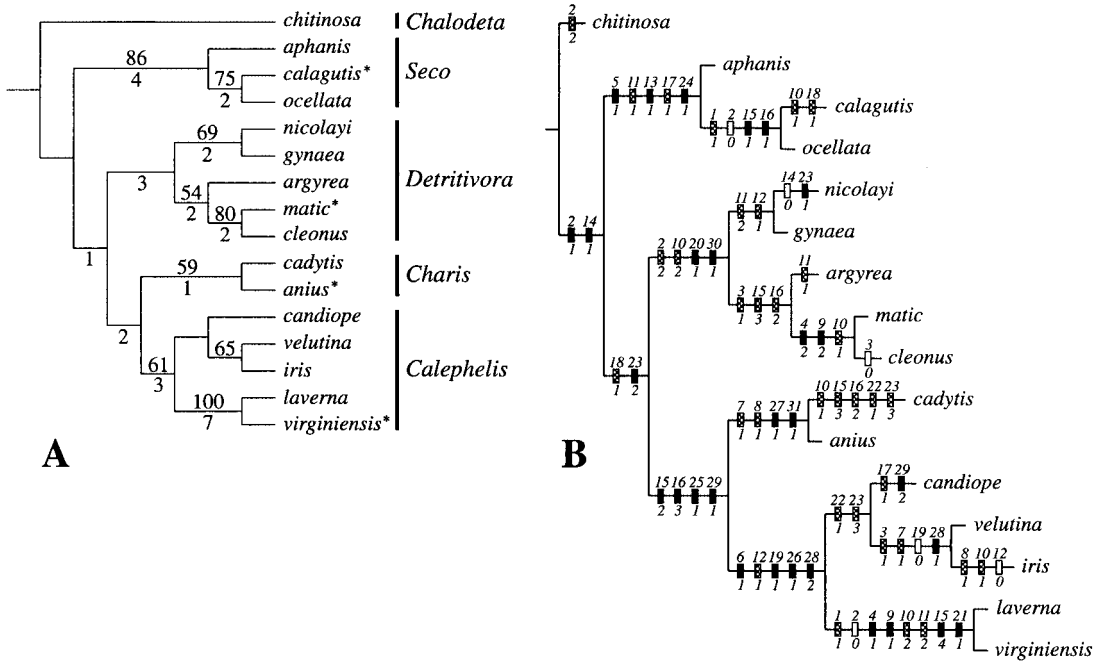

Fig. 9. The single most parsimonious cladogram generated using *Chalodeta* only as the outgroup. (A) Cladogram illustrating estimates of branch support (bootstrap values above branches and decay indices below branches) and generic limits; the type species for each genus is indicated with an asterisk. (B) Cladogram illustrating distribution of character states; black bars indicate unique apomorphies, shaded bars homoplasious apomorphies and white bars reversals.

Increased support for the new generic arrangement adopted here comes from two additional sources. The first is uncertainty concerning the relationships among the four genera. The variable structure of the male genital pedicel is one of the most phylogenetically important characters in this group of riodinids and, therefore, we chose to code its variation in two different ways to assess the impact on the resulting cladograms. Fig. 9 is the result of treating the variation in two binary characters (26 and 27). If the variation is treated in a single three state character, the different outgroup and weighting combinations produce several alternative cladograms (Fig. 10) in which the genera are almost always monophyletic but the position of each relative to the others is inconstant. Although *Charis* and *Calephelis* always group together, in the unweighted analyses using *Dachetola* only or both *Dachetola* and *Chalodeta* as outgroups, *Calephelis* is paraphyletic with respect to *Charis.* However, this scenario is regarded as very implausible on morphological grounds, as the highly modified posteriorly elongate bifurcate pedicel of *Calephelis* would have to be reversed to the simple strap-like pedicel of *Charis.* There is no evidence elsewhere in the Riodinini that such complex structures have ever been lost.

The second source of information supporting the recognition of several genera is the apparent larval foodplant specialization in different clades of the group (Fig. 11; Table 3). Most notably, all oviposition records for *Detritivora* indicate that eggs are laid on dead leaves of the forest floor upon which the larvae feed. This specialization is believed to be unique in the Riodinidae, but parallels that of the lycaenid genus *Calycopis* Scudder, 1876 and relatives (R. Robbins, personal communication). Although *Sarota* larvae feed on the surface of dead leaves, they are actually consuming epiphylls and mosses (DeVries 1988, 1997; DeVries et al. 1994; Hall 1998). Most reliable rearing records for *Charis* and *Calephelis* are in the Asteraceae, with one each in the Ranunculaceae and Euphorbiaceae.

Generic Diagnoses. Below are presented descriptions and synapomorphies (within the context of the ingroup analyzed) for *Seco*, *Detritivora*, *Charis*, and *Calephelis.* Synonymic checklists for these genera are provided in Table 4.

Seco Hall & Harvey, n. gen.
(Figs. 1C, D; 2C, D; 6A; 8A)

Type Species. *Charis calagutis* Hewitson, 1871.

Etymology. The name derives from the Spanish word for "dry," in reference to the relatively arid habitats these species inhabit.

Description. Male. Forewing length 11–13 mm. *Head.* Labial palpi shades of brown with long ventral setae, second segment elongate; eyes brown and bare (*calagutis* and *ocellata*) or very sparsely setose (*aphanis*), brown scaling at margins; frons shades of brown (setae very long in *aphanis*); antennal length ≈70% of forewing length, segments brown with prominent white scaling at base, small disjointed nudum section

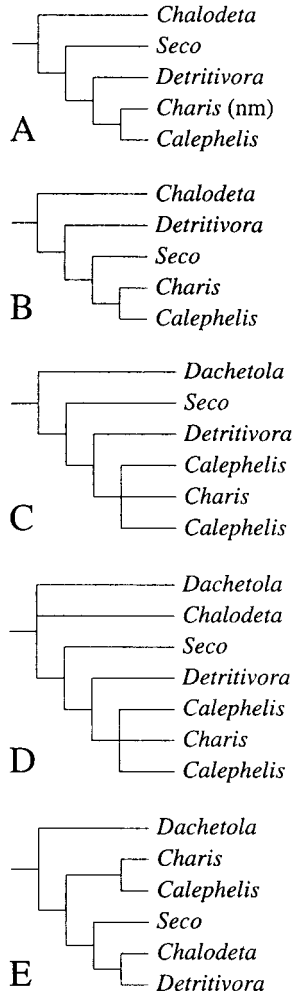

Fig. 10. Cladograms resulting from treating characters 26 and 27 as a single multistate character instead of two binary characters as in Fig. 9. (A) Outgroup *C. chitinosa*, unweighted analysis (strict consensus of two MPCs, length 68); (B) Outgroup *C. chitinosa*, after two iterations of SACW (single MPC, length 35.72); (C) Outgroup *D. azora*, unweighted analysis (single MPC, length 72); (D) outgroups *C. chitinosa* and *D. azora*, unweighted analysis (strict consensus of five MPCs, length 75); (E) Outgroups *C. chitinosa* and *D. azora*, after two iterations of SACW (single MPC, length 35.51). nm = nonmonophyletic.

along inner margin of shaft increases in size toward clubs; clubs black, tips orange-brown. *Body.* Dorsal and ventral surface of thorax and abdomen shades of brown; tarsus of foreleg unimerous, coxa of medium length for family; all legs brown or orange-brown, midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tibia and spines along inner margin of all tarsal segments. *Wing shape.* Both wings compact; forewing somewhat pointed, costa approximately straight, distal margin slightly convex; hindwing rounded. *Venation.* As in *Charis* (see Stichel 1910-11), four forewing radial veins. *Dorsal Surface.* Ground color of both wings alternating shades of brown; four evenly spaced dark brown marks in discal cell of each wing, distal marks often divided, that marking cell end extends as discal line to vein 2A on both wings and to costa on hindwing, two spots toward base of cell Cu2 on both wings, postdiscal band of spots on both wings consists of two sets of distally semicircular markings, one in cells Cu2 and Cu1 and one in cells M3 to M1, small more distal spot toward base of cells R4+5-R1 (single spot only in cells Rs and Sc+R1 on hindwing); submarginal brown band of variable width and prominence, inner silver submarginal line absent (*aphanis*) or composed of small flecks in apical cell R4+5 (*calagutis* and *ocellata*), outer silver submarginal line composed of flecks along vein endings (*aphanis*) or solid line parallel to distal wing margin (*calagutis* and *ocellata*) in each case with submarginal row of black spots proximally surrounded by paler coloration (developed into large "eyespots" in cells Cu2 [both wings] and R4+5 [forewing only] in *ocellata*); fringe on both wings varies from entirely brown (*ocellata*) to entirely white (*calagutis*). *Ventral Surface.* Differs from dorsal surface in following ways: ground color of both wings paler with more contrasted markings, silver markings in apex more prominent in *calagutis* and *ocellata. Genitalia* (Fig. 6A). Uncus rectangular with rounded ventral posterior corner and variably shallow indentation at middle of posterior dorsal margin, falces of average size and shape for family, tegumen with pronounced medial notch at anterior margin; vinculum narrow and sinuate; aedeagus narrow and sigmoidal with pointed tip opening broadly; pedicel highly modified into a posteriorly elongate structure with fine acanthae (acellular projections) restricted to a raised distal area termed a "vogelkop" by Stichel (1910-11); valvae consist of a typically elongate somewhat membranous lower process and a short upper process that is joined above aedeagus to form a transtilla, transtilla developed into a pair of lateral upwardly curved and asymmetrical projections.

Female. Differs externally from male as follows: both wings more rounded; color of both wing surfaces paler. *Head.* Third palpal segment slightly more elongate. *Body.* Foreleg with spines at inner distal tip of tibia and tarsal segments 1–4. *Genitalia* (Fig. 8A). Corpus bursae elongate, signa small spine-like invaginations, ductus bursae membranous with only very distal portion sclerotized, ductus seminalis membranous, ostium bursae a simple hole approximately centrally positioned, only abdominal sternite 8 sclerotized.

Synapomorphies.

- Inner dorsal silver submarginal line reduced to faint apical fleck or absent (character 5:1; e.g., Fig. 1D).
- Ventral ground color of males brown instead of orange-brown or iridescent blue/purple (also *argyrea*) (character 11:1; e.g., Fig. 2D).
- Ventral surface a mixture of light and dark shades instead of a uniform color (character 13:1; e.g., Fig. 2D).

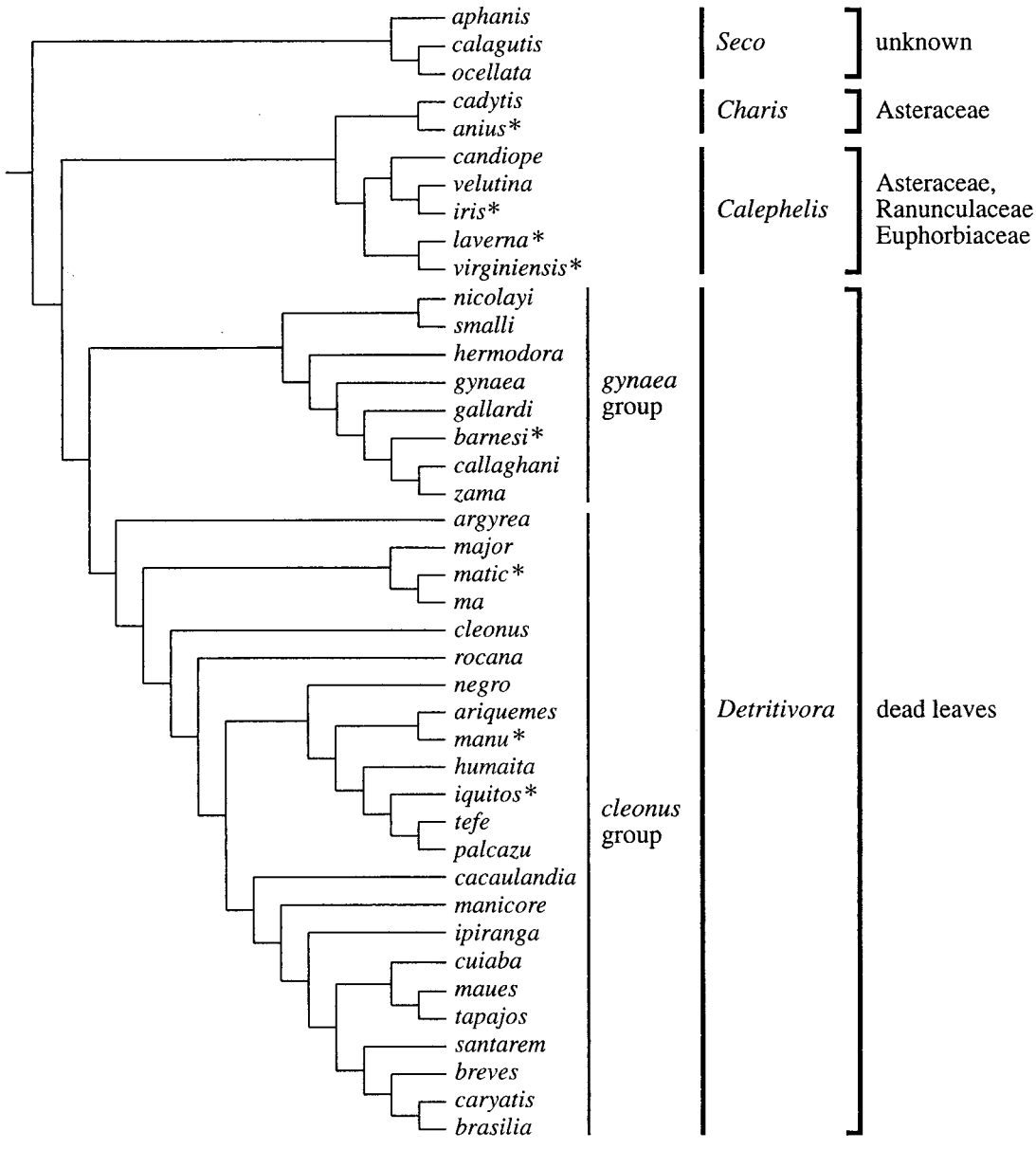

Fig. 11. The cladogram from Fig. 9 of this study combined with those from Hall and Harvey (2001) for the *Detritivora gynaea* group, and Harvey and Hall (2002) for the *Detritivora cleonus* group. Note that *Calephelis* contains an additional forty currently recognized species in the *virginiensis* clade for which the phylogenetic relationships are unknown. The known foodplant families are indicated at right based on the asterisked species. Detailed foodplant information for all *Charis*, *Calephelis* and *Detritivora* species is given in Table 3.

- Individual postdiscal spots on ventral surface outwardly curved instead of straight (also *candiope*) (character 17:1; e.g., Fig. 2D).
- Transtilla tip of male genitalia modified into two long posteriorly and upwardly curved projections (also *Chalodeta*) (character 23:1; Fig. 6A).
- Transtilla projections of male genitalia asymmetrical (character 24:1; Fig. 6A).

***Detritivora* Hall & Harvey, n. gen.**
(Figs. 1E, F; 2E, F; 5C; 6B, C; 8B)

Type Species. *Charis matic* Harvey & Hall, 2002

Etymology. The name refers to the detritivorous feeding habits of the larvae.

Description. Male. Forewing length 10–14 mm. *Head.* Labial palpi brown or black; eyes brown and

Table 3. A list of all rearing records for *Charis*, *Calephelis*, and *Detritivora* (none are known for *Seco*) giving the species (where known), genus and family of hostplant, the location and bibliographic reference

Taxon	Plant taxon	Location	Reference
Charis			
anius	Asteraceae		
	Mikania micrantha	Trinidad	M. Cock (unpublished data)
	Mikania sp.	Ecuador	DeVries et al. (1994)
	Unknown canopy vine	Ecuador	DeVries et al. (1994)
Calephelis			
borealis	Asteraceae		
	Senecio obovatus	USA (NJ)	dos Passos (1936) (D,F:e,l,p)
	Senecio obovatus	USA (WVA)	Allen (1997) (D:l,p; F:l)
iris	Euphorbiaceae		
	Acalypha diversifolia	Costa Rica	Janzen & Hallwachs (2001) (00 SRNP-12644)
laverna	Asteraceae		
	Chromolaena odorata	Trinidad	Cruttwell (1974)
	Eupatorium ivaefolium	Trinidad	Cruttwell (1974)
	Eupatorium macrophylum	Trinidad	Cruttwell (1974)
	Eupatorium microstemon	Trinidad	Cruttwell (1974)
muticum	Asteraceae		
	Cirsium muticum	USA (MI)	McAlpine (1938) (D:e,l,p; F:l,p)
	Cirsium altissimum	USA	Scott (1986) (D:e,l,p)
nemesis	Asteraceae		
	Baccharis glutinosa	USA (CA)	Comstock & Dammers (1932) (D:e,l,p; F:1,p)
	Encelia californica	USA (CA)	Emmel & Emmel (1973) (D,F:l,p)
	Ranunculaceae		
	Clematis drummondii	USA (TX)	Kendall (1959)
	Clematis henryi	USA (TX)	Kendall (1959)
nilus (?)	Bromeliaceae		
	Bromelia antiacantha (?)	Brazil	Biezanko et al. 1979
perditalis	Asteraceae		
	Chromolaena odorata	USA (TX)	Kendall *in* Powell (1975); Kendall (1976); Downey & Allyn (1980) (D,F:e)
	Eupatorium glabratum	Mexico	de la Maza & de la Maza (1976) (D,F:e,l,p)
rawsoni	Asteraceae		
	Eupatorium havanense	USA (TX)	Kendall (1976); Downey & Allyn (1980) (D,F:e)
	Eupatorium greggii	USA (TX)	Kendall (1976)
virginiensis	Asteraceae		
	Cirsium horridulum	USA (TX)	Kendall *in* Powell (1975); Kendall (1976)
wrighti	Asteraceae		
	Bebbia juncia	USA (CA)	Comstock (1928) (D,F:e,l,p)
Detritivora			
barnesi	Dead leaves	Panama	DeVries et al. (1994); DeVries (1997) (D:e,l)
iquitos	Dead leaves	Peru	D. Harvey (unpublished data)
matic	Dead leaves	Ecuador	DeVries et al. (1994)
	Dead leaves	Ecuador	DeVries et al. (1994)
manu	Dead leaves	Peru	D. Harvey (unpublished data)

A question mark indicates a dubious record. Note that for some records the name of the taxon differs from that given in the original publication. Early stage information provided by authors is indicated as follows: D = description of, and F = figures of, (e) egg, (l) larva and (p) pupa.

densely setose, brown or black scaling at margins; frons brown or black; antennal length ≈70% of forewing length, segments brown with prominent white scaling at base, clubs black. *Body.* Dorsal and ventral surface of thorax and abdomen brown or black; tarsus of foreleg unimerous, coxa of medium length for family; all legs brown (forelegs with blue iridescence in *cleonus* group), midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tibia and spines along inner margin of all tarsal segments. *Wing Shape.* Both wings compact; forewing costa approximately straight, distal margin convex, apex sometimes slightly falcate; hindwing rounded. *Venation.* As in *Charis* (see Stichel 1910-11), four forewing radial veins. *Dorsal Surface.* Ground color of both wings shades of brown or black overlaid with dark iridescent blue (*cleonus* group—no discal or postdiscal markings visible in this group); three (*smalli* and *argyrea* only) or four evenly spaced dark brown marks in discal cell of each wing, that marking cell end extends as discal line to vein 2A on both wings and to costa on hindwing, two spots toward base of cell Cu2 on both wings, postdiscal band of spots on both wings consists of two slightly disjointed lines between cells Cu2 and M1 with marks at the base of cells R4+5 and R3 variably prominent (marks in cells Rs and Sc+R1 on hindwing prominent); two parallel submarginal silver lines with orange-brown distally and in between surrounding a black spot in each of cells Cu1 to R4+5 (two in Cu2); fringe on both wings varies from entirely brown to almost entirely white (entire hindwing and anal half of forewing in cleonus group). *Ventral Surface.* Differs from dorsal surface in following ways: ground color of both wings in *gynaea* group orange-brown, often with

Table 4. Synonymic checklists for *Seco*, *Detritiora*, *Charis*, and *Calephelis*

Seco Hall & Harvey (3spp.)
aphanis (Stichel, 1910) n. comb.

calagutis (Hewitson, 1871) n. comb.
ocellata (Hewitson, 1867) n. comb.

Detritivora Hall & Harvey (31spp.)
argyrea (Bates, 1868) n. comb.
ariquemes (Harvey & Hall, 2002) n. comb.
barnesi (Hall & Harvey, 2001) n. comb.
brasilia (Harvey & Hall, 2002) n. comb.
breves (Harvey & Hall, 2002) n. comb.
cacaulandia (Harvey & Hall, 2002) n. comb.
callaghani (Hall & Harvey, 2001) n. comb.
caryatis (Hewitson, 1866) n. comb.
cleonus (Stoll, 1781) n. comb.
cuiaba (Harvey & Hall, 2002), n. comb.
gallardi (Hall & Harvey, 2001) n. comb.
gynaea (Godart, [1824]) n. comb.
hermodora (C. & R. Felder, 1861) n. comb.
humaita (Harvey & Hall, 2002) n. comb.
ipiranga (Harvey & Hall, 2002) n. comb.
iquitos (Harvey & Hall, 2002) n. comb.
ma (Harvey & Hall, 2002) n. comb.
major (Lathy, 1932) n. comb.
manicore (Harvey & Hall, 2002) n. comb.
manu (Harvey & Hall, 2002) n. comb.
matic (Harvey & Hall, 2002) n. comb.
maues (Harvey & Hall, 2002) n. comb.
negro (Harvey & Hall, 2002) n. comb.
nicolayi (Hall & Harvey, 2001) n. comb.
palcazu (Harvey & Hall, 2002) n. comb.
rocana (Harvey & Hall, 2002) n. comb.
santarem (Harvey & Hall, 2002) n. comb.
smalli (Hall & Harvey, 2001) n. comb.
tapajos (Harvey & Hall, 2002) n. comb.
tefe (Harvey & Hall, 2002) n. comb.
zama (Bates, 1868) n. comb.

Charis Hübner, [1819] (2spp.)
Charmona Stichel, 1910
Charmonana Strand, 1932
anius (Cramer, 1776)
--*ania* (Hübner, [1819)
--*cleodora* (Godart, [1824])
cadytis Hewitson, 1866
--*acroxantha* (Stichel, 1910) n.syn.

Calephelis Grote & Robinson, 1869 (45spp.)
Lephelisca Barnes & Lindsey, 1922
acapulcoensis McAlpine, 1972
argyrodines (Bates, 1866)
arizonensis McAlpine, 1971
aymaran McAlpine, 1971
azteca McAlpine, 1971
bajaensis McAlpine, 1971
borealis (Grote & Robinson, 1866)
--*geda* Scudder, 1876
braziliensis McAlpine, 1971
browni McAlpine, 1971
burgeri McAlpine, 1971
candiope (H. Druce, 1904) n. comb.
--*pyritis* Stichel, 1928
clenchi McAlpine, 1971
costaricicola Strand, 1916
dreisbachi McAlpine, 1971
exiguus Austin, 1993
freemani McAlpine, 1971
fulmen McAlpine, 1971
guatemala McAlpine, 1971
huasteca McAlpine, 1971
inca McAlpine, 1971
iris (Staudinger, 1876) rev. comb.
--*irina* Stichel, 1928 n. syn.
laverna (Godman & Salvin, 1886)
-*parva* Austin, 1993
-*trinidadensis* McAlpine, 1971
matheri McAlpine, 1971
maya McAlpine, 1971
mexicana McAlpine, 1971
montezuma McAlpine, 1971
muticum McAlpine, 1937
nemesis (Edwards, 1871)
--*australis* (Edwards, 1871)
--*guadeloupe* (Strecker, 1878)
-*californica* McAlpine, 1971
-*dammersi* McAlpine, 1971
nilus (C. & R. Felder, 1861)
perditalis Barnes & McDunnough, 1918
-*donahuei* McAlpine, 1971
rawsoni McAlpine, 1971
sacapulas McAlpine, 1971
schausi McAlpine, 1971

sinaloensis McAlpine, 1971
-*nuevoleon* McAlpine, 1971
sixola McAlpine, 1971
sodalis Austin 1993
stallingsi McAlpine, 1971
tapuyo McAlpine, 1971
tikal Austin, 1993
velutina (Godman & Salvin, 1878) rev. comb.
virginiensis (Guérin-Méneville, [1832])
--*louisiana* Holland, 1929
--*pumila* (Boisduval & LeConte, [1835])
wellingi McAlpine, 1971
-*baleuensis* McAlpine, 1971
wrighti McAlpine, 1971
yautepequensis R. G. Maza & Turrent, 1977
yucatana McAlpine, 1971

The list for the *Calephelis virginiensis* group (i.e., *Calephelis sensu* McAlpine, 1971) is unchanged from Miller and Brown (1981) and Callaghan and Lamas (2002) as no original alpha-level taxonomic work has been done on the group. However, a significant number of synonymies are expected.

purple iridescence, more contrasted markings, submarginal orange-brown often reduced; typically two parallel submarginal silver lines but in certain *gynaea* and *cleonus* group species inner line may be reduced to apical fleck or absent, and both lines may be merged to form single broad band in derived cleonus group species. *Genitalia.* (Fig. 6B and C); also see illustrations in Hall and Harvey 2001; Harvey and Hall 2002: uncus rectangular with rounded ventral posterior corner and variably shallow indentation at middle of posterior dorsal margin, falces of average size and shape for family, tegumen with pronounced medial notch at anterior margin; vinculum narrow and sinuate; aedeagus narrow and often sigmoidal in shape with pointed tip opening broadly, small spine-like cornuti present in several *cleonus* group species; pedicel highly modified into a posteriorly elongate structure with fine acanthae typically restricted to a raised distal "vogelkop," distributed along its distal half in derived *cleonus* group species; valvae consist of a typically small and somewhat membranous lower process and an upper process that is joined above aedeagus to

form a "hood"-like transtilla; in some species, transtilla reduced or lost, developed into additional paired lateral projections or a pouch of spines (derived *cleonus* group species).

Female. Differs externally from male in following ways: both wings more rounded; ground color of both dorsal wings brown with no iridescence present, ground color of both ventral wings orange-brown with no iridescence in *gynaea* group, brown in *cleonus* group; ventral markings, especially on forewing, more prominent. *Head.* Third palpal segment slightly more elongate. *Body.* Foreleg with spines at inner distal tip of tibia and tarsal segments one to four. *Genitalia* (Fig. 8B; also see illustrations in Hall and Harvey 2001, Harvey and Hall 2002): corpus bursae elongate, signa typically small spine-like invaginations, rarely elongate at corpus wall (*argyrea* and *smalli* only), ductus bursae typically membranous, distal portion sclerotized and occasionally coiled in some *cleonus* group species, ductus seminalis membranous, ostium bursae asymmetrically displaced, typically to right, ostium may be a simple hole or positioned in an invagination forming part of a modified eighth abdominal sternite (*cleonus* group), abdominal sternites 6–8 may be sclerotized.

Synapomorphies.

- Eyes densely setose (also *Chalodeta*) (character 2:2; Fig. 5C).
- Black spots in each of ventral forewing cells R4+5 to R2 absent (character 20:1; e.g., Fig. 2E).
- Ostium bursae of female genitalia asymmetrically displaced, typically to right (not in many derived *cleonus* group species) (character 30:1; Fig. 8B).
- All known larvae detritivores (see Table 3). This character is believed to be unique within the Riodinidae.

Charis Hübner, [1819]
(Figs. 1 G–J; 2 G-J; 5B; 6D, E; 8C)

Charis Hübner, [1819]. *Verz. Bekannt. Schmett.* 2: 21. Type species by selection of Scudder (1875): *Charis ania* Hübner, [1819], op. cit. (=*Charis anius* (Cramer, 1776): 144, Pl. 92, figure B).

= *Charmona* Stichel, 1910. *Berl. Entomol. Zeit.* 55: 15. Type species by original designation: *Papilio anius* Cramer, 1776: 144, Pl. 92, figure B.

= *Charmonana* Strand, 1932. *Folia Zool. Hydrobiol.* 4: 145. Replacement name for *Charmona*, which is a junior homonym of *Charmona* Billberg, 1820 (Zygaenidae).

Synapomorphies.

- Area between dorsal silver submarginal lines brown instead of orange-brown (also *velutina* and *iris*) (character 7:1; e.g., Fig. 1I).
- Black spots positioned immediately proximal to outer dorsal submarginal line instead of equidistant between inner and outer silver lines (also *iris*) (character 8:1; e.g., Fig. 1I).
- Male genital pedicel simple and strap-like (character 27:1; e.g., Fig. 6D). This state is rare in the Riodinini, in which almost all species have a posteriorly modified pedicel, and is the most convincing synapomorphy for *Charis.*
- Sclerotization on eighth abdominal sternite of female abdomen absent (character 31:1; Fig. 8C). This character may be linked to the lack of a posteriorly elongate pedicel.

Calephelis Grote & Robinson, 1869
(Figs. 3 A-H; 4 A-H; 5A; 7 A-C; 8D)

Calephelis Grote & Robinson, 1869. *Trans. Am. Entomol. Soc.* 2: 310. Type species by designation of ICZN (1966, Op. 775): *Erycina virginiensis* Gray, [1832], in Griffith's Cuvier's *Anim. Kingd.* 15: 58, figure 1 (=*Erycina virginiensis* Guérin-Méneville, [1832], *Iconographie Ins.*: 489, Pl. 81, figure 1).

= *Lephelisca* Barnes and Lindsey, 1922. Ann. Entomol. Soc. Am. 15: 93. Type species by original designation: *Erycina virginiensis* Guérin-Méneville, [1832], op. cit. Unnecessary replacement name for *Calephelis.*

Synapomorphies.

- Inner dorsal silver submarginal line jagged instead of straight (character 6:1; e.g., Fig. 3E).
- Ventral ground color of females orange-brown instead of brown (not *iris;* also *Detritivora gynaea* group) (character 12:1; e.g., Fig. 4F).
- Silver spot in ventral forewing cell R3 present (not *velutina* and *iris*) (character 19:1; e.g., Fig. 4G).
- Male genital pedicel bifurcate (character 26:1; e.g., Fig. 7C). The exact configuration of the bifurcate pedicel in *Calephelis* is unique in the Riodinini and thus a solid synapomorphy for *Calephelis*, although different independently derived bifurcate pedicels do occur in a few other riodinine genera, including *Notheme* Westwood, [1851] and *Siseme* Westwood, [1851].

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