Phylogenetic Revision of the *Charis gynaea* Group (Lepidoptera: Riodinidae) with Comments on Historical Relationships Among Neotropical Areas of Endemism

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

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

Ann. Entomol. Soc. Am. 94(5): 631–647 (2001)

ABSTRACT A revision of the *Charis gynaea* group of Neotropical riodinid butterflies is presented. We recognize eight species, including five that are described here: *C. barnesi*, *C. callaghani*, *C. gallardi*, *C. nicolayi*, and *C. smalli*. The taxa *zama* and *candiope*, previously treated as subspecies of *Charis gynaea*, are both returned to species status (stat. revs.), and the latter is excluded from the *gynaea* group. The taxon *pyritis* is synonymized with *C. candiope* (n. syn.). A cladistic analysis using seventeen characters of male and female genitalia and external facies generated a single most parsimonious cladogram indicating the existence of two clades, one containing *smalli* + *nicolayi* and the other containing the remaining species. In the latter *gynaea* clade, all species except *C. hermodora* are distributed parapatrically throughout the Neotropics. An area cladogram indicates the historical relationships among endemic centers for this last group to be southeast Brazil + (Guianas + (Central America + Amazon)). This hypothesis is compared with those generated for birds.

KEY WORDS *Charis*, area cladograms, biogeography, cladistics, endemism, Neotropics

THE RIODINID GENUS *Charis* Hübner, [1819] is a medium-sized group of inconspicuous butterflies in the tribe Riodinini (sensu Harvey 1987) that historically have been understudied because of their small size and often relatively drab coloration. The genus has had a confused nomenclatural and systematic history, in part because of a lack of published synapomorphies defining *Charis* and related genera, and its members have often been confused with those of *Calephelis* Grote & Robinson, 1869 and *Chalodeta* Stichel 1910 (e.g., d'Abrera 1994). Stichel (1910, 1930–1931) treated these butterflies in *Charmona* Stichel, 1910 because of confusion about the correct type species of *Charis*, an error finally corrected by Hemming (1967).

Although most *Charis* species are common in primary and secondary growth habitats throughout the Neotropics, species-level identifications have always been problematic because of great external interspecific similarities, and the true diversity of the genus has not been hitherto fully appreciated. This paper forms part of a series revising monophyletic units within *Charis* (Harvey and Hall 2001) and in this case treats the *gynaea* group, which contains more undescribed than described species. The final part will provide an overview and comprehensive species-level cladistic analysis of the genus to provide stable diagnoses for *Charis* and related riodinine genera. Here we present a phylogenetic analysis of the *gynaea* group and use the resulting cladogram to briefly comment on historical relationships among the broad Neotropical areas of endemism.

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

Materials and Methods

Dissections were made using standard techniques after abdomens were soaked in hot 10% potassium hydroxide solution for approximately 5 min and subsequently stored in glycerol. Dissected specimens are indicated throughout the text with unique reference numbers. Morphological terms for genitalia follow Klots (1956) and Eliot (1973), and the terminology for wing venation follows Comstock and Needham (1918).

Charis gynaea group specimens have been examined and their locality data recorded in the following collections, whose acronyms are used throughout the text. (AME) Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, U.S.A.; (BMNH) The Natural History Museum, London, England; (CJC) Collection of C. J. Callaghan, Bogotá, Colombia; (DA) Collection of D. H. Ahrenholz, St. Paul, MN, U.S.A.; (JBS) Collection of J. B. Sullivan, Beaufort, PA, U.S.A.; (JHKW) Collection of J.P.W. Hall & K. R. Willmott, Washington, DC, U.S.A.; (JS) Collection of J. Shuey, Indianapolis, IN, U.S.A.; (SMF) Senckenberg Museum, Frankfurt, Germany; (SMTD) Staatliches Museum für Tierkunde, Dresden, Germany; (USNM) National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; (ZMHU) Zoologisches Museum für Naturkunde, Humboldt Universität, Berlin, Germany. Only locality data are given in the species accounts of described taxa, but full label data are given for new species.

The phylogenetic analysis presented here is based on morphological characters derived from the wings

0013-8746/01/0631–0647$02.00/0

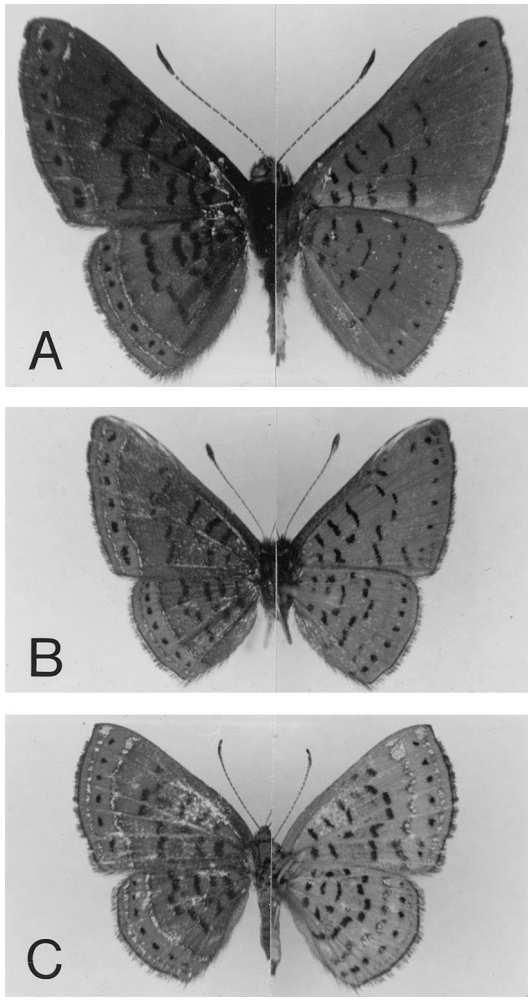

Fig. 1. Adults (dorsal surface on left, ventral surface on right). (A) Holotype ♂ *Charis nicolayi*, Potrerillos, Panama (USNM). (B) Holotype ♂ *C. smalli*, Caña, Panama (USNM). (C) Allotype ♀ *C. smalli*, El Durango, Ecuador (JHKW).

and male and female genitalia of all eight *Charis gynaea* group species (Figs. 1–6). Phylogenetically uninformative autapomorphies were excluded, although these are given in the relevant species accounts below. The phylogenetic analysis was performed using a heuristic search with 1,000 random addition sequence TBR replicates in PAUP 4.0b4a (Swofford 2000). All characters were equally weighted. *Charis argyrea* Bates, 1868 was used as the outgroup because it is hypothesized to be the most closely related species to the ingroup (see *Diagnosis* section). The strength of branch support was estimated by means of 1,000 bootstrap replicates in PAUP (Felsenstein 1985) and by calculating decay indices (Bremer 1988, 1994) using the program AUTODECAY 4.0 (Eriksson 1998) in combination with PAUP. Character distribution was studied using MacClade 3.05 (Maddison and Maddison 1995).

Results of Phylogenetic Analysis

A total of 17 characters was identified (see Appendix 1) from wing pattern (eight), male genitalia (six), and female genitalia (three) (see Table 1 for character matrix). The heuristic searches generated a single most parsimonious cladogram (Figs. 7 and 8) of 23 steps, with a consistency index of 0.74, and a retention index of 0.82. This cladogram provides strong branch support for the existence of two clades, one containing *nicolayi* + *smalli*, the other containing *hermodora* + (*gynaea* + (*gallardi* + (*barnesi* + (*callaghani* + *zama*)))). Branch support for nodes within the *gynaea* clade is generally weak, except for the *callaghani* + *zama* node, because of homoplasy in genitalic characters 9, 11, and 16, and an overall paucity of characters. The branching order of the *gynaea* clade is used to make tentative biogeographical inferences (see *Biogeography* section).

Revision of *Charis gynaea* Group

Charis Hübner, [1819]

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

Charmona Stichel, 1910: 15. Type species by original designation: *Papilio anius* Cramer, 1776: 144, Pl. 92, figure B. A junior homonym of *Charmona* Billberg, 1820 (Zygaenidae).

Charmonana Strand, 1932: 145. A replacement name for *Charmona.*

Diagnosis. The *gynaea* group of *Charis* is characterized by a combination of wing pattern characters that include a brown ground color and two parallel submarginal silver lines on both dorsal wings, and an orange-brown ventral ground color, often overlaid with purple iridescence, with a complete, reduced or absent outer submarginal silver line on both wings and no inner submarginal silver line (in males of all species and females of all but one species). The lack of an inner submarginal silver line on the ventral surface in males occurs elsewhere in the genus only in one species of the closely related *cleonus* group and one species of the unrelated *ocellata* group, whose members exhibit quite different external facies and genitalic morphology, and probably do not belong in *Charis* (unpublished data).

The male and female genitalia of *Charis gynaea* group species are typical for the tribe Riodinini (see Figs. 4–6). The uncus of the male genitalia is rectangular with a straight or shallowly indented dorsal margin, the falci and tegumen are of average size and shape for the tribe, and the vinculum is long, thin, and often posteriorly bowed in its dorsal half. The aedeagus is long, thin, slightly asymmetrical, opens broadly to the right with an anteriorly projecting everted vesica, and often has a broad lateral flange near the tip (Fig. 5D). The pedicel is modified into a posteriorly elongate structure with fine acanthae (acellular pro-

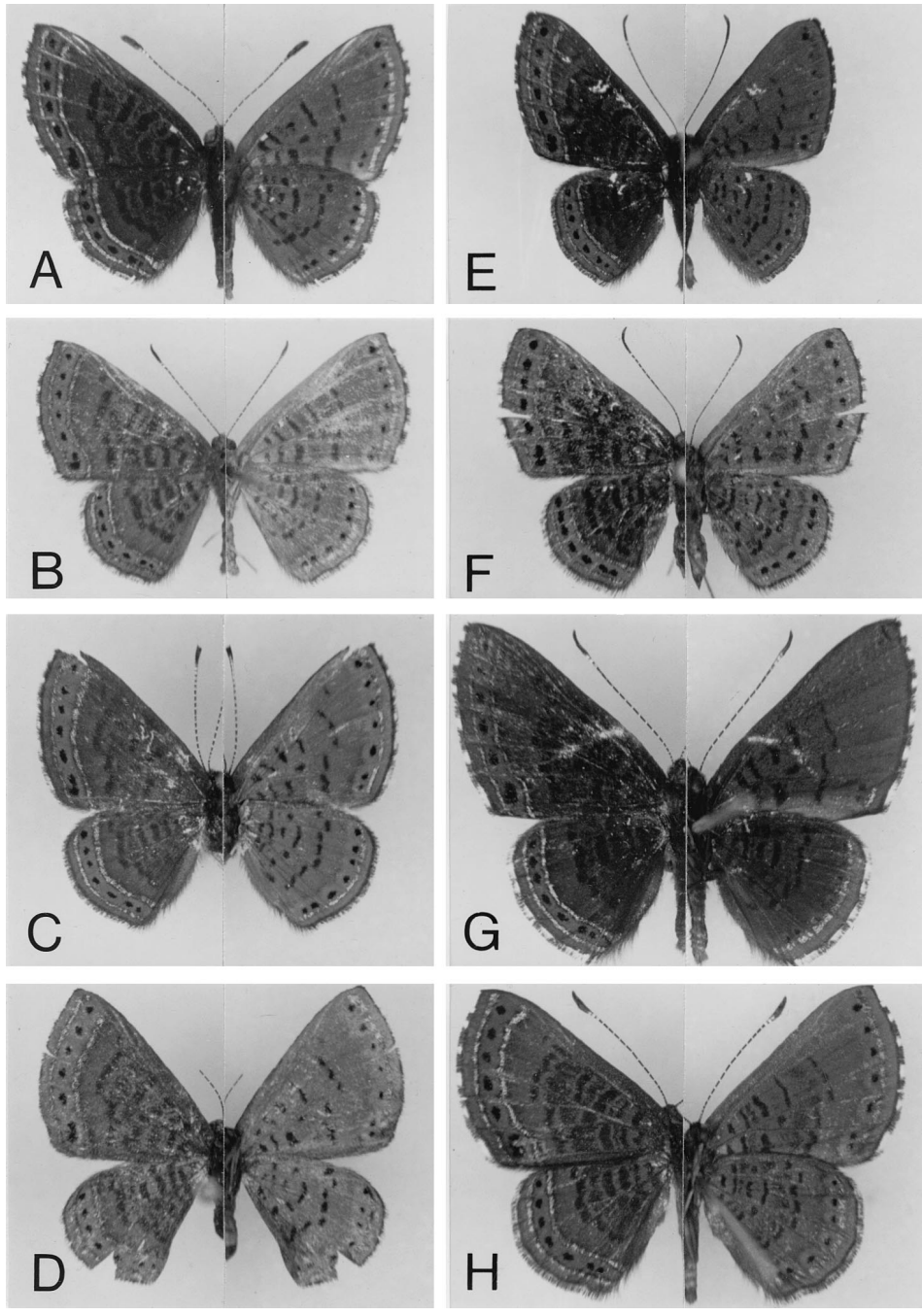

Fig. 2. Adults (dorsal surface on left, ventral surface on right). (A) ♂ *Charis hermodora*, Farfan, Panama (USNM). (B) ♀ *C. hermodora*, Madden Forest, Panama (USNM). (C) ♂ *C. gynaea*, Linhares, Brazil (ES) (AME). (D) ♀ *C. gynaea*, Linhares, Brazil (ES) (AME). (E) Holotype ♂ *C. gallardi*, Saint Élie, French Guiana (USNM). (F) Allotype ♀ *C. gallardi*, Saint Élie, French Guiana (USNM). (G) Holotype ♂ *C. barnesi*, Guapiles, Costa Rica (USNM). (H) Allotype ♀ *C. barnesi*, Caña, Panama (USNM).

jections) distributed atop a raised distal area termed a "vogelkop" by Stichel (1910). The valvae consist of a small and narrow lower process and typically one small upper process joined above the aedeagus to form a broad transtilla. The male genitalia of *gynaea* group species differ only slightly interspecifically compared with other members of the genus, and most specific differences are exhibited in the length and shape of the pedicel, valvae, and transtilla. The female genitalia are even more homogeneous and consist of an elon-

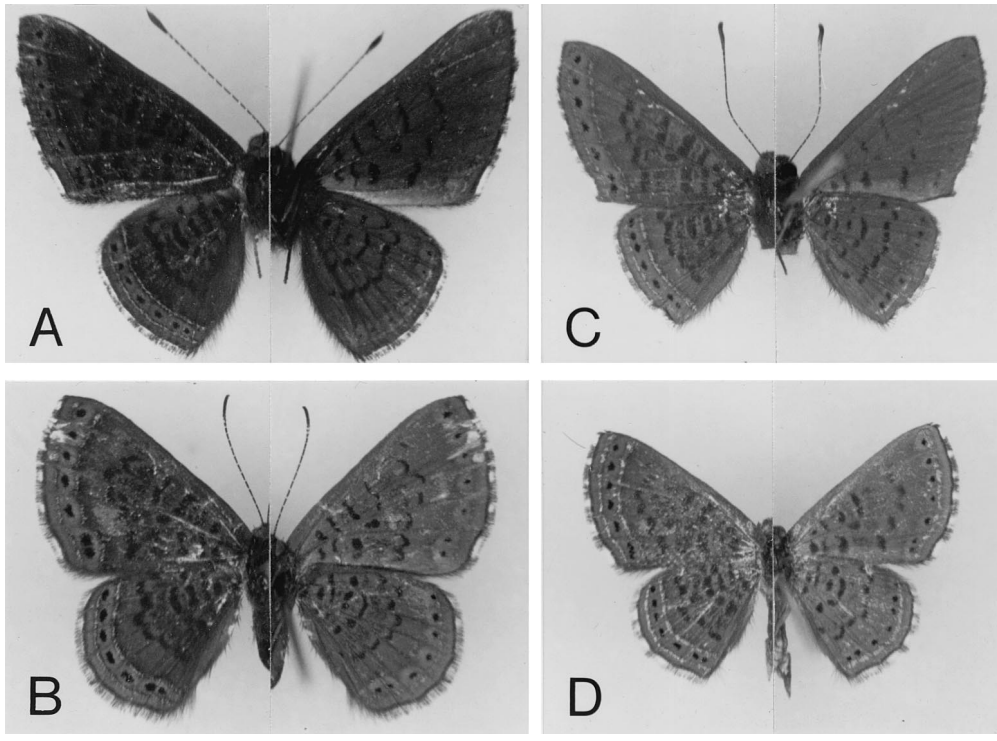

Fig. 3. Adults (dorsal surface on left; ventral surface on right). (A) Holotype ♂ *Charis callaghani*, Pescador, Colombia (AME). (B) Allotype ♀ *C. callaghani*, Pescador, Colombia (AME). (C) ♂ *C. zama*, Chapada, Brazil (MG) (USNM). (D) ♀ *C. zama*, Diamantino, Brazil (MG) (USNM).

gate corpus bursae, typically with a pair of short "horn-like" signa, a membranous ductus bursae, and an ostium bursae that is asymmetrically placed to the right. The last two sternal segments are well sclerotized with the seventh typically more elongate than the eighth.

The most closely related *Charis* species appear to be *C. argyrea* and members of the *cleonus* group (Harvey and Hall 2001), which have similar male and female genitalia, but black or iridescent blue wings with two submarginal silver lines on the ventral surface. *C. argyrea* lacks the entirely white hindwing fringe and half white forewing fringe of *cleonus* group species and has the most similar genitalia to the *gynaea* group.

Proposed Classification. The *Charis gynaea* group as defined here has traditionally been regarded as containing two species, *gynaea* Godart [1824] and *hermodora* C. & R. Felder, 1861, with the only other described taxon, *zama* Bates, 1868, having typically been treated as a subspecies of *C. gynaea* (Stichel 1910, 1930–1931; d'Abrera 1994; Bridges 1994). Godman (1903) described the taxon *candiope* as a full species, but Stichel (1910, 1930–1931) and most subsequent authors have treated it as a subspecies of *C. gynaea.* However, because the male possesses an inner silver submarginal line on the ventral surface, it can be placed outside the *gynaea* group. Its unique genitalic morphology clearly indicates that it is a valid species (stat. rev.) related to *Charis iris* Staudinger, 1876, and *Charis velutina* Godman & Salvin, 1878 (unpublished data). The taxon *pyritis* Stichel, 1928, currently treated as a subspecies of *C. velutina*, is a synonym of *C. candiope* (n. syn.). We recognize eight species for the *Charis gynaea* group in the systematic checklist below, including five newly described here.

Charis gynaea group:

barnesi Hall & Harvey n. sp.
callaghani Hall & Harvey n. sp.
gallardi Hall & Harvey n. sp.
gynaea (Godart, [1824])
hermodora C. & R. Felder, 1861
nicolayi Hall & Harvey n. sp.
smalli Hall & Harvey n. sp.
zama Bates, 1868 stat. rev.

Key to the Identification of Male *Charis gynaea* Group Species

The females of certain species are too similar to identify by means of a key and should be identified by comparison with the specimens in Figs. 1–3 and on the basis of capture locality.

1. Outer silver submarginal line on ventral hindwing absent 2
   Outer silver submarginal line on ventral hindwing present 3
2(1). Forewing length > 13 mm, ventral ground color dark orange-brown, four black marks in discal cell . . . . . *nicolayi*

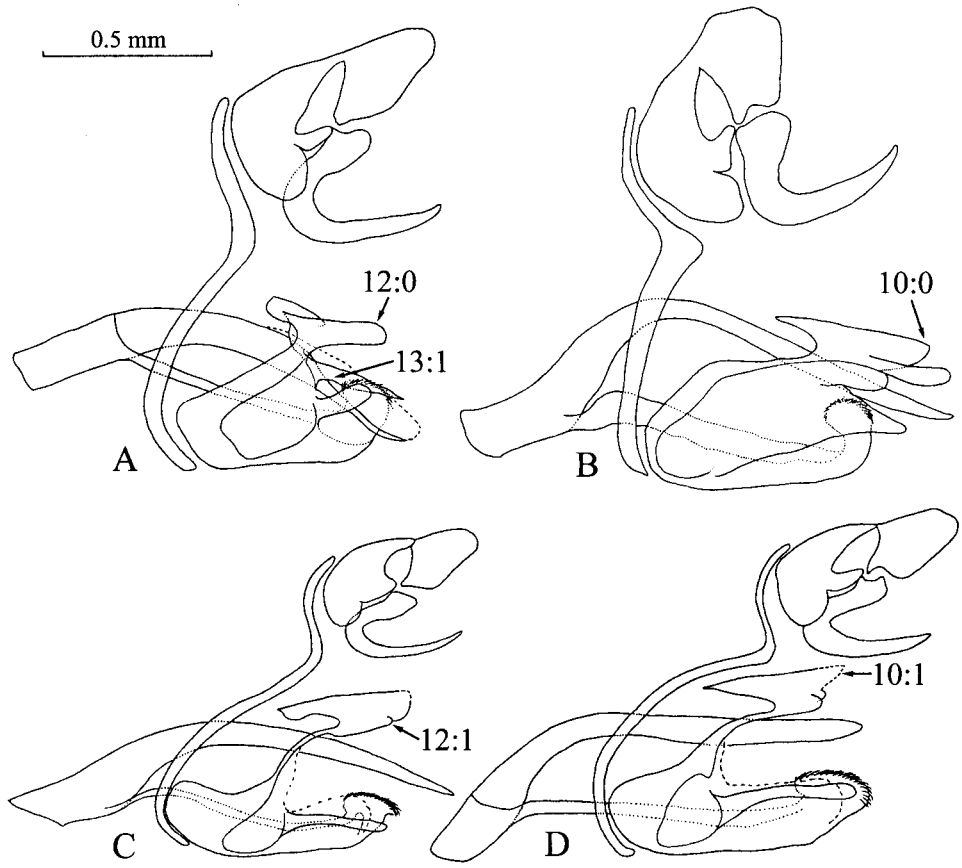

Fig. 4. Male genitalia in lateral view. (A) Holotype *Charis nicolayi*, Potrerillos, Panama (USNM) (JH # USNM-357). (B) Holotype *C. smalli*, Caña, Panama (USNM) (JH # USNM-68). (C) *C. hermodora*, Farfan, Panama (USNM) (DH # 1989–66). (D) *C. gynaea*, Ubatã, Brazil (Ba) (USNM) (DH # 2000–416).

Forewing length < 12 mm, ventral ground color pale orange-brown, three black marks in discal cell . . . . . *smalli*

3(1). Iridescent purple on ventral surface absent, outer silver submarginal line on ventral forewing present and complete 4

Iridescent purple on ventral surface present, outer silver submarginal line on ventral forewing reduced or absent 5

4(3). Ventral surface dark orange-brown, hindwing fringe brown and white, dark markings between discal and postdiscal bands on ventral surface present . . . . *hermodora*

Ventral surface pale orange-brown, hindwing fringe entirely brown, dark markings between discal and postdiscal bands on ventral surface absent . . . . . *gynaea*

5(3). Hindwing fringe entirely brown, submarginal spots on ventral surface prominently present . . . . . *gallardi*

Hindwing fringe brown and white, submarginal spots on ventral surface absent or only weakly present 6

6(5). Forewing length typically < 13 mm, outer silver submarginal line on ventral forewing absent or reduced to fleck in apex, ventral purple iridescence weak . . . . . *zama*

Forewing length typically > 13 mm, outer silver submarginal line on ventral forewing reduced to flecks in apex and tornus, ventral purple iridescence strong 7

7(6). Ventral purple iridescence uniform on both wings, pedicel of male genitalia long . . . . . *callaghani*

Ventral purple iridescence typically darker on hindwing, pedicel of male genitalia short . . . . . *barnesi*

Biogeography. The *Charis gynaea* group is distributed throughout the Neotropics from Mexico to west Ecuador, throughout the Amazon basin and Guianas, and extends as far as southeast Brazil (see Fig. 9). The highest number of species occurs in Colombia (five) (see Table 2). The *nicolayi* + *smalli* clade is Central American, and members of the *gynaea* clade all occupy parapatric distributions throughout the Neotropics ex-

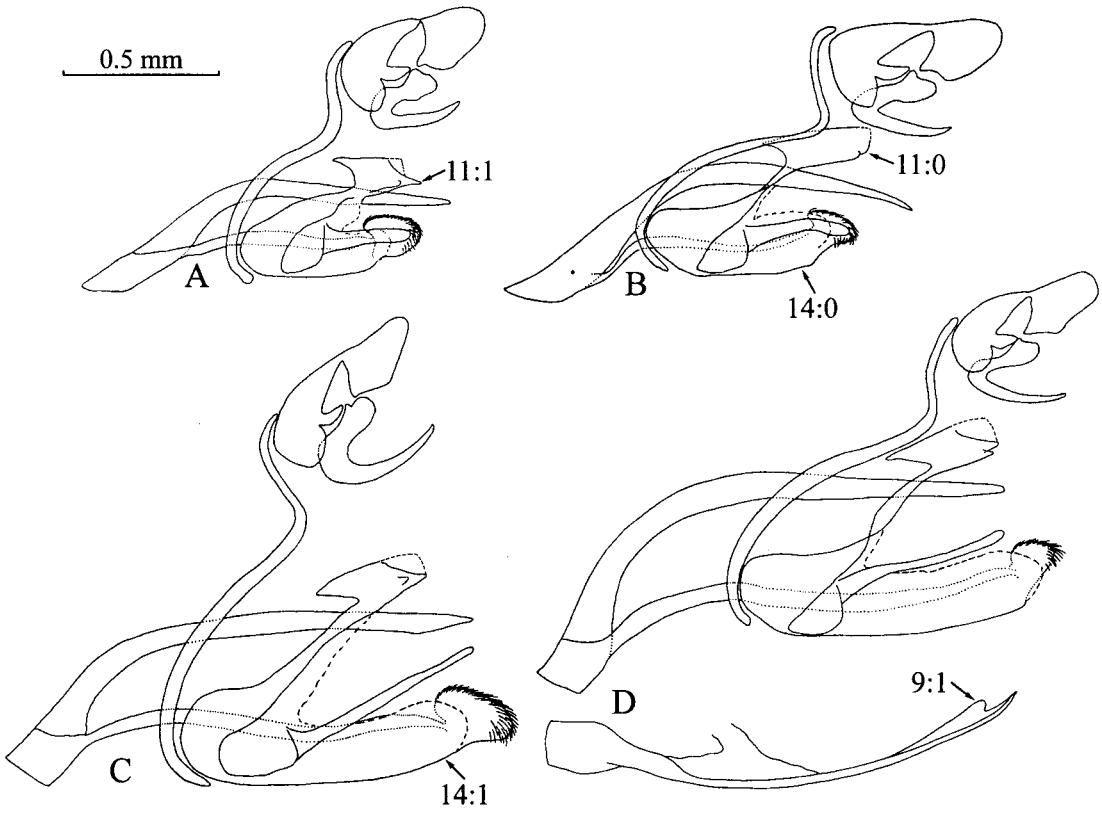

Fig. 5. Male genitalia in lateral view. (A) Holotype *Charis gallardi*, Saint Élie, French Guiana (USNM) (JH # USNM-359). (B) Holotype *C. barnesi*, Guapiles, Costa Rica (USNM) (JH # USNM-358). (C) Holotype *C. callaghani*, Pescador, Colombia (AME) (DH # 2000–340). (D) *C. zama*, Tefé, Brazil (Am) (AME) (DH # 2000–335), aedeagus in dorsal view below.

cept *C. hermodora*, which occurs sympatrically with *C. barnesi* in eastern Central America.

Based on the cladograms presented in Figs. 7 and 8, the historical relationships between the areas of endemism occupied by the *gynaea* clade exclusive of *C. hermodora* can be described as southeast Brazil + (Guianas + (Central America + Amazon)). Fig. 10 illustrates this hypothesis in the form of an area cladogram as well as those based on Neotropical bird distributions (Cracraft and Prum 1988, Prum 1988, Bates et al. 1998). Although there are several differences between these area cladograms, they do exhibit significant congruence, suggesting that these organisms may have shared a common vicariant history. All of the cladograms, except that of Bates et al. (1998) hypothesize southeast Brazil as the most basal area, all except that derived in this study hypothesize the Guianas as one of the two most distal areas, and all hypothesize the Amazon as the other most distal area. The area cladogram for the *Charis gynaea* group differs from those based on birds by hypothesizing Central America as one of the most distal groups instead of one of the two most basal groups. It is not unexpected to find some differences in the topologies of these cladograms, even if hypothesizing a common vicariant history for these organisms, as palaeoclimatic and palaeogeographic events are sure to have influenced the ecology and distribution of each in different ways. Other factors, such as the methods used to construct the cladograms, the number of taxa involved, and whether each was distributed parapatrically or not, could also explain the different hypotheses in Fig. 10. For example, if the most immediate outgroup taxa for the *Charis gynaea* group are included (i.e., including sympatric species) in generating an area cladogram, then Central America additionally becomes the most basal area, as hypothesized by Bates et al. (1998).

Biology. *Charis gynaea* group species inhabit a wide variety of forest habitats from sea-level to 1700 m, although they are most frequently encountered along forest edges and in secondary growth below 1000 m. Males are encountered perching singly or in small groups close to the ground, typically from late morning to early afternoon. They rest beneath the tips of leaves with their wings outspread. Both sexes visit a variety of flowers but predominantly weedy Asteraceae. The early stages are partially known for only one species in the group, *C. barnesi*, and like those species in the closely related *cleonus* group that have been reared, the larvae are detritivorous (DeVries et al. 1994, DeVries 1997 – as *C. gynaea*). The larvae grow very slowly and have only been reared as far as the

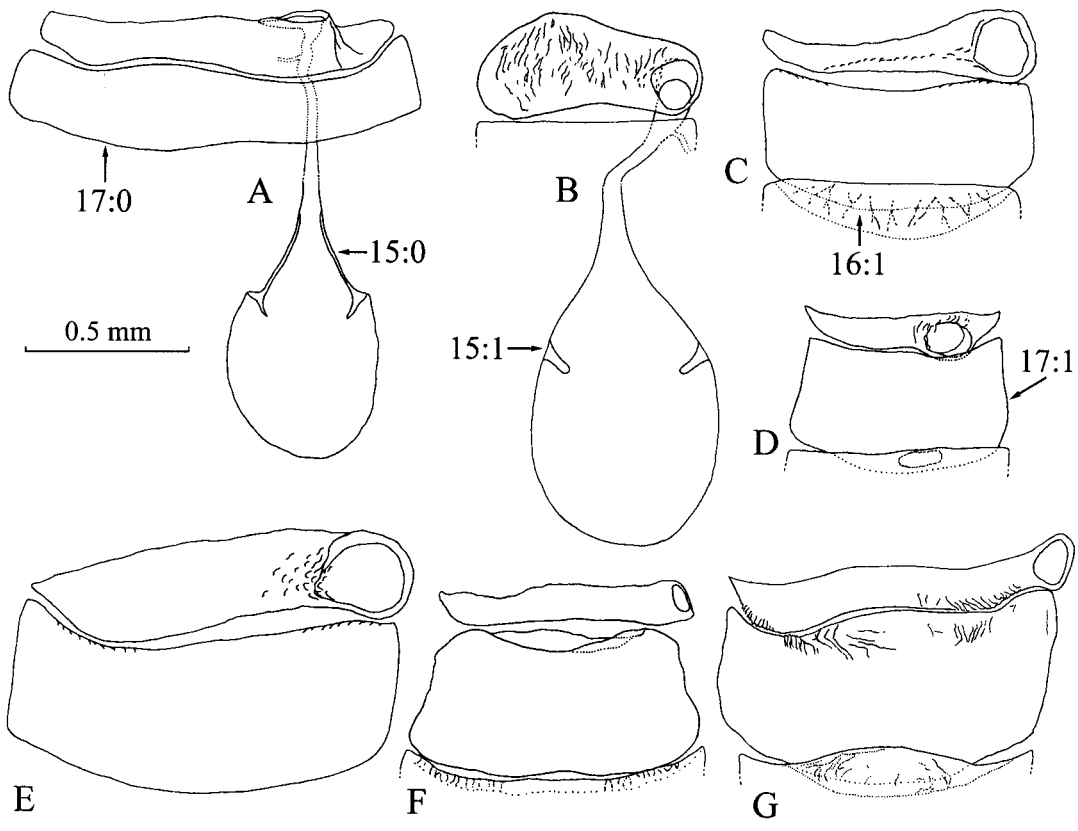

Fig. 6. Female genitalia. Only sclerotized sternites are illustrated, and because the corpus bursae and signa of all species except *C. smalli* are the same, these structures are illustrated for *C. hermodora* only. (A) *Charis smalli*, El Llano, Panama (USNM) (DH # 2000–233). (B) *C. hermodora*, Farfan, Panama (USNM) (DH # 2000–181). (C) *C. gynaea*, old Rio de Janeiro-Petrópolis rd., Brazil (RJ) (AME) (JH # USNM-347). (D) Allotype *C. gallardi*, Saint Élie, French Guiana (USNM) (JH # USNM-360). (E) Allotype *C. barnesi*, Caña, Panama (USNM) (JH # USNM-349). (F) Allotype *C. callaghani*, Pescador, Colombia (AME) (JH # USNM-345). (G) *C. zama*, Diamantino, Brazil (MG) (USNM) (JH # USNM-346).

fourth instar. The brown, densely hirsute larvae are similar to that figured by DeVries (1997) as *Charis anius.*

Charis nicolayi Hall & Harvey, new species
(Figs. 1A, 4A, and 9)

Male. Forewing length 14 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal Surface.* Forewing ground color brown; four black marks in discal cell, one at base, two at middle, one at end, one black mark at base of cell Cu1, three toward base of cell Cu2; a band of black postdiscal marks extends vertically from vein 2A to vein Cu1, shifts distally and extends diagonally inwards to vein M1, then shifts distally to cell R4+5 and proximally to cell R2; two faint and broken parallel submarginal silver lines encompass area of dark orange-brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2; fringe brown with faint white scaling at distal tips of veins Cu2, M3 and R4+5. Hindwing same as forewing except two additional black spots at base of cell Sc+R1, upper half of postdiscal band straight and fringe entirely brown. *Ventral Surface.* Forewing ground color rich dark orange-brown, anal margin gray; black markings same as dorsal surface; submarginal black spots visible only in apex, inner silver submarginal line absent, outer line reduced to a few silver scales in apex. Hindwing ground color rich dark

Table 1. Character matrix for phylogenetic analysis

					5					10					15			
Charis argyrea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charis nicolayi	0	0	0	0	1	1	?	1	0	0	0	0	1	0	?	?	?	
Charis smalli	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	
Charis hermodora	1	1	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	
Charis gynaea	1	1	0	0	0	0	1	0	1	1	0	1	0	0	1	1	1	
Charis gallardi	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	
Charis barnesi	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	1	
Charis callaghani	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	
Charis zama	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	

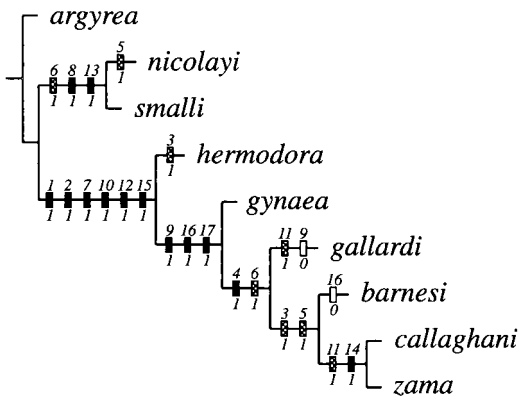

Fig. 7. The single most parsimonious cladogram generated for the *Charis gynaea* group, illustrating the distribution of characters and their states. Black bars indicate unique apomorphies, shaded bars homoplasious apomorphies, and white bars reversals.

orange-brown; black markings same as dorsal surface; silver submarginal lines absent.

Head. Labial palpi brown. Eyes brown and setose. Frons dark brown with brown scaling at margins. Antennal segments black with white scaling at base; clubs black and flattened.

Body. Dorsal and ventral surface of thorax dark brown; dorsal surface of abdomen dark brown with some dark orange-brown scaling, ventral surface pale brown. All legs brown.

Genitalia (Fig. 4A). Uncus rounded and more elongate dorsally, shallowly indented at posterior dorsal margin, tegumen and falci of average size and shape for tribe, small, deep semicircular notch in anterior margin of tegumen; vinculum elongate, narrow and posteriorly bowed in dorsal half; aedeagus long, narrow, pointed, bowed and swollen at base, tip opens broadly to right; pedicel extends from swollen base as narrow tube to form short posterior projection tipped with slightly bifurcate and dorsally medially grooved "vogelkop" containing fine acanthae, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of a short, narrow lower process extending from near base of pedicel, and a short rounded upper process joined to lower one by an elongate ribbon of sclerotized tissue and dorsally over aedeagus by a narrow and slightly posteriorly elongate sclerotized transtilla with a similarly short, triangular process inside upper process.

Female. A specimen is illustrated by DeVries (1997) (as *Chalodeta candiope*), but it was unavailable for examination.

Type Material. HOLOTYPE, ♂: PANAMA: *Chiriquí*, Potrerillos, 3600 feet, 14-II-70, S. S. Nicolay, USNM (JH # USNM-357).

PARATYPES. PANAMA: same locality data as holotype, 1♂: 29-I-66, S. S. Nicolay; 1♂: 5-II-66, G. B. Small; 1♂: 28-XII-66, G. B. Small; 1♂: 11-II-70, S. S. Nicolay; 3♂: 14-II-70, S. S. Nicolay (DH # 1989–67), all USNM. 1♂: Santa Clara, 1350 m, 9-I-77, G. B. Small, USNM. 1♂: "Chiriquí," BMNH.

Etymology. This species is named for Stan S. Nicolay, who was one of the most prolific and successful collectors of Neotropical Riodinidae in the latter half of the 20th Century and collected the bulk of the type series.

Diagnosis. *Charis nicolayi* n. sp. is most closely related to *Charis smalli* (described below). The male is considerably larger, has darker orange-brown scaling between the dorsal submarginal silver lines, a darker orange-brown ventral surface, less prominent black ventral markings, typically no silver flecks in the apex of the ventral forewing, four instead of three black markings in the forewing discal cell, and three instead of two black markings at the base of forewing cell Cu2. The male genitalia of *C. nicolayi* have a smooth instead of weakly toothed distal margin to a more rounded uncus, a slightly bifurcate tip to the pedicel, a shorter and narrower lower valve process, a considerably narrower transtilla, and a slightly shorter upper valve process of even width with a considerably longer, triangular inner process.

Biology. *C. nicolayi* is restricted to premontane cloud forest habitats between 1,100 and 1,600 m. DeVries (1997) reports the following in his *Butterflies of Costa Rica II: Riodinidae*, under the name *Chalodeta candiope* (an unrelated member of *Charis* – Hall and Harvey, unpublished data): "Encountered typically as local solitary individuals along forest edges, streams, and occasionally in light gaps. The males perch in direct sunshine on top of leaves ≈1–5 m above the ground between 0630 and 0800 hours. While perching, an individual male will frantically chase other darkly colored insects of the same size and, more often than not, return to the same perch. The females fly low to the ground along forest edges between 0900 and 1230 hours. Both sexes visit flowers of *Phoebe*, *Ocotea*,

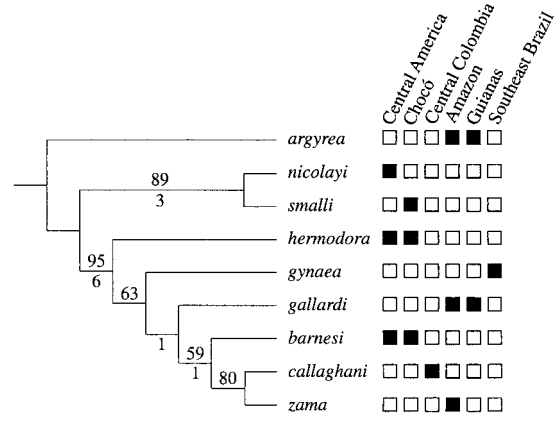

Fig. 8. The single most parsimonious cladogram generated for the *Charis gynaea* group. Estimates of branch support are given in the form of bootstrap values above branches and decay indices below branches. Black squares to the right indicate the presence of a taxon in a particular geographic region, white squares its absence.

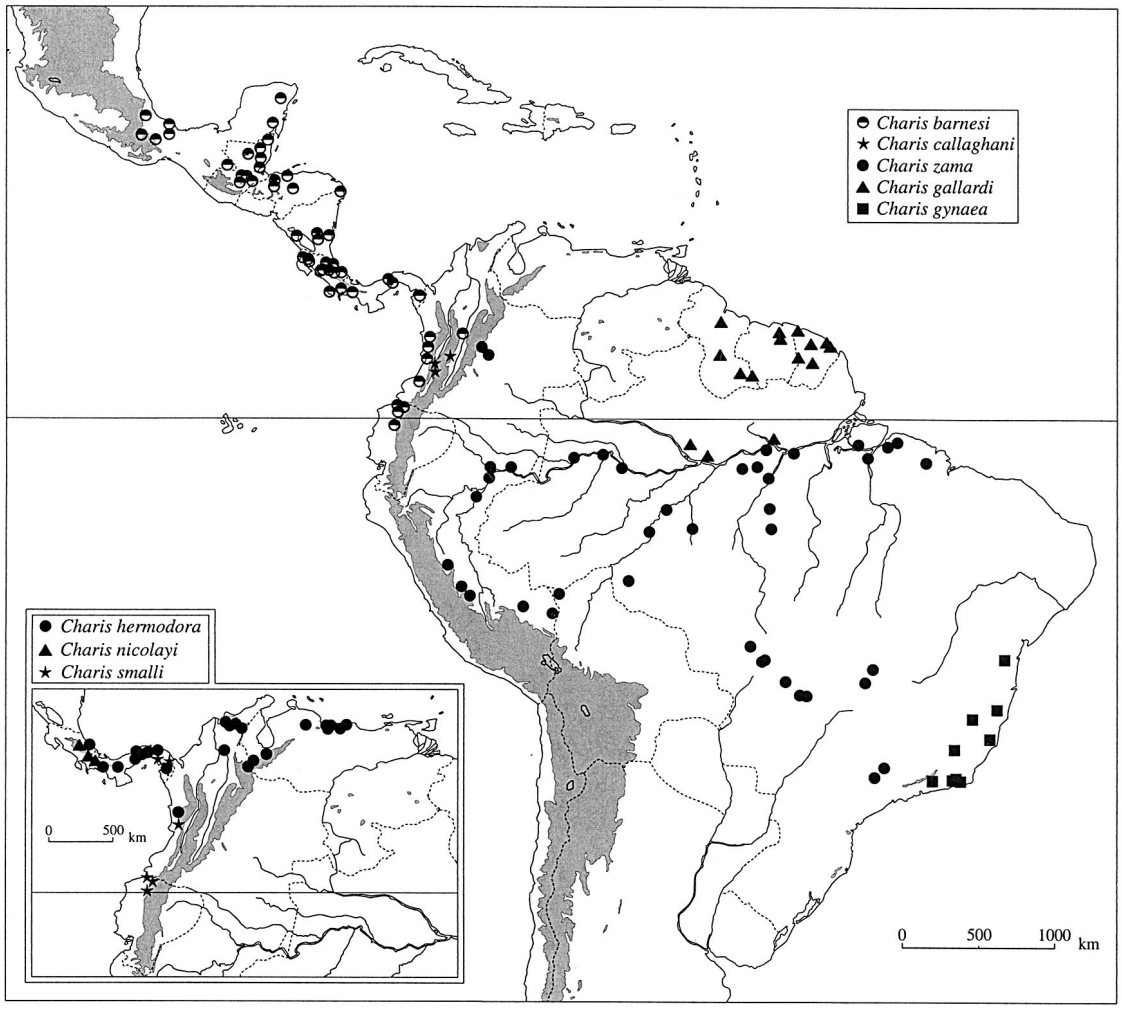

Fig. 9. Neotropic distributions of *Charis gynaea* group species.

Nectandra, *Dendopanax*, *Lantana camara*, and various weedy Asteraceae that grow along sunlit forest edges."

Distribution. *C. nicolayi* appears to be endemic to the Cordillera de Talamanca in east Costa Rica and west Panama, although it should be looked for on the west Andean slope of Colombia and Ecuador (see Fig. 9). DeVries (1997) lists the following additional locality for COSTA RICA: *San José*, LA, Montura.

Charis smalli Hall & Harvey, new species
(Figs. 1B, C, 4B, 6A, and 9)

Male. Forewing length 11 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal Surface.* Forewing ground color brown; three black marks in discal cell, one black mark at base of cell Cu1, two toward base of cell Cu2; a jagged band of black postdiscal marks extends vertically from vein 2A to vein Cu1, shifts distally and extends as a semicircle to vein M1, then shifts distally to cell R4+5 and proximally to cell R2; two parallel submarginal silver lines encompass area of orange-brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2, distal margin orange-brown; fringe entirely brown. Hindwing same as forewing except two additional black spots at base of cell Sc+R1. *Ventral Surface.* Forewing ground color rich orange-brown, anal margin gray; black markings same as dorsal surface; inner silver submarginal line reduced to a few silver scales in apex and brown line at tornus, outer line reduced to a few silver scales in apex and tornus. Hindwing ground color rich orange-brown; black markings same as dorsal surface; inner silver submarginal line replaced with faint black line, outer silver line absent.

Head. Labial palpi brown. Eyes brown and setose. Frons dark brown with brown scaling at margins. An-

Table 2. Distribution of *Charis gynaea* group species by country

Taxon	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Venezuela	Colombia	Ecuador	Peru	Bolivia	Argentina	Brazil	Paraguay	Guyana	Surinam	French Guiana
nicolayi							●	●											
smalli								●		●	●								
hermodora							●	●	●	●	?								
gynaea															●				
gallardi									?						●		●	●	●
barnesi	●	●	●	?	●	●	●	●		●	●								
callaghani										●									
zama									●	●	?	●	●	?	●	?			
Total recorded	1	1	1	0	1	1	3	4	2	5	2	1	1	0	3	0	1	1	1
Total expected	1	1	1	1	1	1	3	4	3	5	4	1	1	1	3	1	1	1	1

Solid circles represent known records and question marks represent expected records.

tennal segments black with white scaling at base; clubs black and flattened.

Body. Dorsal surface of thorax and abdomen dark brown, ventral surface pale brown. All legs brown.

Genitalia (Fig. 4B). Uncus rectangular and shallowly indented at weakly toothed posterior dorsal margin, tegumen and falci of average size and shape for tribe, small, deep semicircular notch in anterior margin of tegumen; vinculum narrow and posteriorly bowed and slightly elongate medially; aedeagus long, narrow, pointed, bowed and swollen at base, tip opens broadly to right; pedicel extends from swollen base as narrow tube to form short posterior projection tipped with a vertically rounded "vogelkop" containing fine acanthae, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of a short, triangular weakly sclerotized lower process extending from near base of pedicel, and a short spatulate-shaped upper process joined to lower one by an elongate ribbon of sclerotized tissue and dorsally over aedeagus by a posteriorly elongate sclerotized transtilla with a small rounded process inside upper process.

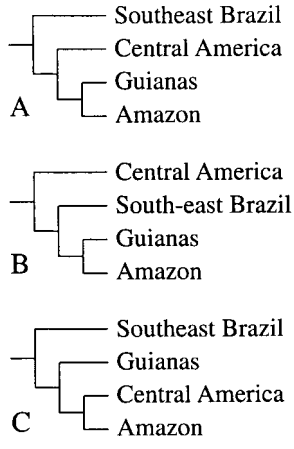

Fig. 10. Area cladograms. (A) Maximum parsimony analysis (MP) for several clades of parrots, toucans, woodpeckers, manakins and cotingas (Prum 1988; Cracraft and Prum 1988). (B) Parsimony analysis of endemicity (PAE) for all Neotropical passerine birds (Bates et al. 1998). (C) MP for the *Charis gynaea* clade (*gynaea* through *zama*) of riodinid butterflies (this study).

Female. Differs from the male in the following respects: Distal margin of forewing slightly more convex. *Dorsal Surface.* Ground color paler; fringe brown with white scaling in cell R4+5. *Ventral Surface.* Ground color paler; faint sparse black scaling between discal and postdiscal bands on both wings; inner silver submarginal line on both wings present and broken with some black scaling proximally, outer silver line present and continuous on forewing, present and continuous but faint on hindwing.

Genitalia (Fig. 6A). Corpus bursae elongate, signa elongate at corpus wall with short pointed invagination at posterior tip; ductus bursae membranous; seventh and eighth abdominal sternites narrow and heavily sclerotized, latter with ovoid ostium bursae displaced to its anterior right margin.

Type Material. HOLOTYPE, ♂: PANAMA: *Darién,* Caña, 500 m, 7-VII-83, G. B. Small, USNM (JH # USNM-68).

ALLOTYPE, ♀: ECUADOR: *Esmeraldas,* km 40 Lita-San Lorenzo Rd., El Durango, 250 m, 22-VIII-96, K. R. Willmott, JHKW.

PARATYPES. PANAMA: *Panamá,* 1♂: Bayano, 25-I-75, G. B. Small, USNM. 1♀: 6 miles N. of El Llano, 1,300 feet, 30-XII-74, G. B. Small, USNM (DH # 2000–233). *Darién,* 1♂: Cerro Pirre, Caña, 7° 56′ N, 77° 43′ W, 500 m, VII-83, G. B. Small, USNM (DH # 2000–455).

COLOMBIA: *Chocó,* 2♀: Río San Juan, ZMHU.

ECUADOR: *Esmeraldas,* 1♀: Estación Experimental La Chiquita, km 10 San Lorenzo-Lita rd., 50 m, 3-III-01, D. H. Ahrenholz, DA. *Carchi,* 1♀: near Lita, ridge to east of Río Baboso, 900 m, 6-VII-98, K. R. Willmott, JHKW (dissected). *Imbabura,* 1♀: Rumiñahui, 37 km N. Pedro Vicente Maldonado, 500 m, 9-III-01, J.P.W. Hall, JHKW.

Etymology. This species is named for the late Gordon B. Small, who, while tirelessly documenting the

butterfly fauna of Panama, collected the largest series of specimens.

Diagnosis. *Charis smalli* n. sp. is most closely related to *Charis nicolayi*. The two species are distinguished in the latter species account.

Biology. *C. smalli* appears to be associated with intact wet lowland forest habitats up to 900 m. The Ecuadorian females were encountered flying slowly along the forest edge from late morning to early afternoon.

Distribution. *C. smalli* is currently known from east Panama to west Ecuador (see Fig. 9).

Charis hermodora C. & R. Felder, 1861
(Figs. 2 A and B, 4C, 6B, and 9)

Charis hermodora C. & R. Felder, 1861. *Wien. Ent. Monats.* 5(4): 99. Type locality: Venezuela. Syntype ♂ BMNH (Examined). Syntype label data: "Vene/zuela/Dr Moritz/type," "Hermodora n.," "Hermo/dora F," "FELDER/COLL$^{N.}$" and "Type."

Identification and Taxonomy. Typical forewing length: both sexes 12 mm. Male *Charis hermodora* is most readily distinguished from the similar *C. barnesi* (sympatric), *C. gallardi*, *C. callaghani* (described below), and *C. zama* by its more compact wing shape and dark orange or reddish-brown ventral ground color which lacks any purple iridescence. Both sexes of *C. hermodora* therefore closely approximate the females of the aforementioned species, and female *C. hermodora* is difficult to distinguish externally from that of the sympatric *C. barnesi*. It is typically slightly smaller, has a slightly darker orange-brown ventral surface and a slightly more angular postdiscal line of spots on the ventral hindwing. The female genitalia differ from those of all other species in the *gynaea* group by possessing an unsclerotized seventh abdominal sternite.

Biology. *C. hermodora* occurs in wet lowland forest habitats up to 1,300 m. Nothing is known of its biology.

Distribution. *C. hermodora* ranges from Costa Rica to north Venezuela (see Fig. 9) and is sympatric with *C. smalli* and *C. barnesi* in the western portion of its range. DeVries (1997) lists Trinidad as being within the range of this species, but it is not listed by Barcant (1970) for that country, nor have we found any such specimens in collections. The following additional localities are listed by DeVries (1997) for COSTA RICA: *Limón*, Limón; and by Huntington (1932) for PANAMA: *Canal Zone*, Corozal, Paitilla Point, Fort Davis.

Material Examined. PANAMA: *Chiriquí*, Santa Cruz (JH M# USNM-340); *Veraguas*, Santa Fé, Calobre; *Colón*, Santa Rita; *Canal Zone*, Albrook Air Base, Ancón Hill, Barro Colorado Island, Cocoli, Farfan (DH M# 1989–66; F# 2000–181), Fort Clayton, Gamboa, Gatun, Madden Forest, Matachin, Paraiso, Piña, Rodman, Summit; *Panamá*, Cerro Campana, Chepo, Río Trinidad; *San Blas*, Río Armila; *Darién*, Caña, Canglon, Cerro Pirre. COLOMBIA: *Chocó*, El Tigre de Río Tamaná; *Magdalena*, Atanquez, Cincinati, El Campano, El Banco, Onaca, Pueblo Bello, Río Guachaca, Río Magdalena, San Pedro de la Sierra, Santa Marta; *César*, Manaure; *Norte de Santander*, Cúcuta. VENEZUELA: *Tachira*, 5 km N. of San Juan de Colon; *Mérida*, km 2 Lagunillas-Mérida Rd.; *Yaracuy*, Aroa; *Carabobo*, San Esteban, Puerto Cabello, Las Quiguas, Valencia; *Aragua*, 2 km N. of Ocumare de la Costa, Rancho Grande (JH M# USNM-341), Playa de Cata (9 km E. of El Playon) (JH F# USNM-348); *Distrito Federal*, Caracas; *Miranda*, 5 miles N of La Sabana, Ocumare del Tuy.

Charis gynaea (Godart, [1824])
(Figs. 2C and D, 4D, 6C and 9)

Erycina gynaea Godart, [1824]. *Ency. Méth.* 9 (Ins.) (2): 573. Type locality: Casimiro de Abreu, SE Brazil. Neotype ♂ USNM [Designated].

Identification and Taxonomy. Typical forewing length: both sexes 12 mm. Because Godart ([1824]) did not illustrate his newly described taxon *gynaea* nor indicate a precise type locality for it (only "Brazil"), and the type is unknown, the identity of this species has been subsequently somewhat uncertain. Given the large number of related species in the *Charis gynaea* group, including three species in Brazil, in the interests of nomenclatural stability, we designate a neotype. The most common depository for the types of species described by Godart is the Musée Nationale d'Histoire Naturelle, Paris, France (MNHN). However, despite thorough searching there, neither the first author nor Callaghan (1995) have been able to locate a potential syntype specimen of *gynaea*, and G. Lamas (personal communication) has not located one in any other European museum. Because the material described by Godart is believed to have been obtained by collectors in the vicinity of Rio de Janeiro in southeast Brazil (G. Lamas personal communication), we designate a male neotype in the USNM with the following label data: "Brazil, RJ, Casimiro/de Abreu (Aldeia Velha)/22° 39′S, 42° 23′ W/8 March 1995, 200–400 m/leg. Robbins & Caldas" and "Charis gynaea/NEOTYPE/det. J. Hall & D. Harvey."

Charis gynaea is readily distinguished from the remaining species of the *gynaea* clade by its rounded wing shape, pale orange-brown ventral surface without purple iridescence in males, complete outer silver submarginal line on the ventral forewing of males (also in *C. hermodora*) and entirely brown hindwing fringe (also in *C. gallardi* described below).

Biology. Nothing is known about the biology of this species.

Distribution. Due to uncertainty regarding the true identity of *C. gynaea* and the fact that the group has never been revised, this species has often been regarded as Pan Neotropical. However, the species as defined here is restricted to the lowland coastal Atlantic forest of southeast Brazil between the states of Bahia and Rio de Janeiro (see Fig. 9).

Material Examined. BRAZIL: *Bahia*, Itamaraju, Ubatã (DH M# 2000–416); *Espírito Santo*, Linhares (DH M# 2000–334; JH F# USNM-361); *Minas Gerais*,

Serra do Caraça, Teófilo Otoni (San Jacintho Valley); *Rio de Janeiro*, Rio de Janeiro, Laguna de Sacuarema, Corcovado, Casimiro de Abreu (Aldeia Velha), Parque Nacional de Itatiaiá; Petrópolis (JH M# USNM-124), old Rio de Janeiro-Petrópolis Rd. (JH F# USNM-347), km 96 Niterói-Campos Rd. (Mun. Silvia Jardin) (DH M# 2000–333), Nova Friburgo.

Charis gallardi Hall & Harvey, new species
(Figs. 2 E and F, 5A, 6D, and 9)

Male. Forewing length 11 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal Surface.* Forewing ground color brown; four faint black marks in discal cell, one at base, two at middle, one at end, one faint black mark at base of cell Cu1, three toward base of cell Cu2; two faint black postdiscal bands extend from vein 2A and curve inwards toward costa; two parallel submarginal silver lines encompass area of dark orange-brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2, dark orange-brown at distal margin; fringe brown with faint white scaling at distal tips of veins Cu1 to R4+5. Hindwing same as forewing except inner postdiscal band faint, outer postdiscal band curves diagonally outwards in anal half and vertical in upper half; fringe entirely brown. *Ventral Surface.* Forewing ground color rich dark orange-brown with faint purple iridescence, anal margin gray; black markings same as dorsal surface except inner postdiscal band absent; inner silver submarginal line absent, outer line broken and largely reduced to silver scaling in apex and tornus. Hindwing ground color rich dark orange-brown with faint purple iridescence; black markings same as dorsal surface except inner postdiscal band very faint; inner silver submarginal line brown.

Head. Labial palpi brown. Eyes brown and setose. Frons dark brown with brown scaling at margins. Antennal segments black with white scaling at base; clubs black and flattened.

Body. Dorsal surface of thorax and abdomen dark brown, ventral surface pale brown. All legs brown.

Genitalia (Fig. 5A). Uncus rounded and more elongate dorsally, shallowly indented at posterior dorsal margin, tegumen and falci of average size and shape for family, small, deep semicircular notch in anterior margin of tegumen; vinculum narrow and posteriorly bowed in dorsal half; aedeagus long, narrow, pointed, bowed and slightly swollen at base, tip opens broadly to right; pedicel extends from swollen base as narrow tube to form short posterior projection tipped with a horizontally rounded "vogelkop" containing somewhat coarse acanthae, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of a short, rounded lower process extending from near middle of pedicel, and a very small upper process joined to lower one by an elongate ribbon of sclerotized tissue and dorsally over aedeagus by an anteriorly and posteriorly elongate transtilla that is desclerotized at dorsal posterior corner and elongate and pointed at its ventral posterior corner.

Female. Differs from the male in the following respects: Distal margin of forewing more convex. *Dorsal Surface.* Ground color paler; white fringe elements larger. *Ventral Surface.* Ground color paler with no purple iridescence, distal margins of both wings paler; additional faint medial black spot in forewing discal cell, faint black scaling between discal and postdiscal bands present on both wings; outer silver submarginal line on forewing continuous.

Genitalia (Fig. 6D). Corpus bursae elongate, signa small spine-like invaginations; ductus bursae membranous; seventh and eighth abdominal sternites heavily sclerotized, latter narrow with ovoid ostium bursae displaced toward right, small patch of sclerotization within invaginated pouch along posterior margin of sixth sternite.

Type Material. HOLOTYPE, ♂: FRENCH GUIANA: *Cayenne*, camp Saint Élie, pk 15.5 on D21, 5° 16′ N, 53° 02′ W, 100 m, 16-XI-88, D. J. Harvey, USNM (JH # USNM-359).

ALLOTYPE, ♀: FRENCH GUIANA: same locality data as holotype, 12-XI-88, D. J. Harvey, USNM (JH # USNM-360).

PARATYPES. FRENCH GUIANA: *Saint Laurent du Maroni*, Saint Laurent du Maroni, 1♂: III-04, USNM; 15♂: BMNH. Saint Jean du Maroni, USNM, 1♂: III-04; 1♀: IV-04. 1♀: Riviere Maroni, VIII-04, USNM. *Cayenne*, same locality data as holotype, D. J. Harvey, USNM, 1♂, 1♀: 4-XI-88; 1♀: 5-XI-88 (DH # 2000–232); 1♂: 12-XI-88. 1♂: Montsinéry, 4° 55′ N, 52° 32′ W, 100 m, 23-XI-88, D. J. Harvey, USNM. Saül, 200–450 m, 3° 37′ N, 53° 43′ W, D. J. Harvey, USNM, 1♂: 15-XI-93; 1♀: 17-XI-93; 1♀: 22-XII-93; 1♂: 24-XII-93; following all J.-Y. Gallard, 1♂: 3-V-92; 2♂: 6-VI-92 (JH # USNM-127); 2♂: 7-V-92. 1♂: Remire, X-86, USNM.

SURINAM: *Para*, 1♂: Bersaba, 1898–9, Michael, ZMHU. *Brokopondo*, 1♂: Berg en dal, IV-1892, C. W. Ellacombe, BMNH. 1♂: "interior Surinam," VIII-1892, C. W. Ellacombe, BMNH. 1♂: "Surinam," SMTD.

GUYANA: *Upper Demerara-Berbice*, 1♂: Rockstone, IX-04, USNM (DH# 2000–417). *East Berbice-Corentyne*, 1♂: New River Triangle, Camp Jaguar, 500 feet, 6-XI-80, S. R. Steinhauser, AME (DH # 2000–338). 1♂: upper Corentyne river, VIII-35, G. A. Hudson, BMNH. *Upper Takutu-Upper Essequibo*, 1♂: Annai, H. Whitely, BMNH.

BRAZIL: *Amazonas*, km 26 on AM-010, Reserva Ducke, 2° 55′S 59° 59′ W, J. B. Sullivan & R. W. Hutchings, JBS, 1♂: 12-XII-93; 1♂: 14-XII-93. 1♂: Ipiranga, ex. coll. Le Molt, AME (DH # 2000–336). *Pará*, Obidos, M. de Mathan, BMNH, 1♂: X-XI-04; 2♂: −07.

Etymology. This species is named for Jean-Yves Gallard, who, with Christian Brévignon, has made great strides in furthering our knowledge of Guianan riodinids.

Diagnosis. *Charis gallardi* n. sp. is most similar to *C. zama* and *C. callaghani* and *C. barnesi* (described below), but it has an entirely brown hindwing fringe, more prominent submarginal black spots on the ventral forewing of males and a straighter line of postdiscal black spots on the ventral hindwing. The ventral posterior corner of the transtilla of the male genitalia

is elongate and pointed, as in *C. zama* and *C. callaghani*, but the pedicel is short, as in the Central American *C. barnesi*, the character that perhaps most unambiguously distinguishes *C. gallardi* from its parapatric Amazonian relative, *C. zama.*

Biology. Brévignon and Gallard (1998) report finding *C. gallardi* (as *C. gynaea zama*) in the understory of large forested hilltops.

Distribution. This species occurs throughout the Guianas and southward as far as the north bank of the eastern Amazon river (see Fig. 9). The following additional localities are listed by Brévignon & Gallard (1998) (as *C. gynaea zama*) for FRENCH GUIANA: *Saint Laurent du Maroni*, Maripasoula; *Cayenne*, Cacao, Montagne de Kaw.

Charis barnesi Hall & Harvey, new species
(Figs. 2 G and H, 5B, 6E, and 9)

Male. Forewing length 14 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal surface.* Forewing ground color brown; four faint black marks in discal cell, one at base, two at middle, one at end, one faint black mark at base of cell Cu1, three toward base of cell Cu2; faint black postdiscal band extends from vein 2A and curves inwards toward costa; two parallel submarginal silver lines encompass area of paler brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2; fringe brown with white scaling at distal tips of veins Cu1 to R4+5. Hindwing same as forewing except two additional black spots at base of cell Sc+R1. *Ventral Surface.* Forewing ground color dark orange-brown with iridescent purple, anal margin gray-brown; black markings same as dorsal surface except submarginal spots reduced to apex and tornus; inner silver submarginal line absent, outer line reduced to silver scaling in apex and tornus. Hindwing ground color darker orange-brown with faint purple iridescence, distal margin brown; black markings same as dorsal surface; inner silver submarginal line absent.

Head. Labial palpi brown. Eyes brown and setose. Frons dark brown with brown scaling at margins. Antennal segments black with white scaling at base; clubs black and flattened.

Body. Dorsal surface of thorax and abdomen dark brown, ventral surface brown. All legs brown.

Genitalia (Fig. 5B). Uncus rounded and more elongate dorsally, shallowly indented at posterior dorsal margin, tegumen and falci of average size and shape for family, small, deep semicircular notch in anterior margin of tegumen; vinculum elongate, narrow and posteriorly bowed in dorsal half; aedeagus long, narrow, pointed, bowed and slightly swollen at base, tip opens broadly to right, broadens sharply on right-hand side before tip; pedicel extends from swollen base as narrow tube to form short posterior projection tipped with a horizontally rounded "vogelkop" containing somewhat coarse acanthae, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of a short, rounded lower process extending from near middle of pedicel, and a very small upper process joined to lower one by an elongate ribbon of sclerotized tissue and dorsally over aedeagus by an anteriorly and posteriorly elongate transtilla that is desclerotized at dorsal posterior corner with a rounded ventral posterior corner.

Female. Differs from the male in the following respects: Distal margin of forewing more convex. *Dorsal Surface.* Ground color paler; prominent brown scaling between discal and postdiscal bands, orange-brown between submarginal silver lines paler, pale orange-brown at distal margins of both wings. *Ventral Surface.* Ground color paler with no purple iridescence, distal margins of both wings even paler; prominent brown scaling between discal and postdiscal bands; inner silver submarginal line absent on both wings, outer silver line present on both wings.

Genitalia (Fig. 6E). Corpus bursae elongate, signa small spine-like invaginations; ductus bursae membranous; seventh and eighth abdominal sternites heavily sclerotized, latter narrow with ovoid ostium bursae displaced toward right.

Type Material. HOLOTYPE, ♂: COSTA RICA: *Limón*, Guapiles, 850 feet, 1-III-07, coll. W. Schaus, USNM (JH # USNM-358).

ALLOTYPE, ♀: PANAMA: *Darién*, Caña, 1,000 m, 12-VI-83, G. B. Small, USNM (JH # USNM-349).

PARATYPES. MEXICO: *Veracruz*, Santa Rosa, USNM, coll. W. Schaus, 1♂: I-06; 2♂: V-06 (DH # 2000–401); 1♂, 1♀: VIII-06. 1♂: Córdoba, 13-VIII-64, P. J. Spangler, USNM. 1♂: Catemaco, 23-IX-72, USNM. *Oaxaca*, 1♂: Valle Nacional, 26-VI-66, A. B. Lau, USNM. *Yucatán*, 2♂: X-can, E. C. Welling, USNM, 1♂: 18-VII-59; 1♂: 13-VI-62. *Quintana Roo*, 1♂: Bac-halal, 28-X-58, E. C. Welling, USNM.

BELIZE: *Cayo*, Camp Sibun, 200 m, E. C. Welling, USNM, 1♀: 14-XI-58; 1♂: 3-VII-60 (DH # 2000–402); *Orange Walk*, Río Bravo Conservation Area, J. A. Shuey, JS, 1♀: 16-VII-96; 1♂: 4-IX-95; 1♂: 6-IX-95.

GUATEMALA: *Alta Verapaz*, 1♂: San Juan, Champion, BMNH. 1♂: Lanquin, Champion, BMNH. 1♂: Cahabón, Champion, BMNH. *Baja Verapaz*, 2♂: Panimá, Champion, BMNH. *El Petén*, 1♀: Tikal, 2-IX-72, G. F. & S. Hevel, USNM. *Izabal*, Cayuga, USNM, 1♀: II; 2♂: IV; 2♀: V (DH # 2000–231); 1♂: VII, all coll. of Schaus & Barnes; 1♂, 1♀: coll. of E. T. Owen.

HONDURAS: *Atlantida*, 1♀: 18 km W. of La Ceiba, 2-VI-79, R. D. Lehman, USNM. *Cortés*, San Pedro Sula, Bella Vista, R. D. Lehman, USNM, 1♂, 1♀: 12-II-72; 1♂, 1♀: 8-IV-73. 1♂: El Jaral, 600 m, 21-IX-21, J. Lienhart, BMNH. *Olancho*, 1♂: Portillo, coll. W. Schaus, USNM.

NICARAGUA: *Managua*, 1♂: 13 km S. of Managua, 31-VII-76, R. A. Anderson, JBS (DH # 2000–403). *Zelaya*, 1♂: Cabo Gracias, I-05, M. G. Palmer, BMNH. 1♂: Yolaina, 25-VIII-76, R. A. Anderson, JBS. 1♂: Volcan Mombacho, 18-IX-1976, R. A. Anderson, JBS. 2♂: Rama, 6-III-76, R. A. Anderson, JBS. 5♂: Bluefields, 9-XII-75, R. A. Anderson, JBS.

COSTA RICA: *Guanacaste*, 5 km NW of Cañas, Hacienda La Pacifica, 50 m, P. Opler, USNM, 1♂: 15-I-71; 1♀: 30-I-71; 1♂: 27-VIII-78; 1♂: 3-XII-70. 1♂:

4 km N.W. of Bagaces, 100 m, 18-XI-70, P. Opler, USNM. 1♂: 8 km N.W. of Bagaces, 100 m, 21-X-71, P. Opler, USNM. *Alajuela*, 1♂: 2 km N. of Bijuaga, 14–15-XI-91, A. S. Menke, USNM. 1♂: 6 km W. of Atenas, 2-V-71, P. Opler, USNM. San Mateo, coll. W. Schaus, USNM, 1♀: IX; 1♂: X. *Cartago*, 4 km S.E. of Turrialba, 550 m, W. A. Haber, USNM, 1♀: 3-III-74; 1♂: 13-III-74; 1♀: 19-III-74. Turrialba USNM, 1♂: 25-V-51, O. L. Cartwright; 1♂: 12-VII-65, G. B. Small; 1♀: V. 1♀: Tres Rios, 5,000 feet, XII-06, coll. W. Schaus, USNM. 1♀: Juan Viñas, V, USNM. *Heredia*, Finca La Selva, 75 m, P. Opler, USNM, 1♂: 18-V-72; 1♂, 3♀: 4-VIII-71; 1♂: 24-XI-71. *Limón*, Limón, coll. W. Schaus, USNM, 1♂: I-07; 1♀: II-07. 2♂, 1♀: La Florida, 500 feet, III-07, coll. W. Schaus, USNM (DH # 2000–404). Guapiles, coll. W. Schaus, USNM, 1♀: II-04; 1♂: V-07. 1♀: Banana river, III-07, coll. W. Schaus, USNM. 1♀: Zent, II-07, coll. W. Schaus, USNM. *Puntarenas*, 4♂: 7 km S. of Río Naranjo, 19-III-71, P. Opler, USNM. 1♀: Miramar, 9-I-74, W. A. Haber, USNM.

PANAMA: *Chiriquí*, 1♂: Chiriquicito, coll. W. Schaus, USNM (DH # 2000–406). 1♂: David, Champion, BMNH. *Colón*, 1♀: Santa Rita, 1,000 feet, III-69, G. B. Small, USNM. *Canal Zone*, 1♂: Fort Sherman, 12-I-73, G. B. Small, USNM (DH # 2000–405). 1♂: Piña, 2-II-73, G. B. Small, USNM. *Darién*, Caña, 400–1,000 m, G. B. Small, USNM, 1♂: 6-I-84; 1♀: 10-I-84; 1♂: 14-I-84 (DH # 2000–408); 1♂: 18-III-83; 1♂: 20-V-83; 1♂: 18-VI-81; 1♂: 17-VII-81 (DH # 2000–407); 1♂: 18-VII-81; 1♂: 3-VIII-81; 2♂: 29-XII-83.

COLOMBIA: *Caldas*, Victoria, 2,400 feet, S. S. Nicolay, USNM, 3♂, 1♀: 17-I-72 (DH M# 2000–409); 1♂: 6-XI-65. *Valle de Cauca*, 2♂: Bajo Calima, 300 feet, 20-I-88, J. B. Sullivan, JBS (DH # 2000–456, 486). *Cauca*, 1♂: Río Micay, W. Hopp, ZMHU. *Chocó*, 3♂: El Tigre, Río Tamaná, 3,200 feet, II-09, G. M. Palmer, BMNH. 1♂, 1♀: San Pablo, Río San Juan, Ex. coll. Staudinger, BMNH.

ECUADOR: *Esmeraldas*, 1♂: Cachabé, I-97, Rosenberg, BMNH. 1♂: Río San Miguel, San Miguel, 100 m, 9–11-VI-94, J. P. W. Hall, JHKW. 1♂: km 16 Lita-San Lorenzo Rd., El Encanto, 800 m, 1-XII-96, K. R. Willmott, JHKW (dissected). Km 40 Lita-San Lorenzo Rd., El Durango, 300 m, K. R. Willmott, JHKW, 2♂: VI-00; 1♂, 1♀: 2-VII-98. Km 44 Lita-San Lorenzo Rd., La Punta, 300 m, K. R. Willmott, JHKW, 1♀: 7-VII-94; 1♀: 24-VIII-96. 1♀: km 46 Lita-San Lorenzo rd., Mina Vieja, 250 m, K. R. Willmott, JHKW. *Pichincha*, 1♀: Tinalandia, Río Tanti, 750 m, 2–3-VIII-93, J. P. W. Hall, JHKW.

Etymology. This species is named for Jack Barnes, who, with his collecting companion William Schaus, made a considerable contribution to our knowledge of Central American riodinids.

Diagnosis. *C. barnesi* n. sp. is most similar to *C. zama* and *C. callaghani* (described below). Males typically have a ventral hindwing that is darker than the forewing (although specimens from Mexico to Honduras have a more uniform ventral ground color), a rounded line of postdiscal black spots on the ventral hindwing and silver flecks in the apex and tornus of the ventral forewing as in *C. callaghani*, but unlike *C. zama.* The male genitalia of *C. barnesi* have a considerably shorter pedicel than either *C. zama* or *C. callaghani*, a shorter, rounded upper valve process and a rounded instead of elongate and pointed ventral posterior corner to the transtilla. Females must be identified by comparison with sympatric males and locality.

Biology. *C. barnesi* is perhaps the most common member of the *gynaea* group and occurs from sea level to ≈1,000 m. Both sexes are encountered along forest edges, streamsides, and in secondary growth habitats, and occasionally feed on flowers of the Asteraceae. Males perch singly or in small groups from ≈1100 to 1400 hours.

DeVries et al. (1994) report that the larvae feed on dead leaves (as *C. gynaea*). DeVries (1997) provides the following description of the early stages (as *C. gynaea*): "*Egg*—lozenge-shaped, pale green deposited on the confluence of the veins on dead leaves. *Early instar caterpillars*—very densely covered in long brown setae. The caterpillars feed on the epidermis of dead leaves, and they may be found wandering across the forest floor." Due to the difficulties in raising detritivorous larvae, the mature larva and pupa of *C. barnesi* are unknown.

Distribution. *C. barnesi* is distributed from central Mexico to west Ecuador (see Fig. 9). The following additional localities are listed by Raguso and Llorente (1991) (as *Charmona gynaea zama*) for MEXICO: *Veracruz*, Laguna Encantada; by Luis et al. (1991) (as *Charmona gynaea zama*) for MEXICO: *Oaxaca*, Soyolapan El Bajo; by de la Maza and de la Maza (1993) for MEXICO: *Chiapas*, No specific locality; by Meerman (1999) for BELIZE: districts of Corozal and Toledo; and by DeVries (1997) for COSTA RICA: *Guanacaste*, Santa Rosa, Tilaran; *Alajuela*, Cariblanco, San Gabriel, Dos Rios; *Cartago*, Tuis; *San José*, Carillo, El Rodeo; *Heredia*, Chilamate, Tirimbina; *Puntarenas*, San Vito, Piedras Blancas, Sirena, San Luis at Río Guacimal.

Charis callaghani Hall & Harvey, new species
(Figs. 3 A and B, 5C, 6F, and 9)

Male. Forewing length 14 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal Surface.* Forewing ground color brown; four faint black marks in discal cell, one at base, two at middle, one at end, one faint black mark at base of cell Cu1, three toward base of cell Cu2; two faint black postdiscal bands extend from vein 2A and curve inwards toward costa; two parallel submarginal silver lines encompass area of dark orange-brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2; fringe brown with white scaling at distal tips of veins Cu1 to R4+5. Hindwing same as forewing except two additional black spots at base of cell Sc+R1. *Ventral Surface.* Forewing ground color dark iridescent purple, anal margin gray-brown; black markings same as dorsal surface except markings between discal and postdiscal bands absent and submarginal spots reduced to apex and tornus; inner silver submarginal line absent, outer line reduced to silver scaling in apex and tornus.

Hindwing ground color dark iridescent purple, submargin and margin orange-brown; black markings same as dorsal surface; inner silver submarginal line absent.

Head. Labial palpi brown. Eyes brown and setose. Frons dark brown with brown scaling at margins. Antennal segments black with white scaling at base; clubs black and flattened.

Body. Dorsal surface of thorax and abdomen dark brown, ventral surface brown. All legs brown.

Genitalia (Fig. 5C). Uncus rounded and more elongate dorsally, shallowly indented at posterior dorsal margin, tegumen and falci of average size and shape for family, small, deep semicircular notch in anterior margin of tegumen; vinculum elongate, narrow and posteriorly bowed in dorsal half; aedeagus long, narrow, pointed, bowed and slightly swollen at base, tip opens broadly to right, broadens sharply on right-hand side before tip; pedicel extends from swollen base as narrow tube to form long posterior projection tipped with a horizontally rounded "vogelkop" containing somewhat coarse acanthae, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of a long, rounded lower process extending from near middle of pedicel, and a very small upper process joined to lower one by an elongate ribbon of sclerotized tissue and dorsally over aedeagus by an anteriorly and posteriorly elongate transtilla that is desclerotized at dorsal posterior corner with an elongate and pointed ventral posterior corner.

Female. Differs from the male in the following respects: Distal margin of forewing more convex. *Dorsal Surface.* Ground color paler; orange-brown between submarginal silver lines paler, pale orange-brown at distal margins of both wings. *Ventral Surface.* Ground color paler with no purple iridescence, distal margins of both wings even paler; faint brown scaling between discal and postdiscal bands; inner silver submarginal line absent on both wings, outer silver line present on both wings.

Genitalia (Fig. 6 F). Corpus bursae elongate, signa small spine-like invaginations; ductus bursae membranous; seventh and eighth abdominal sternites heavily sclerotized, latter narrow with ovoid ostium bursae displaced toward right, area of sclerotization within invaginated pouch along posterior margin of sixth sternite.

Type Material. HOLOTYPE, ♂: COLOMBIA: *Cauca,* Pescador, 1450 m, 20-I-74, S. R. & L. M. Steinhauser, AME (DH # 2000–340).

ALLOTYPE, ♀: COLOMBIA: *Cauca,* Pescador, 1,450 m, 8-XI-75, S. R. & L. M. Steinhauser, AME (JH # USNM-345).

PARATYPES. COLOMBIA: *Valle de Cauca,* 1♂: Pance, 4,000 feet, 26-I-88, J. B. Sullivan, JBS. Cali, 4,000 feet, J. B. Sullivan, JBS, 2♂: 9-I-92 (DH # 2000–489); 1♂: 30-I-89. 2♂: near Cali, Pico de Aguila, 1,700 m, 26-I-87, J. B. Sullivan, JBS (DH # 2000–488). 2♂: near Cali, El Saladito, 1,700 m, 23-I- 87, J. B. Sullivan, JBS (DH # 2000–487). *Tolima,* 1♂: Mina Vieja Area, Río Frio, Payande, 950 m, 24-III-74, S. R. & L. M. Steinhauser, AME (DH # 2000–341).

Etymology. This species is named for Curtis J. Callaghan, who has avidly collected riodinids and studied their biology throughout the Neotropics and particularly enhanced our knowledge of the Colombian fauna.

Diagnosis. *C. callaghani* n. sp. is most similar to *C. zama* and *C. barnesi,* which replace it in east Colombia and the lower central Colombian valleys and Chocó, respectively, and shares a variety of characters in common with each. *C. callaghani* is consistently the largest of the three species, and males have a darker uniform iridescent purple ventral surface, with a rounded line of postdiscal black spots on the ventral hindwing and silver flecks in the apex and tornus of the ventral forewing as in *C. barnesi,* but a long pedicel to the male genitalia and a long and pointed ventral posterior corner to the transtilla as in *C. zama.* Females must be identified by comparison with sympatric males and locality.

Biology. Nothing is known about the biology of this species, although it appears to be restricted to premontane cloud forest habitats between 950 and 1,700 m. Its close relatives *C. zama* and *C. barnesi* are confined to lowland forest.

Distribution. *C. callaghani* appears to be endemic to the upper Cauca and Magdalena valleys of central Colombia (see Fig. 9). Another *Charis* species similarly endemic to this region is *C. candiope.*

Charis zama Bates, 1868 stat. rev.
(Figs. 3 C and D, 5D, 6G, and 9)

Charis zama Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 392. Type locality: Amazon. Lectotype ♂ BMNH (Designated).

Identification and Taxonomy. Typical forewing length: both sexes 12.5 mm. This taxon was described as a full species by Bates (1868), but was treated as a subspecies of *Charis gynaea* by Stichel (1910, 1930–1931) and most subsequent authors (d'Abrera 1994, Bridges 1994). Although *zama* has occasionally been accorded species status in recent faunistic works (e.g., Callaghan 1985), its taxonomic status has never been critically assessed. We here return it to specific rank. It is actually quite distinct from *C. gynaea,* as outlined in that species account, and is most similar to and closely related to *C. callaghani* and *C. barnesi,* which replace *C. zama* west of the Andes. *C. zama* is typically smaller, males have a paler ventral surface of a uniform shade, typically no silver submarginal markings on the ventral forewing and a straighter line of postdiscal black spots on the ventral hindwing. The pedicel of the male genitalia is similar in length to that of *C. callaghani,* but considerably longer than that of *C. barnesi,* and the ventral posterior margin of the transtilla is elongate and pointed, also as in *C. callaghani.* Females must be identified by comparison with sympatric males and locality.

Since Bates (1868) described *zama* stating the type locality to be "the Amazons, and[ellipsis]other parts of Tropical America," it is necessary to designate a

lectotype to fix the type locality. We therefore designate an Amazonian male syntype in the BMNH as a lectotype, which bears the following labels: "B.C.A. Lep. Rhop./Charis/zama,/Bates/Godman-Salvin/Coll. 1914.–5.," "Tapajos,/Amazons./H.W. Bates," "M/Tapajos," "M" and "zama."

Biology. Nothing is known about the biology of this species.

Distribution. *C. zama* has the broadest range of any species in the *gynaea* group, occurring from Venezuela to Bolivia, throughout the Amazon basin (except in the northeast region where *C. gallardi* occurs) and as far south as São Paulo state in southeast Brazil (see Fig. 9). The following additional localities are listed by Huntington (1933) (as *C. gynaea zama*) for VENEZUELA: *Amazonas*, Mount Duida; and by Brown and Mielke (1967) (as *Charmona gynaea zama*) for BRAZIL: *Distrito Federal*, Sobradinho; *Goiás*, Vianópolis.

Material Examined. COLOMBIA: *Boyaca*, Muzo (DH M# 2000–339); *Meta*, San Martín. PERU: *Loreto*, Río Sucusari, Explornapo-ACEER, Iquitos (Río Cachiyacu), Río Ucayali, Pebas, Yahuas Territory; *Huánuco*, Tingo Maria; *Pasco*, Río Pachitea; *Junín*, Río Paucartambo; *Madre de Dios*, Parque Nacional Manu (Pakitza), 50 km W.S.W. of Puerto Maldonado. BOLIVIA: *Pando*, El Porvenir. BRAZIL: *Amazonas*, Tonantins, Fonte Boa, Tefé (DH M# 2000–413), Humaitá, Manicoré, Beneficiente (Rio Aripuanã) (DH M# 2000–414), Maués, Massauari; *Rondônia*, vicinity of Cacaulândia; *Mato Grosso*, Diamantino (Alto Rio Arinos) (JH F# USNM-346), Chapada (DH M# 2000–413), Cuiabá, Melguira, Buriti; *Pará*, Río Tapajós, Itaituba, km 1,270 Cuiabá-Santarém highway (DH M# 2000–412), km 1,666 Cuiabá-Santarém highway, Juruti, Mujo, Santarém, Breves, Cametá, Belém (DH M# 2000–337), Mosqueiro, Igarapé-Açu; *Goiás*, km 123 Jataí-Santa Rita do Araguaia rd. (Mineiros) (DH M# 2000–441), km 163 Jataí-Santa Rita do Araguaia rd.; *Maranhão*, Montes Aureos; *Distrito Federal*, Parque do Gama; *São Paulo*, Rio Claro (DH M# 2000–415), Casa Branca.

Acknowledgments

We thank the following for access to riodinid collections: P. Ackery (BMNH), W. Mey (ZMHU), L. and J. Miller (AME), W. Nässig (SMF), M. Nuss (SMTD) and J. Pierre (MNHN); and C. Callaghan, J. B. Sullivan and J. Shuey for the loan of *gynaea* group specimens from their private collections. The costs of fieldwork and museum research for J.P.W.H. during 1993–1996 were contributed to by Oxford and Cambridge Universities, The Royal Entomological Society, Sigma Xi and Equafor, and during 1997–2000 covered by The National Geographic Society (Research and Exploration Grant #5751–96) and a Smithsonian Postdoctoral Fellowship. J.P.W.H. thanks the Pontificia Universidad Católica, the Museo Nacional de Ciencias Naturales and INEFAN, in Quito, for arranging the necessary permits for research in Ecuador.

References Cited

Barcant, M. 1970. Butterflies of Trinadad & Tobago. Collins, London.

Bates, H. W. 1868. A catalogue of Erycinidae, a family of diurnal Lepidoptera. J. Linn. Soc. Lond. Zool. 9: 373–459.

Bates, J. M., S. J. Hackett, and J. Cracraft. 1998. Area-relationships in the Neotropical lowlands: an hypothesis based on raw distributions of Passerine birds. J. Biogeogr. 25: 783–793.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bremer, K. 1994. Branch support and tree stability. Cladistics 1: 295–304.

Brévignon, C., and J.-Y. Gallard. 1998. Inventaire des Riodinidae de Guyane Française III. Riodininae: Riodinini. Description de nouveaux taxa. (Lepidoptera). Lambillionea 98(1): 7–24.

Bridges, C. A. 1994. Catalogue of the Family-Group, Genus-Group and Species-Group Names of the Riodinidae and Lycaenidae (Lepidoptera) of the World. C. Bridges, Urbana, IL.

Brown, K. S., Jr., and O.H.H. Mielke. 1967. Lepidoptera of the central Brazil plateau. I. Preliminary list of Rhopalocera (continued): Lycaenidae, Pieridae, Papilionidae, Hesperiidae. J. Lepid. Soc. 21(3): 145–168.

Callaghan, C. J. 1985. Notes on the zoogeographic distribution of butterflies in the subfamily Riodininae in Colombia. J. Res. Lepid. Suppl. 1: 51–69.

Callaghan, C. J. 1995. Les types des Riodinidae du muséum national d'histoire naturelle de Paris (Lepidoptera, Rhopalocera). Bull. Soc. Entomol. Fr. 100(2): 153–155.

Comstock, J. H., and J. G. Needham. 1918. The wings of Insects. Am. Nat. 32: 231–257.

Cracraft, J., and R. O. Prum. 1988. Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. Evolution 42(3): 603–620.

d'Abrera, B. 1994. Butterflies of the Neotropical Region, part VI. Riodinidae. Hill House, Victoria, Australia.

DeVries, P. J. 1997. The Butterflies of Costa Rica and their Natural History, vol. II. Riodinidae. Princeton University Press, Princeton, NJ.

DeVries, P. J., I. A. Chacón, and D. Murray. 1994. Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera). J. Res. Lepid. 31(1/2): 103–126.

Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. Bull. Br. Mus. Nat. Hist. (Entomol.) 28: 373–506.

Eriksson, T. 1998. AUTODECAY, version 4.0. Computer program distributed by the author. Department of Botany, Stockholm University, Stockholm.

Felsenstein, J. F. 1985. Confidence limits on phylogenies: an approach using bootstrap. Evolution 39: 783–791.

Godart, J. B. 1824. *In* P. A. Latreille and J. B. Godart [eds.], Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire Naturelle des Crustacés, des Arachnides et des Insectes. Veuve Agasse, Paris. Pp. 329–828.

Godman, F. D. 1903. Notes on some Central and South American Erycinidae, with descriptions of new species. Trans. Entomol. Soc. Lond. 1903(4): 529–550.

Harvey, D. J. 1987. The Higher Classification of the Riodinidae (Lepidoptera). Ph.D. dissertation, University of Texas, Austin.

Harvey, D. J., and J.P.W. Hall. 2001. Phylogenetic revision of the *Charis cleonus* complex (Lepidoptera: Riodinidae). Syst. Entomol. 26 (in press).

Hemming, A. F. 1967. The generic names of the butterflies and their type species (Lepidoptera: Rhopalocera). Bull. Br. Mus. Nat. Hist. (Entomol.) Suppl. 9: 1–509.

Huntington, E. I. 1932. A list of the Rhopalocera of Barro Colorado Island, Canal Zone, Panama, with descriptions of two new species of Theclinae. Bull. Am. Mus. Nat. Hist. 63(3): 191–230.

Huntington, E. I. 1933. Erycinidae and Lycaenidae (Lepidoptera, Rhopalocera) from the regions of Mt. Roraima and Mt. Duida. Am. Mus. Novit. 611: 1–5.

Klots, A. B. 1956. Lepidoptera, pp. 97–110. *In* S. L. Tuxen [ed.], Taxonomists' glossary of genitalia in insects. Munksgaard, Copenhagen, Denmark.

Luis, A. M., I. F. Vargas, and J. E. Llorente. 1991. Lepidopterofauna de Oaxaca I: distribución y fenología de los Papilionoidea de la Sierra de Juárez. Publ. Espec. Mus. Zool. 3: 1–119.

Maddison, W. P., and D. R. Maddison. 1995. MacClade: analysis of phylogeny and character evolution, version 3:05. Sinauer, Sunderland, MA.

Maza, R. G., de la, and J. de la Maza. 1993. Mariposas de Chiapas. Gobierno del Estado de Chiapas, Mexico.

Meerman, J. 1999. Lepidoptera of Belize.1. Butterflies. 2. Emperor moths and hawk moths. Trop. Lepid. 10(suppl. 1): 1–61.

Prum, R. O. 1988. Historical relationships among avian forest areas of endemism in the Neotropics, pp. 2562–2568. *In* H. Ouellet [ed.], Acta XIX Congressus Internationalis Ornithologici. International Ornithological Congress, Ottawa.

Raguso, R. A., and J. E. Llorente. 1991. The butterflies (Lepidoptera) of the Tuxtlas Mts., Veracruz, Mexico, revisited: species richness and habitat disturbance. J. Res. Lepid. 29(1/2): 105–133.

Scudder, S. H. 1875. Historical sketch of the generic names proposed for butterflies. Proc. Am. Acad. Arts Sci. 10: 91–293.

Stichel, H.F.E J. 1910. Lepidoptera Rhopalocera. Fam. Riodinidae, pp. 1–238. *In* J. Wytsman [ed.], Genera insectorum112A. Wytsman, Brussels.

Stichel, H.F.E.J. 1930–1931. Riodinidae, pp. 1–795. *In* E. Strand [ed.], Lepidopterorum catalogus. W. Junk, Berlin.

Swofford, D. L. 2000. PAUP: phylogenetic analysis using parsimony (and other methods), version 4:0b4a. Sinauer, Sunderland, MA.

Received for publication 01 November 2000; accepted 1 May 2001.

Appendix 1. Characters Used in Phylogenetic Analysis

Dorsal Wing Pattern (Figs. 1–3).

1. *Broken dark scaling between discal and postdiscal bands in male:* absent (0); present (1).
2. *Forewing fringe with white elements:* only in a few cells (0); in every cell (1).
3. *Hindwing fringe:* entirely brown (0); brown with white elements in variable number of cells (1).

Ventral Wing Pattern (Figs. 1–3).

4. *Iridescent purple in male:* absent (0); present (1).
5. *Submarginal black spots on forewing:* present (0); typically absent or reduced to apex and tornus (1).
6. *Forewing outer silver submarginal line in male:* present (0); absent or reduced to apical or tornal flecks (1).
7. *Forewing inner silver submarginal line in female:* present (0); absent (1).
8. *Hindwing outer silver submarginal line in male:* present (0); absent (1).

Male Genitalia (Figs. 4–5).

9. *Lateral flange towards tip of aedeagus:* absent (0); present (1) (Fig. 5D).
10. *Dorsal posterior corner of transtilla:* sclerotized (0) (e.g., Fig. 4B); unsclerotized (1) (e.g., Fig. 4D).
11. *Ventral posterior corner of transtilla:* short and rounded (0) (e.g., Fig. 5B); elongate and pointed (1) (e.g., Fig. 5A).
12. *Outer upper valve process:* elongate, extending posterior to medial transtilla tip (0) (e.g., Fig. 4A); small, shorter than medial transtilla tip (1) (e.g., Fig. 4C).
13. *Inner upper valve process:* absent (0); present (1) (e.g., Fig. 4A).
14. *Pedicel:* short, < 0.8 mm (0) (e.g., Fig. 5B); long, > 1 mm (1) (e.g., Fig. 5C).

Female Genitalia (Fig. 6).

15. *Signa at corpus wall:* elongate (0) (Fig. 6A); short (1) (Fig. 6B).
16. *Sixth abdominal sternite:* entirely unsclerotized (0); sclerotized only within a posterior invagination (1) (e.g., Fig. 6C).
17. *Seventh abdominal sternite:* approximately same length as eighth abdominal sternite (0) (e.g., Fig. 6A); at least twice length of eighth abdominal sternite (1) (e.g., Fig. 6D).