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Phylogenetic revision of the *Charis cleonus* complex (Lepidoptera: Riodinidae)

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Abstract. A revision of the *Charis cleonus* group of Neotropical riodinid butterflies is presented, including discussions on the taxonomy, biogeography and biology of its species, and illustrations of the adults and male and female genitalia (where known) of all taxa. We recognize twenty-two species, including nineteen new species: *C. ariquemes* sp.n., *C. brasilia* sp.n., *C. breves* sp.n., *C. cacaulandia* sp.n., *C. cuiaba* sp.n., *C. humaita* sp.n., *C. ipiranga* sp.n., *C. iquitos* sp.n., *C. ma* sp.n., *C. manicore* sp.n., *C. manu* sp.n., *C. matic* sp.n., *C. maues* sp.n., *C. negro* sp.n., *C. palcazu* sp.n., *C. rocana* sp.n., *C. santarem* sp.n., *C. tapajos* sp.n and *C. tefe* sp.n. A cladistic analysis using thirty-six characters of male and female genitalia and external facies generated a single most parsimonious cladogram highlighting the existence of two clades, the *major* and *cleonus* subgroups. As each species largely occupies a parapatric range, this cladogram provides the opportunity to reassess historical relationships among areas of endemism in the Amazon basin.

Introduction

The riodinid genus *Charis* Hübner is a medium-sized group of small, inconspicuous butterflies in tribe Riodinini (*sensu* Harvey, 1987) that are common in primary and secondary growth habitats throughout the Neotropics. The genus has had a confused nomenclatural and systematic history. Stichel (1910, 1930) treated these butterflies in *Charmona* Stichel (later emended by Strand, 1932, to *Charmonana*) because he mistakenly regarded *gyas* Cramer (the type species of *Sarota* Westwood) as the type species of *Charis* instead of *anius* Cramer, an error finally corrected by Hemming (1967). *Charis* species have often been confused with members of *Calephelis* Grote & Robinson and *Chalodeta* Stichel. d'Abrera (1994) treated *Charis* and *Chalodeta* as congeneric, although substantial differences in their morphology and ecology suggest that they are not particularly closely related (Hall, 2002). A phylogenetic analysis for *Charis* and related taxa will end such confusion by providing synapomorphic characters to define these genera (Hall & Harvey, 2002a).

The purpose of this paper is to provide a phylogenetic revision for a large monophyletic portion of *Charis*, the *cleonus* group. This group is of broad evolutionary importance for several reasons. (1) Although the group exhibits little wing pattern variation, the interspecific genital variation is substantial, a factor that has led to the gross underestimation of its true species diversity. The group contains three described species and another nineteen are described here as new. Because externally identical individuals may have quite different genitalia, this study highlights the importance of examining internal morphology when attempting to identify riodinid specimens. (2) Because members of this group exhibit highly fragmented parapatric distributions throughout the Amazon basin, they are potential indicators of areas of endemism of other lepidopteran groups. (3) The pattern of parapatric distributions in this group provides an opportunity, through the generation of a phylogenetic hypothesis, to examine historical relationships among areas of endemism in the Amazon basin and compare an area cladogram against those presented for other groups of organisms.

Materials and methods

Dissections were made using standard techniques, abdomens being soaked in hot 10% potassium hydroxide solution for approximately 5 min, and subsequently stored in glycerol. A total of 262 dissections were made, including 193 males and sixty-nine females. Dissected specimens are indicated throughout the text with unique reference numbers. The identification

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of remaining specimens was confirmed by descaling the abdominal tip and examining the partially revealed genitalia. Morphological terms for genitalia follow Klots (1956) and Eliot (1973), and the terminology for wing venation follows Comstock & Needham (1918).

Charis cleonus group specimens have been examined and their label data recorded in the following collections, whose acronyms are used throughout the text: AME, Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, Florida, U.S.A.; AMNH, American Museum of Natural History, New York, New York, U.S.A.; AN, Collection of Andrew Neild, London, U.K.; BMNH, The Natural History Museum, London, U.K.; CJC, Collection of Curtis Callaghan, Bogotá, Colombia; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; FSCA, Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, Florida, U.S.A.; JBS, Collection of J. Bolling Sullivan, Beaufort, North Carolina, U.S.A.; JHKW, Collection of Jason Hall & Keith Willmott, Washington, DC, U.S.A.; MNHN, Museé National d'Histoire Naturelle, Paris, France; SMF, Senckenberg Museum, Frankfurt, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; ZMHU, Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany; ZSM, Zoologische Staatssammlung, Munich, Germany. Localities listed in the *Material examined* sections follow the format given in Hall (1999). As all species possess female genitalia with an elongate corpus bursae with a pair of short 'horn-like' signa, these structures are only illustrated once in the female genitalia figures.

The phylogenetic analysis is based on morphological characters derived from the wings and male and female genitalia of twenty-three species of *Charis*. Autapomorphies were excluded, although these are given in the relevant species accounts below. The analysis was performed using a heuristic search with 1000 random addition sequence TBR replicates in PAUP 4.0b4a (Swofford 2000). All characters were equally weighted and unordered. *Charis argyrea* Bates was used as the outgroup because it is hypothesized to be among the most closely related species in the genus (see *Diagnosis* section). 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) using the program AUTODECAY 4.0 (Eriksson, 1998) in combination with PAUP. Character distributions were studied using MacClade 3.05 (Maddison & Maddison, 1995) and mapped onto the cladogram in Fig. 1. Instances of ambiguous character optimization were resolved by adopting the most plausible evolutionary scenario.

Results and discussion

A total of thirty-six characters were identified (Appendix 1), predominantly from male genitalia (twenty-eight characters),

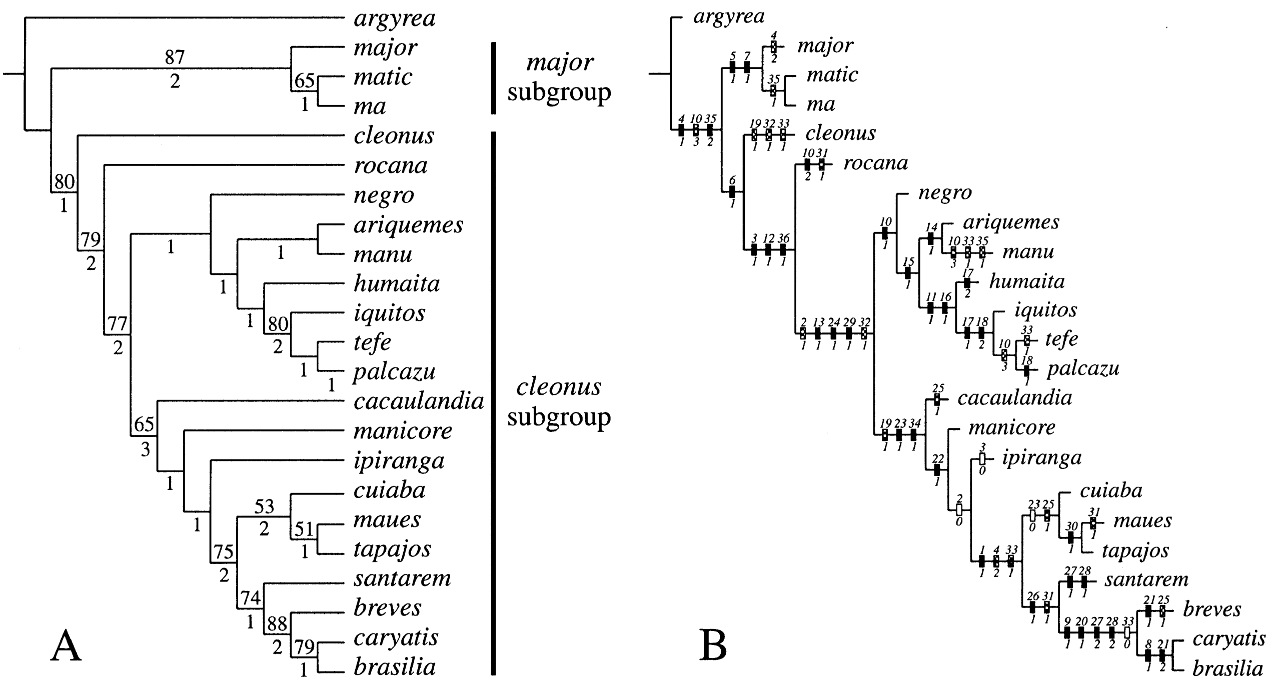

Fig. 1. The single most parsimonious cladogram generated for the *cleonus* group. A, Cladogram illustrating estimates of branch support (bootstrap values above branches and decay indices below branches) and position of the *major* and *cleonus* subgroups. B, Cladogram illustrating distribution of character states (black bars indicate unique apomorphies, shaded bars homoplasious apomorphies and white bars reversals).

but also wing pattern (four characters) and female genitalia (four characters) (see Appendix 2 for data matrix). The heuristic search generated a single most parsimonious cladogram (Fig. 1) of 62 steps, with a consistency index of 0.73 and a retention index of 0.88. Character state changes are indicated on Fig. 1B.

This analysis indicates the existence of two reasonably well supported monophyletic clades, which we refer to as the *major* and *cleonus* subgroups. The unique and unreversed characters supporting the *major* subgroup are the possession of male genitalia with a deeply notched vinculum ventrally (ch. 5) and a pedicel that joins the aedeagus at its very base (ch. 7). Within the *cleonus* group, only *major* subgroup species possess an undivided 'vogelkop' at the tip of the pedicel (see *Diagnosis*). The *cleonus* subgroup is united by all members possessing an even instead of swollen ventral anterior base to the aedeagus of the male genitalia (ch. 6). The *cleonus* subgroup is further divided into two basal Guianan species, and sister clades of upper and lower Amazonian species. The lower Amazon clade is defined by its members possessing a base to the upper male genital valve processes that is positioned anteriorly to the base of the lower valve processes (ch. 23) (reversed in the *C. cuiaba* clade) and a largely membranous female eighth abdominal sternite with only scattered punctate sclerotization (ch. 34). No universal character could be found to define the western Amazon clade.

Of the four different wing patterns exhibited by the group (labelled A–D in Fig. 17), which were broken down into characters 1–4 in the analysis, pattern C is an autapomorphy for *C. rocana*, and only pattern D defines a polytypic monophyletic group (species 13–19 in Fig. 17). Species with pattern A (species 3–11) are paraphyletic with respect to those with pattern D (species 1–2, 12), and species with pattern B are polyphyletic. The cladogram suggests that the pattern B exhibited by *C. ipiranga* (species 12) is not homologous with that exhibited by the more basal members of the group. The biogeographical implications of this cladogram are discussed elsewhere (see *Biogeography* section).

***Charis* Hübner, [1819]**

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

Charmona Stichel, 1910: 15. Type species by original designation: *Papilio anius* Cramer, 1776: 144, Pl. 92, Fig. B.

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

Diagnosis

The *cleonus* group of *Charis* is characterized by a combination of wing pattern characters that include an entirely white hindwing fringe, an entirely white fringe to the anal half of the forewing (males only), a black ground colour overlaid with blue iridescence on both wings (males only) and two parallel submarginal silver lines on both dorsal wings (see Figs 2–4). An entirely white hindwing fringe occurs elsewhere in the genus only in the unrelated *C. iris* Staudinger and *C. cadytis* Hewitson, whereas the pattern of white fringe on the forewing is unique to the cleonus group. *Charis major* subgroup species all have two parallel submarginal silver lines on the ventral surface, whereas *Charis cleonus* subgroup species exhibit this pattern and three others, involving the merging of these two lines (unique in the genus) or the reduction or absence of the inner line.

The male and female genitalia of *cleonus* group species are typical for tribe Riodinini (see Figs 5–15). The uncus of the male genitalia is rectangular with a straight or shallowly indented posterior dorsal margin, the falces are of average size and shape for the family, the tegumen has a deep notch medially at its anterior margin, and the vinculum is long, thin and posteriorly bowed in its dorsal half. The aedeagus is long, thin and slightly asymmetrical, and the pedicel, which joins the aedeagus at its base, is highly modified into a posteriorly elongate structure with fine acanthae (acellular projections) distributed along its distal half or restricted to a raised distal area termed a 'vogelkop' by Stichel (1910) (see Fig. 6). The valvae consist of a typically smaller lower process and an upper process that is joined above the aedeagus to form a transtilla in basal members of the group. The reduction or loss of the transtilla in the more derived species is unique within the genus. In the lower Amazon clade of the *cleonus* subgroup, the upper valve processes become jagged along their dorsal margin and the most derived species possess variably shaped pouches of spines at their anterior dorsal margin, a character not seen elsewhere in Riodinidae. The often extreme modifications of the pedicel and valvae in the *cleonus* subgroup provide the most important characters for distinguishing species. The fact that these structures vary so much among species that do not differ externally suggests that their evolution has been relatively rapid.

All species possess an elongate corpus bursae with a pair of short 'horn-like' signa. The ductus bursae is typically membranous, except for a short, sclerotized posterior section that in certain species is coiled (as in the *Theope lycaenina* group, Hall, 1999). The ostium bursae may be placed centrally or displaced to the right, in the extreme case of *C. matic*, to the junction of the eighth sternite and the pleural membrane. The contours of the region surrounding the ostium are highly interspecifically variable, and the last three sternal segments are variably sclerotized.

The most closely related *Charis* species appear to be *C. argyrea*, which differs in males by lacking blue iridescence and in both sexes by lacking continuous white fringe elements, and members of the *gynaea* group, which includes *C. gynaea* (Godart), *C. zama* Bates, *C. hermodora* C. & R. Felder and five recently described species (Hall & Harvey, 2001). The genitalia of some of these latter species are very similar to those of *major* subgroup species and the females of both groups are also similar. However, the dorsal surface of males in the *gynaea* group is brown and the ventral surface orange-brown, often with purple

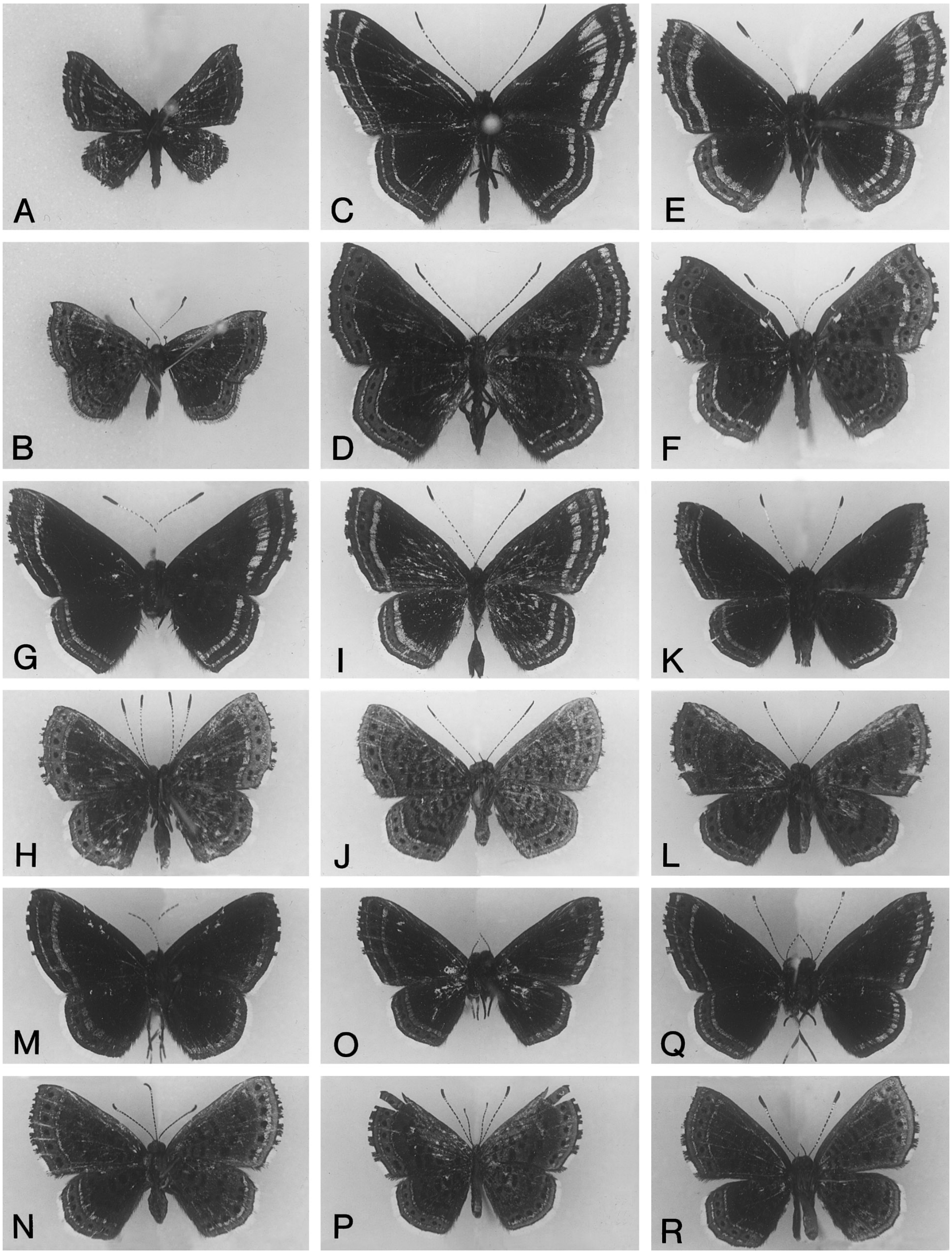

Fig. 2. Adults (dorsal surface on left, ventral surface on right, unless otherwise stated). A, ♂ *Charis argyrea* Bates, Pakitza, Peru (USNM), dorsal surface on right; B, ♀ *C. argyrea* Bates, Cacaulândia, Brazil (Ro) (USNM), dorsal surface on right; C, ♂ *C. major* (Lathy), Loja-Zamora Road, Ecuador (JHKW); D, ♀ *C. major* (Lathy), Loja-Zamora Road, Ecuador (JHKW); E, holotype ♂ *C. matic*; F, allotype ♀ *C. matic*; G, holotype ♂ *C. ma;* H, allotype ♀ *C. ma*; I, ♂ *C. cleonus* (Stoll), Kaiteur Falls, Guyana (USNM); J, ♀ *C. cleonus* (Stoll), Montsinéry, French Guiana (USNM); K, holotype ♂ *C. rocana;* L, allotype ♀ *C. rocana*; M, holotype ♂ *C. negro*; N, allotype ♀ *C. negro*; O, holotype ♂ *C. ariquemes*; P, allotype ♀ *C. ariquemes*; Q, holotype ♂ *C. manu*; R, allotype ♀ *C. manu*.

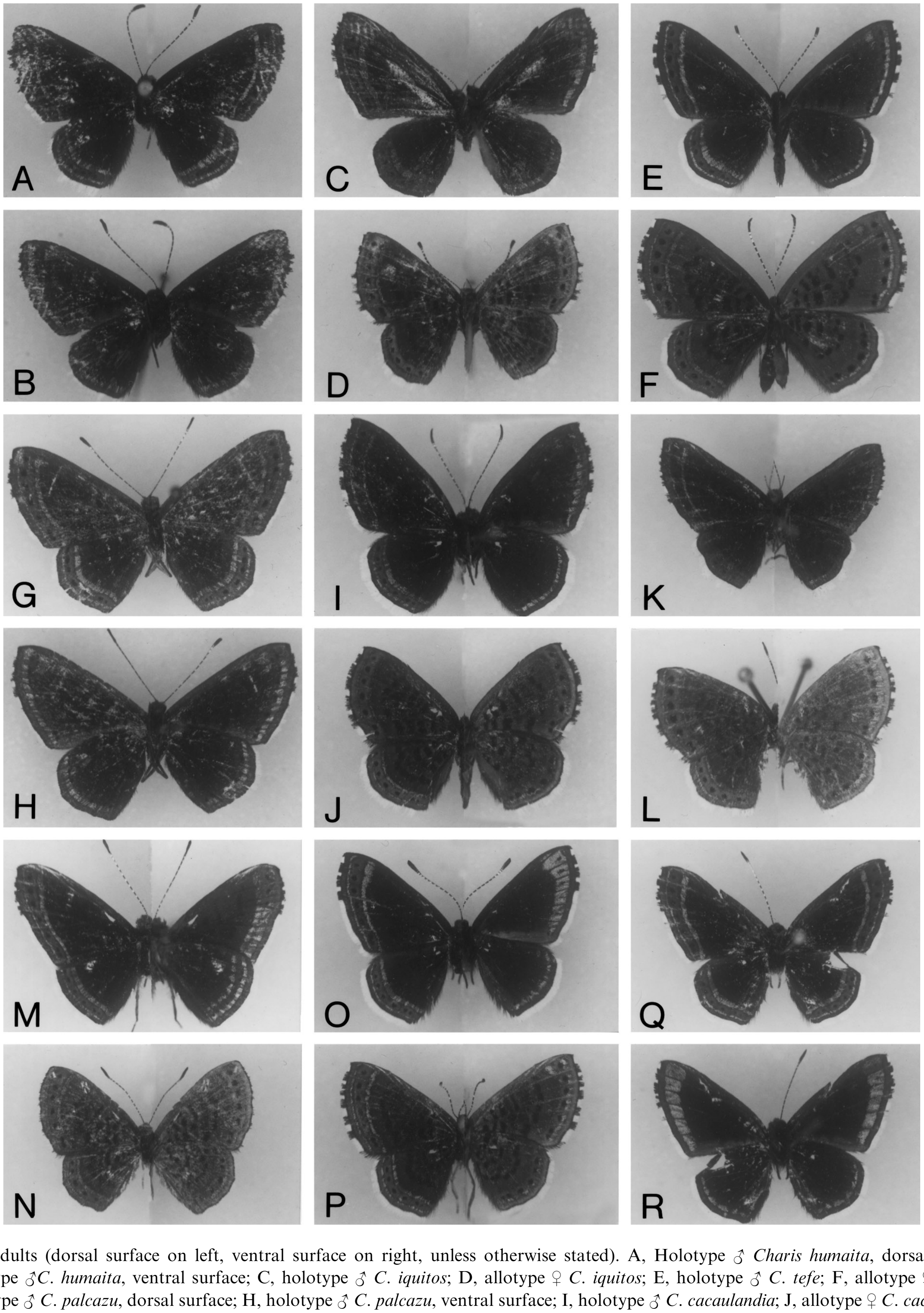

Fig. 3. Adults (dorsal surface on left, ventral surface on right, unless otherwise stated). A, Holotype ♂ *Charis humaita*, dorsal surface; B, holotype ♂*C. humaita*, ventral surface; C, holotype ♂ *C. iquitos*; D, allotype ♀ *C. iquitos*; E, holotype ♂ *C. tefe*; F, allotype ♀ *C. tefe*; G, holotype ♂ *C. palcazu*, dorsal surface; H, holotype ♂ *C. palcazu*, ventral surface; I, holotype ♂ *C. cacaulandia*; J, allotype ♀ *C. cacaulandia*; K, holotype ♂ *C. manicore*; L, allotype ♀ *C. manicore*; M, holotype ♂ *C. ipiranga*; N, allotype ♀ *C. ipiranga*; O, holotype ♂ *C. cuiaba*; P, allotype ♀ *C. cuiaba*; Q, holotype ♂ *C. maues*, dorsal surface; R, holotype ♂ *C. maues*, ventral surface.

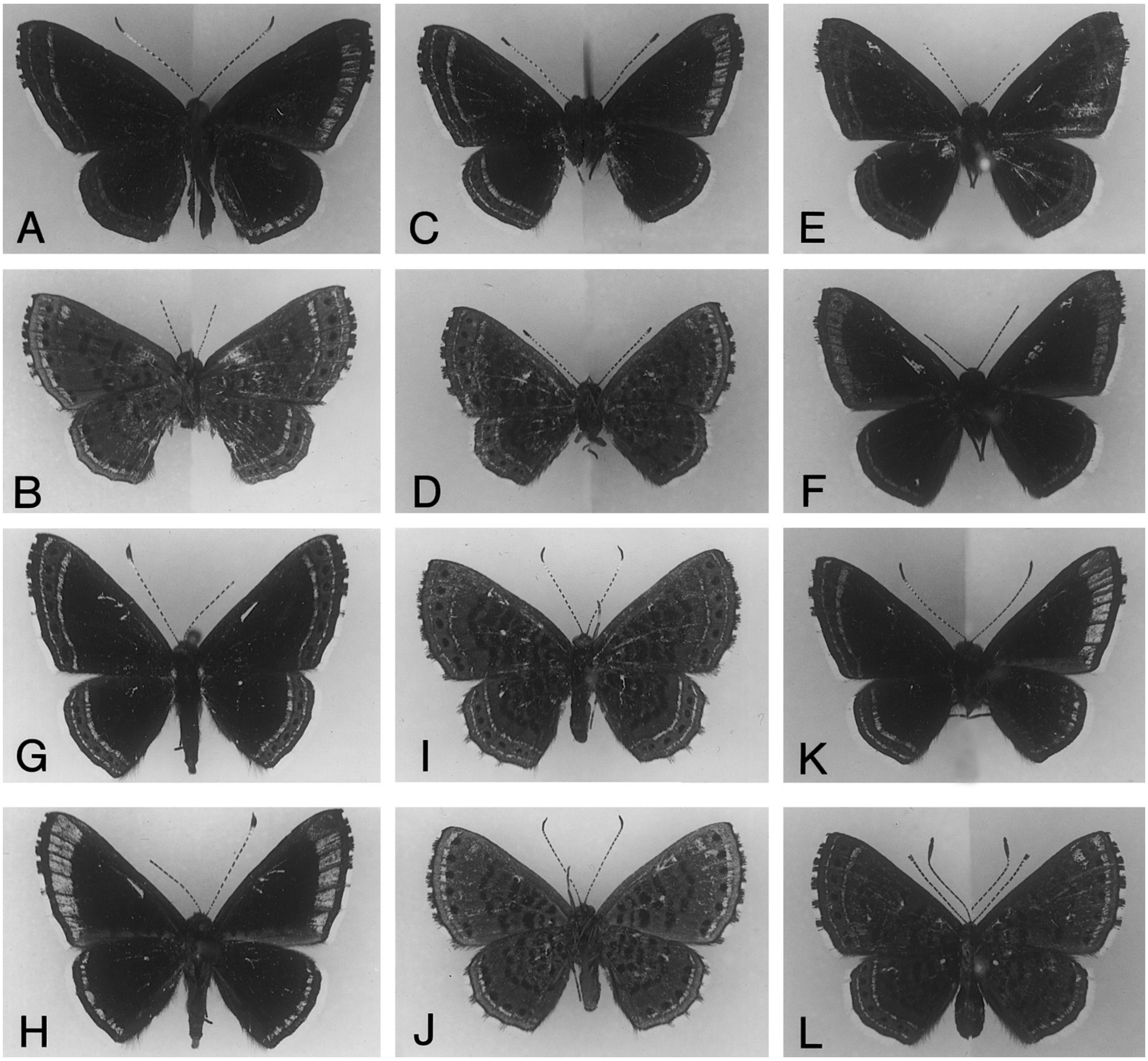

Fig. 4. Adults (dorsal surface on left, ventral surface on right, unless otherwise stated). A, Holotype ♂ *Charis tapajos*; B, allotype ♀ *C. tapajos*, dorsal surface on right; C, holotype ♂ *C. santarem*; D, allotype ♀ *C. santarem*; E, holotype ♂ *C. breves*, dorsal surface; F, holotype ♂ *C. breves*, ventral surface; G, ♂ *C. caryatis*, Benevides, Brazil (Pa) (CMNH), dorsal surface; H, ♂ *C. caryatis*, ventral surface; I, ♀ *C. caryatis*, Benevides, Brazil (Pa) (CMNH), dorsal surface; J, ♀ *C. caryatis*, ventral surface; K, holotype ♂ *C. brasilia,* L, allotype ♀ *C. brasilia.*

iridescence, and both sexes lack an inner silver submarginal line on the ventral surface.

Proposed classification

The *Charis cleonus* group as defined here has traditionally been treated as containing two species, *C. cleonus* (Stoll) and *C. caryatis* Hewitson (Stichel, 1910, 1930; Bridges, 1994; d'Abrera, 1994), but the taxon *major* (Lathy) was recently correctly treated as a species by Lamas (1997). Having examined more than 1000 specimens and made 262 dissections, we recognize twenty-two species for the *cleonus* group.

Given the parapatric distribution of *cleonus* group species, a brief comment on species concepts is warranted. We treat the entities described and discussed in this paper as species because we believe both of the species concepts in widest usage, the phylogenetic species concept (PSC) (e.g. Nixon & Wheeler, 1990) and the biological species concept (BSC) (e.g. Mayr, 1940, 1963) accord them that status. As discrete 100% diagnosable units for which a

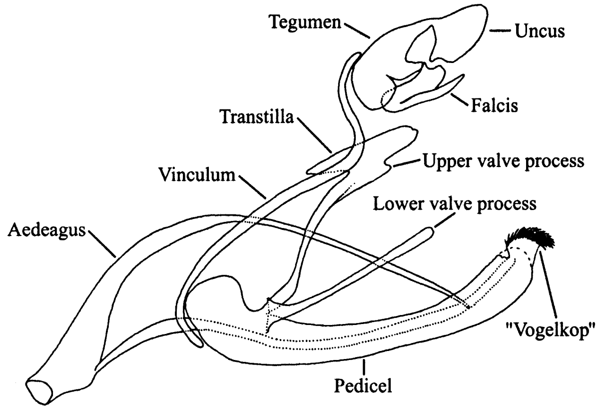

Fig. 5. Male genitalia of *Charis matic* with structures discussed in the text illustrated.

fully resolved cladogram has been generated they certainly constitute species under the PSC, and the interspecific genital differences in the group appear to be sufficient to preclude the possibility of potential interbreeding, the criterion used to define species under the BSC. In fact, these genital differences are greater than those between species of many widely recognized genera (Hall & Harvey, unpublished data).

Below we present our systematic checklist for the group.

Charis major subgroup

ma Harvey & Hall, sp.n.
major (Lathy, 1932)
matic Harvey & Hall, sp.n.

Charis cleonus subgroup

ariquemes Harvey & Hall, sp.n.
brasilia Harvey & Hall, sp.n.
breves Harvey & Hall, sp.n.
cacaulandia Harvey & Hall, sp.n.
caryatis Hewitson, 1866
cleonus (Stoll, 1781)
cuiaba Harvey & Hall, sp.n.
humaita Harvey & Hall, sp.n.
ipiranga Harvey & Hall, sp.n.
iquitos Harvey & Hall, sp.n.
manicore Harvey & Hall, sp.n.
manu Harvey & Hall, sp.n.
maues Harvey & Hall, sp.n.
negro Harvey & Hall, sp.n.
palcazu Harvey & Hall, sp.n.
rocana Harvey & Hall, sp.n.
santarem Harvey & Hall, sp.n.
tapajos Harvey & Hall, sp.n.
tefe Harvey & Hall, sp.n.

Key to the males of *Charis cleonus* group species

As the females are not known for all species and the genitalia provide insufficient well defined character systems to construct a dichotomous key, a key is provided for males only, based largely on genitalia.

1\. Inner silver submarginal line on VFW separated from outer silver line (or absent) 2
– Inner silver submarginal line on VFW merged with outer silver line 16
2(1). Inner silver submarginal line on VFW complete ... 3
– Inner silver submarginal line on VFW reduced to small apical fleck or absent 7
3(2). Forewing fringe brown with solid white from anal margin to vein Cu1 and 4 white flecks in subsequent 4 cells; average FW length 12.5 mm; FW apex not angular 4
– Forewing fringe brown with solid white from anal margin to vein M3 and 3 white flecks in subsequent 3 cells; average FW length 14.5 mm; FW apex angular .... *major*
4(3). Ventral silver submarginal lines prominent and broad; base of valve complex does not extend anterior to vinculum 5
– Ventral silver submarginal lines faint and narrow, inner HW line sometimes absent; base of valve complex does extend anterior to vinculum .... *ipiranga*
5(4). Forewing apex slightly falcate; ventral blue iridescence prominent; tip of aedeagus pointed; tip of pedicel not bifurcate 6
– Forewing apex rounded; ventral blue iridescence weak; tip of aedeagus bulbous; tip of pedicel bifurcate .... *cleonus*
6(5). Pedicel long (1.19–1.5 mm), tip relatively small and flat with small spines .... *matic*
– Pedicel short (0.76–1.14 mm), tip relatively large and more vertically elongate with large spines .... *ma*
7(2). Inner silver submarginal line on VFW reduced to small apical fleck; pedicel posteriorly elongate 8
– Inner silver submarginal line on VFW absent; pedicel simple and straplike .... *rocana*
8(7). Tip of pedicel rounded 10
– Tip of pedicel bifurcate 9
9(8). Dorsal margin of upper valve processes jagged; base of valve complex does not extend anterior to vinculum .... *cacaulandia*
– Dorsal margin of upper valve processes smooth; base of valve complex does extend anterior to vinculum .... *manicore*
10(8). Lower valve process shorter than upper process; pedicel medium to long 11
– Lower valve process significantly longer than upper process; pedicel short .... *manu*
11(10). Distal portion of pedicel elongate and asymmetrical.. 13
– Distal portion of pedicel short and symmetrical 12

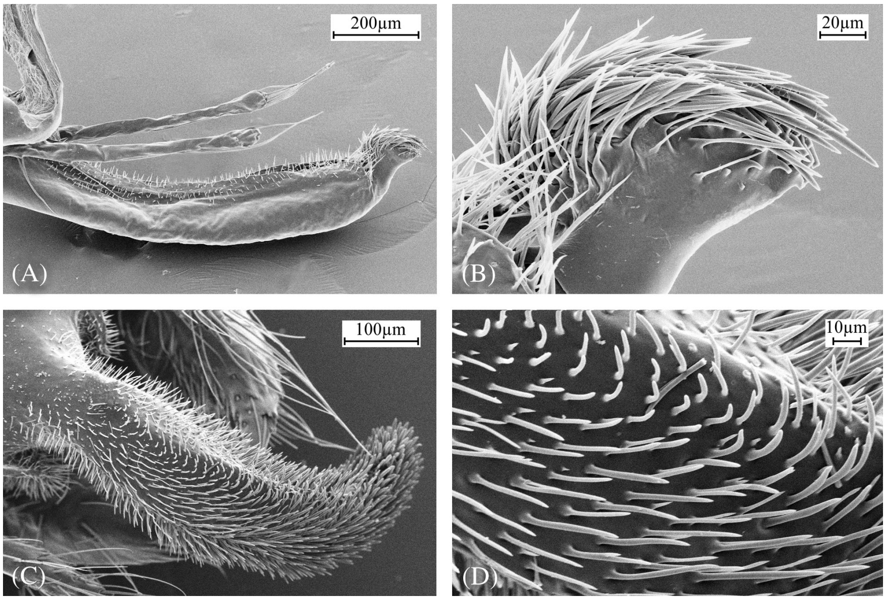

Fig. 6. Scanning electron micrographs of *cleonus* group male genitalia. A, *Charis matic*, lateral view of pedicel and lower valve processes; B, *C. matic*, a magnified view of the pedicel 'vogelkop'; C, *C. iquitos*, ventral view of pedicel; D, a magnified view of 'C'.

12(11). Aedeagus strongly arched; cornuti long and vesica curved to right; upper valve process relatively broad; acanthae on dorsal margin of pedicel tip only .... *negro*

– Aedeagus approximately straight; cornuti short and vesica straight; upper valve process relatively narrow; acanthae on ventral margin of pedicel tip only .... *ariquemes*

13(11). Pedicel long and curved to left in ventral view ... 14

– Pedicel very long and curved to right in ventral view .... *humaita*

14(13). Cornuti absent 15

– Cornuti present .... *iquitos*

15(14). Pedicel curved strongly to left in ventral view; tip of aedeagus pointed; upper valve process shorter than pedicel .... *tefe*

– Pedicel curved weakly to left in ventral view; tip of aedeagus bifurcate; upper valve process longer than pedicel .... *palcazu*

16(1). Anterior portion of upper valve processes approximately flat 17

– Anterior portion of upper valve processes developed into raised area of long spines 19

17(16). Inner upper valve process present 18

– Inner upper valve process absent .... *cuiaba*

18(17). Outer upper valve process out-turned at tip; dorsal margin of inner upper valve process smooth; tip of aedeagus with anteriorly directed triangular point .... *maues*

– Outer upper valve process straight; dorsal margin of inner upper valve process jagged; tip of aedeagus pointed .... *tapajos*

19(16). Raised area of long spines on anterior portion of upper valve processes fine and largely contained within medial invaginated pouch; ventral margin of aedeagal tip indented; ventral tip of pedicel with one or more small projections 20

– Raised area of long spines on anterior portion of upper valve processes coarse and largely external; ventral margin of aedeagal tip straight; ventral tip of pedicel smooth .... *santarem*

20(19). Lateral spine at right tip of aedeagus present; ventral tip of pedicel with several nodules 21

– Lateral spine at right tip of aedeagus absent; ventral tip of pedicel with single small horn ..... *breves*

21(20). Raised area of long spines on anterior portion of upper valve processes directed anteriorly; ventral indentation at tip of aedeagus weak, lateral spine at right of tip small .... *caryatis*

– Raised area of long spines on anterior portion of upper valve processes directed vertically; ventral indentation at tip of aedeagus prominent, lateral spine at right of tip large .... *brasilia*

Biogeography

The *Charis cleonus* group is distributed throughout the Amazon basin and Guianas, and extends as far as southern Brazil. By far the highest number of species occurs in Brazil (eighteen recorded, twenty expected) (see Table 1). The biogeography of this group is unique in several ways and the primary purpose of generating the cladogram is to aid more detailed biogeographical discussions and allow the generation of an

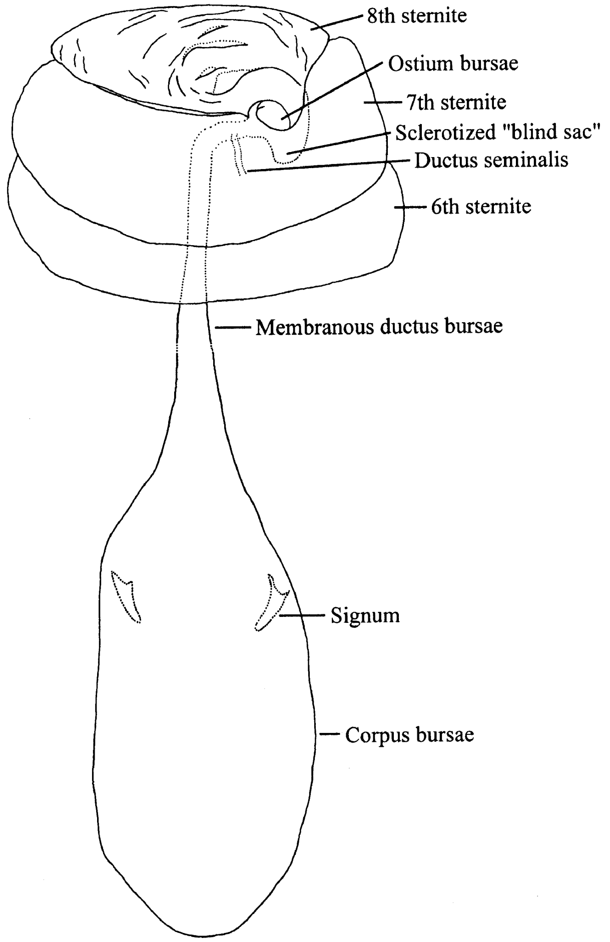

Fig. 7. Female genitalia of *Charis manu* with structures discussed in the text illustrated.

area cladogram that can be compared with those for other organisms. Although this information will be presented elsewhere (Hall & Harvey, 2002b), a brief discussion is warranted here. All members of the *major* and *cleonus* subgroups, respectively, have parapatric distributions, although representatives of the two groups are sympatric in the western Amazon (see Figs 16, 17). *Charis matic* and *C. ma* of the *major* subgroup are macrosympatric but microparapatric, never co-occurring in the same locality yet often present in different localities only kilometres apart. We are not aware of this phenomenon having been reported elsewhere for butterflies. Each species would appear to have subtle microhabitat preferences, although what these might be is currently unclear. The fact that *C. ma* is rarest in the wettest part of its range, from southern Colombia to northern Peru, suggests that the species perhaps prefers slightly drier forest.

All nineteen species of the *cleonus* subgroup are essentially parapatric throughout the Amazon basin, with all the cases of apparent minor overlap probably due to historical labelling error. No specimens with modern label data have been found to be sympatric. Such a fragmented pattern of species distributions across a relatively uniform habitat is not known elsewhere for butterflies. The *cleonus* subgroup species distributions match reasonably well with the centres of endemism proposed for ithomiine, heliconiine and papilionid butterflies (Brown, 1982, 1987; Tyler *et al.*, 1994), although there are numerous discrepancies, particularly in the central and lower Amazon. Interestingly, though, the unusually highly fragmented pattern of distributions on the Madeira and Tapajós Rivers closely matches that of the marmoset genus *Callithrix* Erxleben (Mittermeier *et al.*, 1992), including endemics confined to the vicinities of Humaitá and Maués (species 6 and 14 in Fig. 17, respectively).

Much field work remains to be done to clarify the distributions of *Charis cleonus* group species, especially those only known from one or two localities, and it is probable that additional species remain to be discovered in remote parts of the Amazon basin. The areas most in need of more collecting include southern Venezuela, southeastern Colombia, central Peru and the Brazilian states of Acre, Rondônia, Mato Grosso, Amazonas (southeastern and northeastern), Pará (northern and southeastern) and Amapá.

Biology

All species in the *Charis cleonus* group inhabit intact wet forest, except for *C. brasilia*, which also occurs in drier and more open woodland habitats. All species are confined to the lowlands, typically below 1000 m, except for *C. major*, which is a cloud forest species occurring between 1200 and 1900 m. Males are encountered perching as solitary individuals or in small groups during the early to mid-afternoon in understory sunflecks or small lightgaps below 2 m above the ground. They rest beneath and on top of the tips of leaves with their wings outspread and often engage in rapid spiralling flights with conspecific males. Females fly throughout the day during sunny periods and oviposit single eggs on moist decaying leaves on the forest floor. The early stages are partially known for three species in the group, *C. matic* (DeVries *et al.*, 1994, as *C. cleonus*), *C. manu* and *C. iquitos* (Harvey, unpublished data), and, as is common for the genus, the larvae are detritivores. The larvae grow very slowly and have only been reared as far as the third instar. The brown, densely hirsute larvae are similar to that figured by DeVries (1997) as *Charis anius*.

***Charis major* subgroup**

***Charis major* (Lathy, 1932)** (Figs 2C,D; 8B; 14B; 16)

Charmona anius major Lathy, 1932: 67–68. Type locality: El Topo, eastern Ecuador. Holotype ♂ BMNH (examined): 'El Topo/Rio Pastaza/E. Ecuador/4200 feet/ M. G. Palmer', 'Type/H.T', 'Charmona auius/major, Lathy/Specimen typicum' and 'Joicey Bequest./Brit. Mus./1934–120.'.

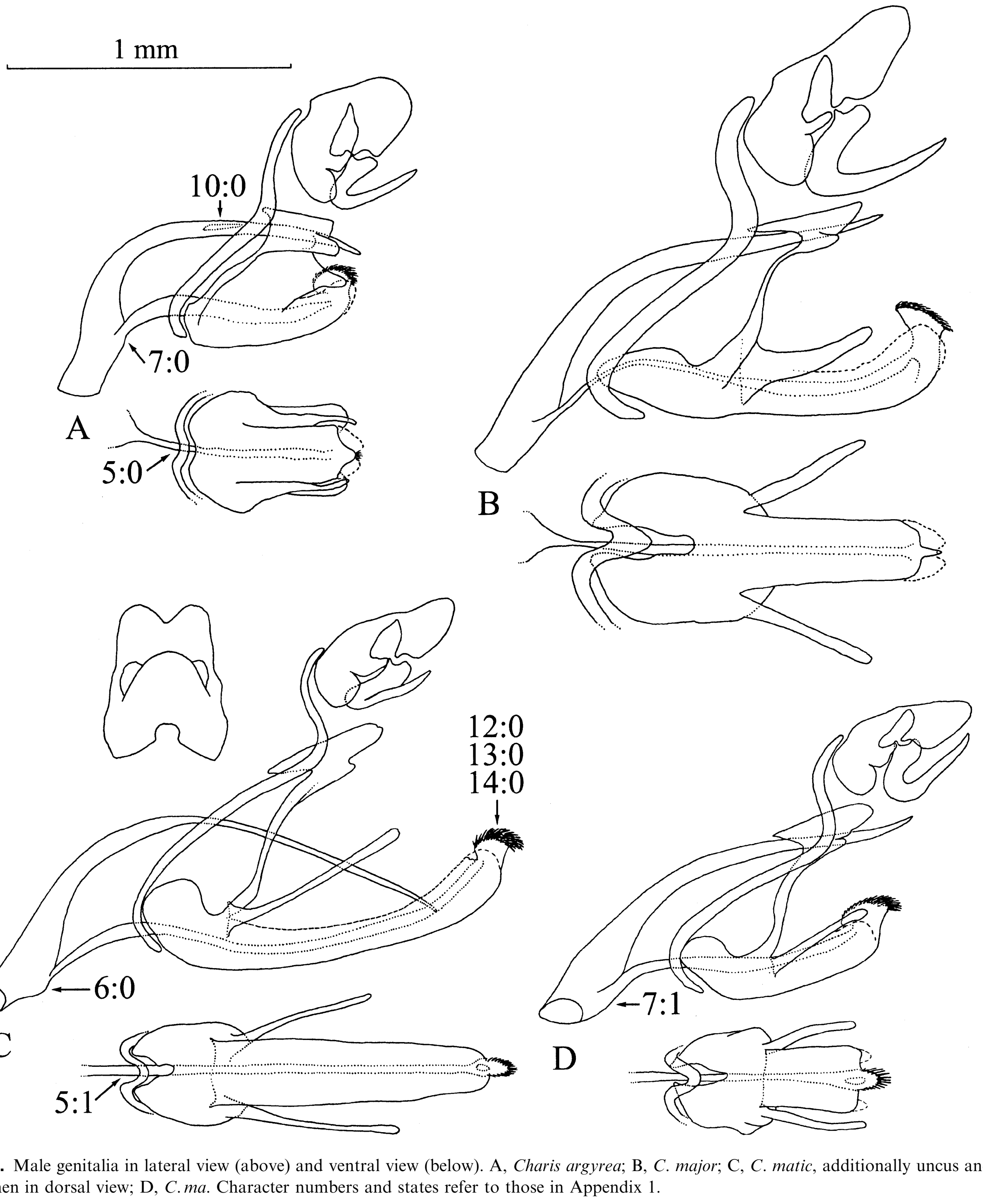

Fig. 8. Male genitalia in lateral view (above) and ventral view (below). A, *Charis argyrea*; B, *C. major*; C, *C. matic*, additionally uncus and tegumen in dorsal view; D, *C. ma*. Character numbers and states refer to those in Appendix 1.

Diagnosis. Typical forewing length: male 14.5 mm, female 14.5 mm. *Charis major* was described as a subspecies of *C. anius*, treated as a subspecies of *C. caryatis* by d'Abrera (1994) and finally correctly treated as a full species by Lamas (1997). The male closely resembles that of *C. cleonus*, *C. matic* and *C. ma*, but is in fact the only species of the four that can be identified from external characters alone. It is a larger species (FW length 14.5 instead of 12.5 mm) with an angular forewing apex, typically a broader area of silver in the apex of the inner submarginal ventral forewing line, and only three

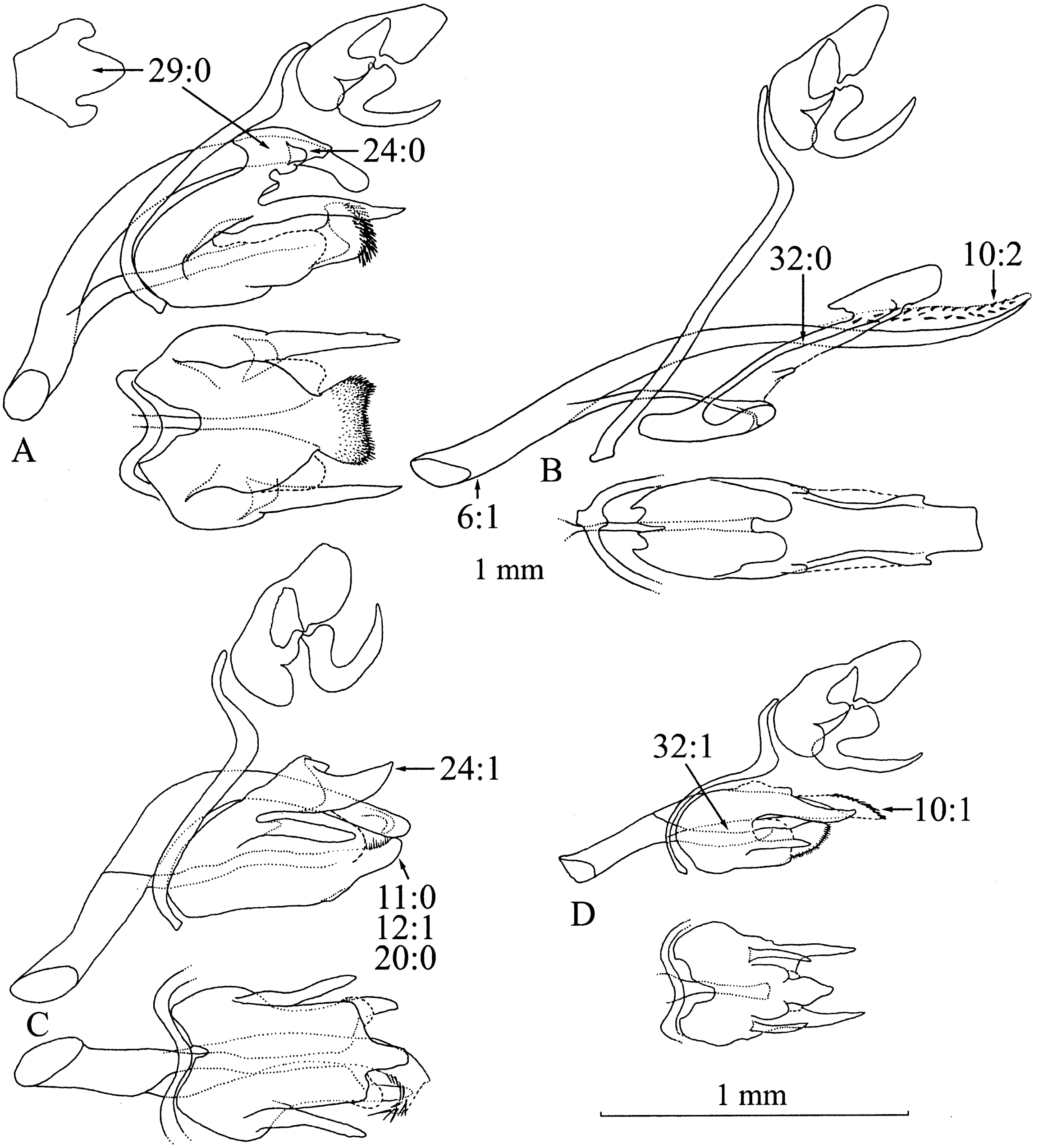

Fig. 9. Male genitalia in lateral view (above) and ventral view (below). A, *Charis cleonus*, additionally transtilla in dorsal view; B, *C. rocana*; C, *C. negro*; D, *C. ariquemes*. Character numbers and states refer to those in Appendix 1.

black forewing fringe elements in the apex instead of four, as in *C. caryatis* and close relatives. The simple tubular pedicel of the male genitalia tipped with a rounded 'vogelkop' places *C. major* in a group with *C. matic* and *C. ma*, but the 'vogelkop' tip is more vertically elongate than in those species and, although the pedicel is of a similar length to that of *C. matic* (1.18–1.28 mm; $n = 3$), it is longer than that of *C. ma*.

Female *C. major* differs externally from *C. cleonus*, *C. matic* and *C. ma* only by the same size differential described for the male. The female genitalia differ from those of *C. matic* and *C. ma* in having a centrally instead of asymmetrically positioned ostium bursae and considerably broader sclerotized abdominal sternites seven and eight with the eighth tergite and intersegmental membrane also being markedly more sclerotized. The female genitalia of *C. cleonus* are distinguished in that species' account.

Biology. *Charis major* is uncommon in premontane forest habitats between 1200 and 1900 m. Males have been observed perching as solitary individuals or in small groups at 08.45 hours and between 13.00 and 16.00

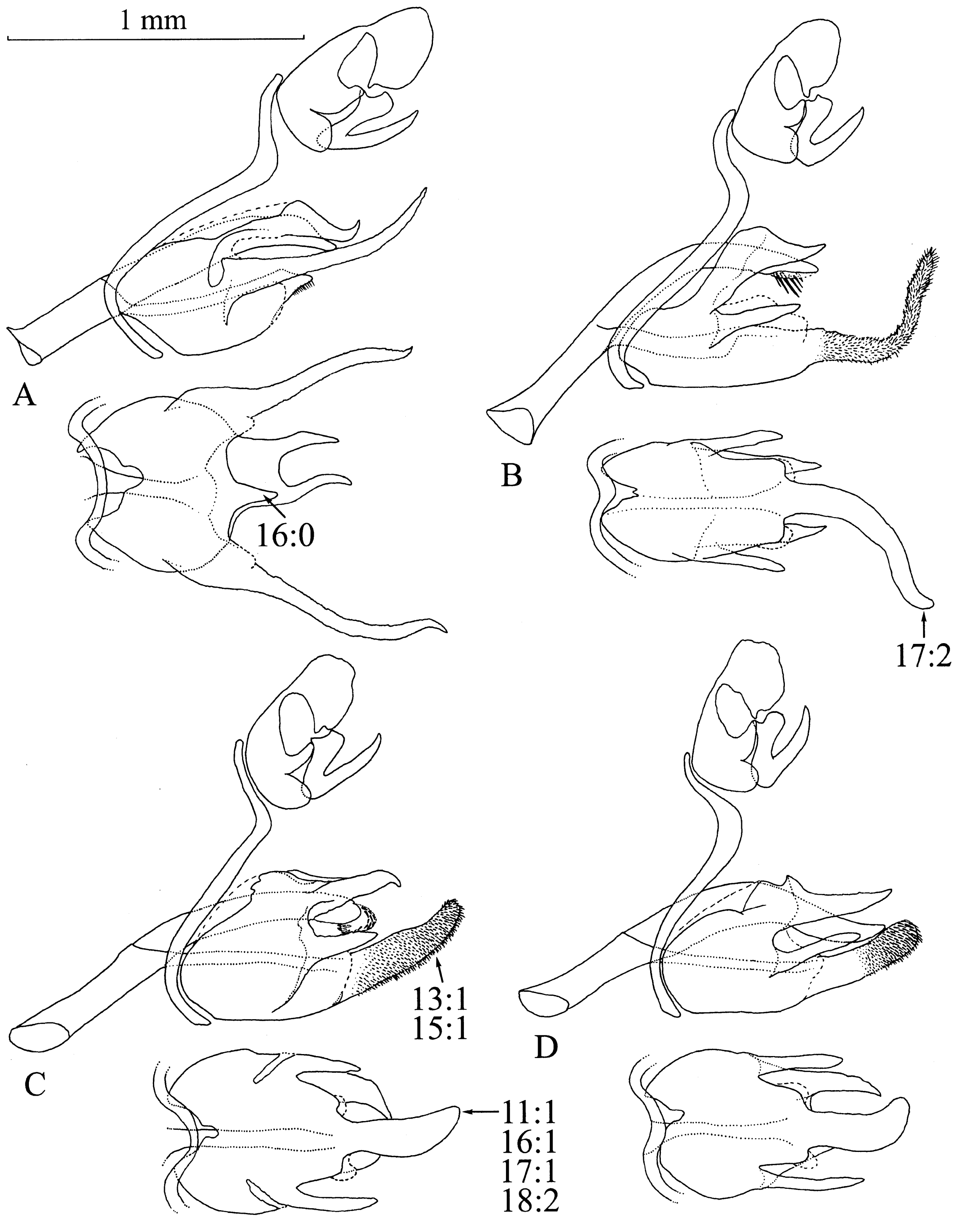

Fig. 10. Male genitalia in lateral view (above) and ventral view (below). A, *Charis manu*; B, *C. humaita*; C, *C. iquitos*; D, *C. tefe*. Character numbers and states refer to those in Appendix 1.

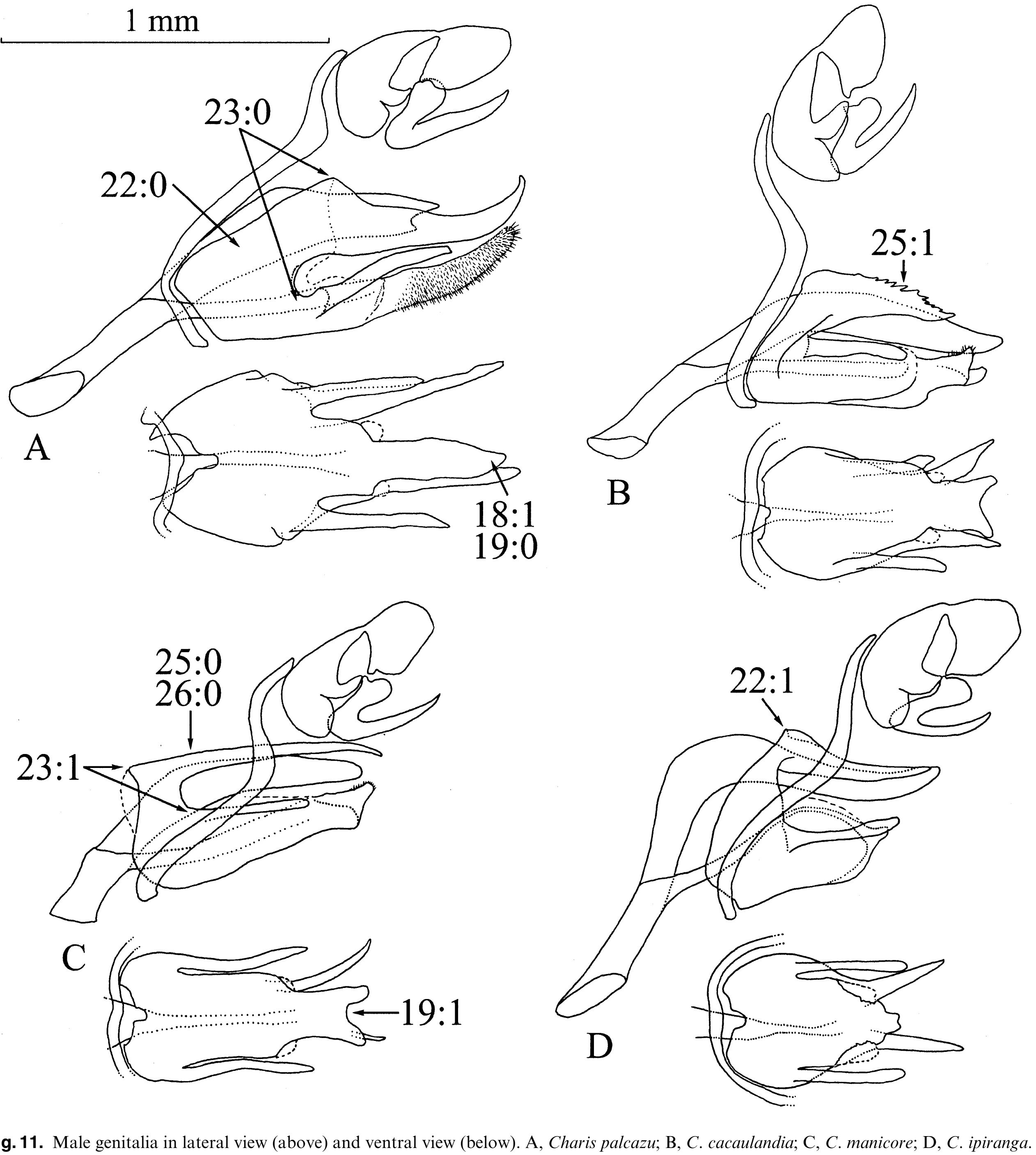

Fig. 11. Male genitalia in lateral view (above) and ventral view (below). A, *Charis palcazu*; B, *C. cacaulandia*; C, *C. manicore*; D, *C. ipiranga*. Character numbers and states refer to those in Appendix 1.

hours on top of small bushes 1–3 m above the ground along the forest edge, and a female was encountered at 08.15 hours flying low to the ground along the edge of a small field near forest (Hall & Willmott, unpublished data).

Distribution. Charis major is currently only known from the central and southern Andes of eastern Ecuador and the extreme northern Andes of Peru, but it surely has a broader eastern Andean distribution (see Fig. 16). The following additional locality is listed by Lamas (1997): PERU: Amazonas, Cordillera del Condór, PV3 (Alfonso Ugarte), 1200–1730 m.

Material examined. ECUADOR: Tungurahua, El Topo, 1♂ (BMNH); Banos-Canelos, 1♂ (BMNH); Morona-Santiago,

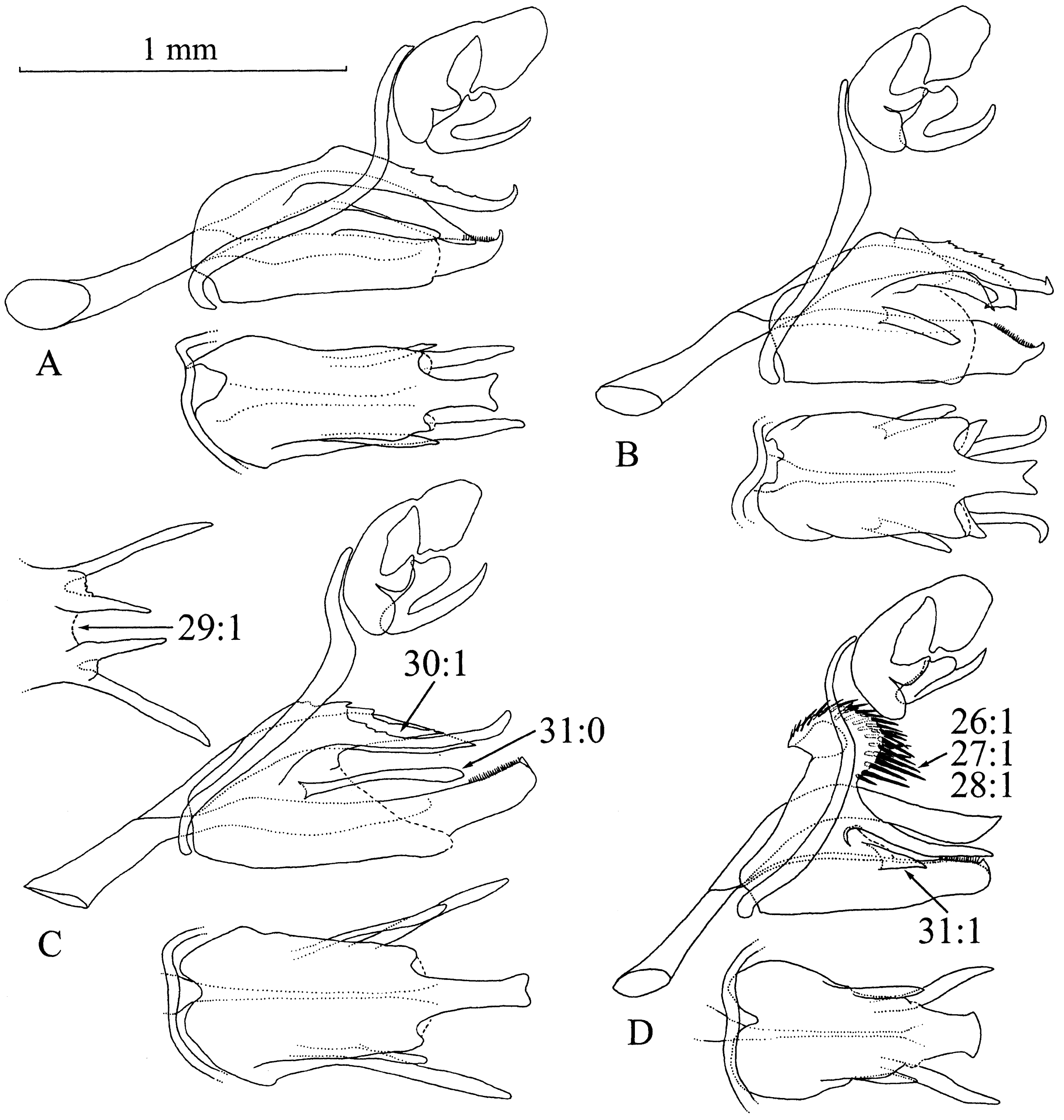

Fig. 12. Male genitalia in lateral view (above) and ventral view (below). A, *Charis cuiaba*; B, *C. maues*; C, *C. tapajos*, additionally upper valve complex in dorsal view; D, *C. santarem*. Character numbers and states refer to those in Appendix 1.

km 12 Chiguinda-Gualaquiza Road (1300 m), 1♂ (JHKW) (dissected); Zamora-Chinchipe, Qbda. San Ramon, Zamora-Loja Road (1700 m), 2♂ (JHKW); Río San Francisco, Zamora-Loja Road 1900 m, 1♀ (JHKW) (# 2000–57); Namírez Bajo, Zamora-Yanzatza Road (1300 m), 2♂ (JHKW) (# 2000–452); no locality data, 3♂, 3♀ (BMNH); 1♂ (USNM) (# 1989–69). Mislabelled: Curaray, 1♂ (BMNH); Sarayacu, 1♂ (BMNH).

***Charis matic* Harvey & Hall, sp.n.** (Figs 2E,F; 5; 6A,B; 8C; 14C; 16)

Male. Does not differ externally from *C. cleonus* except that the ventral blue iridecence is more prominent. *Genitalia* (Fig. 8C): Uncus rounded and more elongate dorsally, shallowly indented at posterior dorsal margin, tegumen and falces of average size and shape for family, vinculum elongate, narrow,

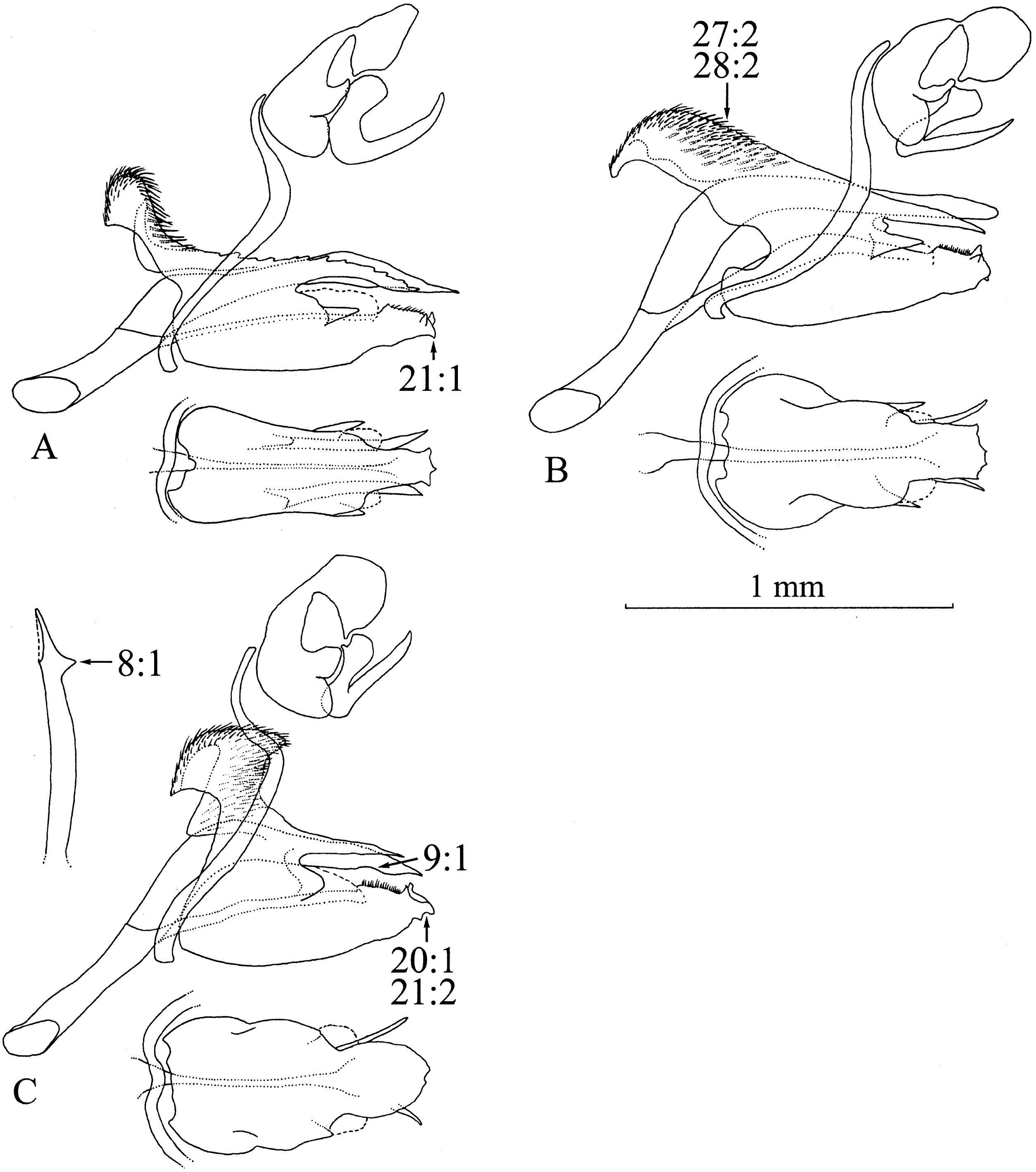

Fig. 13. Male genitalia in lateral view (above) and ventral view (below). A, *Charis breves*; B, *C. caryatis*; C, *C. brasilia*, additionally aedeagus in dorsal view. Character numbers and states refer to those in Appendix 1.

posteriorly bowed in dorsal half and sharply indented at base of valvae in ventral view; aedeagus long, narrow, pointed, bowed and swollen at base; pedicel extends from swollen base of aedeagus as narrow tube to form very elongate posterior projection tipped with 'vogelkop' containing coarse acanthae, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of long, narrow lower process with broader base extending from near base of pedicel, and very small rounded upper process joined to lower one by elongate ribbon of sclerotized tissue and dorsally over aedeagus by posteriorly and anteriorly elongate sclerotized transtilla.

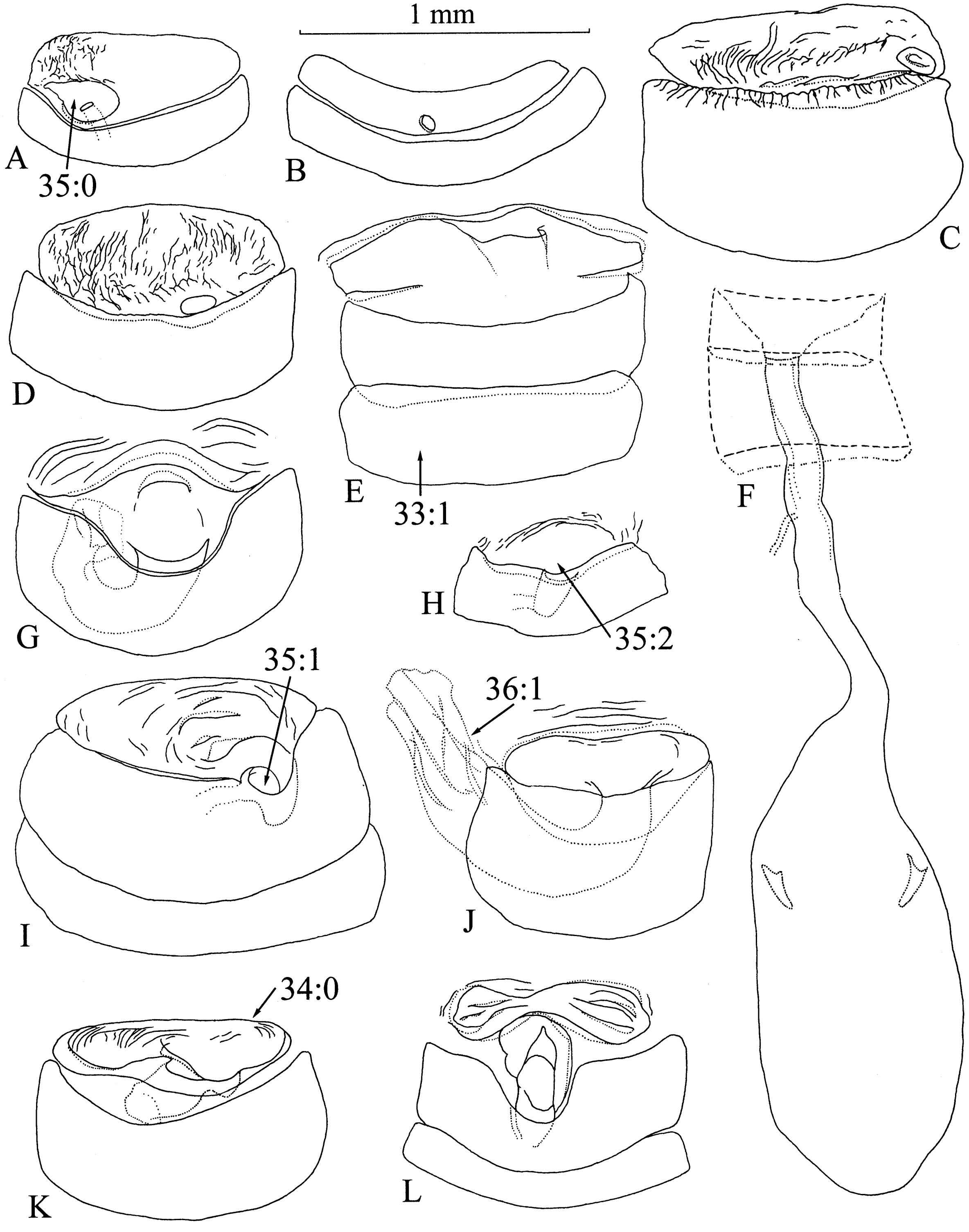

Fig. 14. Female genitalia in ventral view (corpus bursae omitted, see Materials and methods). A, *Charis argyrea*; B, *C. major*; C, *C. matic*; D, *C. ma*; E, *C. cleonus*; F, *C. rocana*, additionally with remainder of ductus bursae and corpus bursae; G, *C. negro*; H, *C. ariquemes*; I, *C. manu*; J, *C. humaita* (possible female, see text); K, *C. iquitos*; L, *C. tefe*. Character numbers and states refer to those in Appendix 1. The scale applies to all species except *C. major*, whose genitalia have been reduced by one-third.

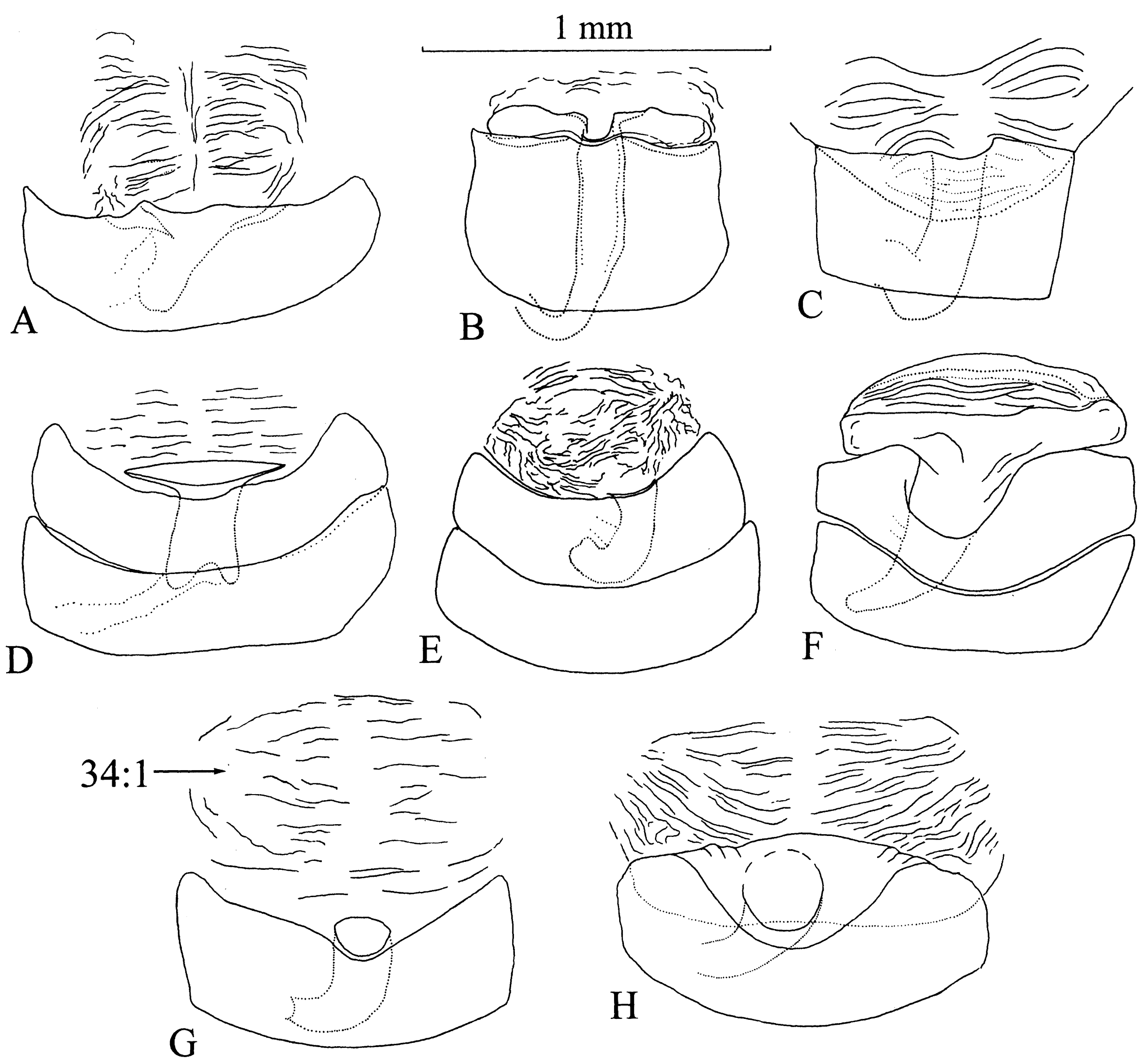

Fig. 15. Female genitalia in ventral view (corpus bursae omitted, see Materials and methods). A, *Charis cacaulandia*; B, *C. manicore*; C, *C. ipiranga*; D, *C. cuiaba*; E, *C. tapajos*; F, *C. santarem*; G, *C. caryatis*; H, *C. brasilia*. Character numbers and states refer to those in Appendix 1.

Female. Does not differ externally from *C. cleonus*. *Genitalia* (Fig. 14C): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, ductus bursae membranous, ostium bursae positioned at right edge of sclerotized eighth abdominal sternite in a shallow medial groove, seventh sternite long and sclerotized.

Material examined. *Holotype*, ♂, COLOMBIA: Putumayo, Río Putumayo, Puerto Asis, 1 February 1969 (S. Nicolay) (USNM) (# 2000-64). *Allotype*, ♀, ECUADOR: Sucumbíos, Lumbaquí, 700 m, 24 September 1975 (S. Nicolay) (USNM) (# 2000-84). *Paratypes*, COLOMBIA: Boyacá, 1♂, Muzo (*ex* coll. LeMoult) (AME) (# 2000-185); Meta, 1♂, Villavicencio, Río Ocoa, 27 January 1944 (W. Hovanitz) (AME) (# 2000-186); Caquetá, 1♂, Montañita, 350 m, 24 January 1971 (S. Nicolay) (USNM) (# 1989-73); Río Bodoquero, 1300 ft (S. Nicolay) (USNM), 1♀, 22 January 1969 (# 2000-52), 1♀, 27 January 1969; Putumayo, 1♂, Río Putumayo, Puerto Asis, 1 February 1969 (S. Nicolay) (USNM) (# 2000-73), 1♂, Villagarson, 20 October 1982 (C. Callaghan) (CJC) (# 2000-422), 1♀, Mocoa, 700 m, 16 December 1994 (C. Callaghan) (CJC) (# 2000-425); Amazonas, 1♂, 1♀, Parque Amayacu, 6–10 October 1999 (C. Callaghan) (CJC) (♂# 2000-420). ECUADOR: Sucumbíos, 1♂, Lumbaquí, 700 m, 24 September 1975 (S. Nicolay) (USNM) (# 2000-72); 1♂, Garzacocha, La Selva, 16–22 September 1994 (R. Hesterberg) (AME) (# 2000-197); Napo, 1♂, km 49 Tena-Loreto Road, 1300 m, 21 September 1996 (K. Willmott) (JHKW) (dissected), 1♂, Río Jondachi, 1000 m, 0°50′ S 77°49′ W, 9 November 1988

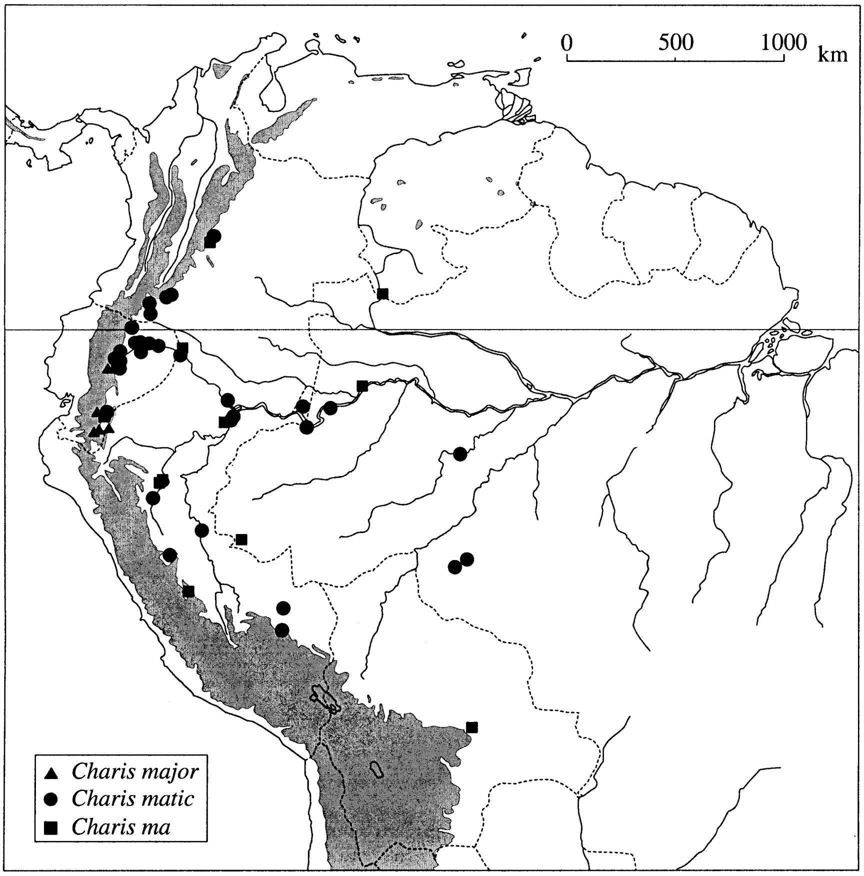

Fig. 16. Map of South America illustrating distributions of *major* subgroup species.

(R. Robbins) (USNM), 2♂, Pano, 731 m, 8 May 1982 (H. Frania & F. Sperling) (USNM), 1♂, Río Anzu, 700 m, *c.* 1°20′ S 78°00′ W, 15 December 1968 (Velastegui) (USNM), 1♂, Satzayacu, November 1968 (R. de Lafebre) (AME) (# 2000-193), 1♂, 1♀, Apuya, 600 m, 27–30 August 1993 (J. Hall) (JHKW), 2♂, 1♀, Río Napo, Puerto Napo, 500 m, 1°03′ S 77°47′ W, 6–10 November 1988 (USNM) (♂# 1998-3), 1♂, Tena, 23 January 1985 (D. & J. Jenkins) (AME) (# 2000-192), 1♂, 1♀, Via Venezia, February 1971 (R. de Lafebre) (AME) (♂# 2000-266; ♀# 2000-272), 2♂, Río Napo, Chichicorrumi, 450 m, 9 July 1993 (J. Hall) (JHKW), 1♀, km 21 Coca-Loreto Road, 300 m, 8 March 1995 (J. Hall) (JHKW), 1♂, Coca, 250 m, 4 February 1971 (S. Nicolay) (USNM), 1♂, Río Coca, July 1971 (R. de Lafabre) (AME) (# 2000-271), 1♀, Coca-Tiguino Road, Río Tiputini, 300 m, 1 July 1994 (J. Hall) (JHKW); Limoncocha, 240 m (S. Nicolay) (USNM), 1♂, 8 February 1971, 1♂, 9 February 1971 (# 1998-2), 1♂, 10 February 1971 (# 1989-68); Pastaza, 1♂, 1♀, Shell, 1050 m, 7–8 February 1995 (J. Hall) (JHKW); Puyo (F. Broen & H. Brown) (AMNH), 1♂, 1♀, 6 December 1938 (♂ dissected), 1♂, 11 December 1939, 1♀, 13 March 1971 (T. Taylor) (AME) (# 2000-270), 1♂, 18 km N of Puyo, 26 January 1985 (D. & J. Jenkins) (AME) (# 2000-194), 1♂, 1♀, km 31.4 Puyo-Macas Road, 900 m, 1°41′ S 77°57′ W, 13 November 1988 (R. Robbins) (USNM); Morona-Santiago, 1♂, Gualaquiza, 22 December 1941 (D. B. L) (AMNH) (dissected). PERU: Loreto, Arcadia, 0°59′37′ S 75°18′55′ W, 150 m (USNM), 1♂, 1♀, 2 November 1993 (G. Lamas) (♂# 2000-70), 1♀, 31 October 1993 (R. Robbins), Río Sucusari, Explornapo-ACEER, 03°14′ S 72°55′ W, 140 m (USNM), 1♂, 4 September 1995 (D. Harvey) (# 2000-68), 3♂, 4♀, 5 September 1995 (D. Harvey, R. Robbins & J. Grados) (♂# 2000-392-394), 3♂, 4♀, 6 September 1995 (J. Grados & D. Harvey) (♂# 2000-395-397), 3♂, 2♀, 7 September 1995 (G. Lamas, J. Grados & A. Caldas), 1♂, 8 September 1995 (D. Harvey), 4♂, 1♀, 9 September 1995 (G. Lamas, J. Grados & D. Harvey), 6♂, 3♀, 10 September 1995 (G. Lamas, J. Grados & D. Harvey), 1♂, 11 September 1995 (J. Grados), 9♂, 1♀, 12 September 1995 (D. Harvey & A. Caldas), 1♂, 1♀, 13 September 1995 (D. Harvey & G. Lamas), 3♂, 14 September 1995 (J. Grados), 1♂, 1♀, 18 September 1995 (J. Grados), 1♂, 22 September 1995 (A. Caldas), 1♂, 23–24 March 1981 (J. Miller) (AME) (# 2000-268); 40 km NE Iquitos, Explorama Inn, 2♂, 24 June–20 July 1990 (Menke & Awertschenko) (USNM) (# 2000-69), 1♀, 26 March 1981 (J. Miller) (AME) (# 2000-269), 1♀, Iquitos, 15 November 1930 (USNM) (# 2000-74); San Martín, 1♂, Juanjui, 400 m, November 1988 (M. Buche) (CJC) (# 2000-421); Ucayali, Pucallpa (*ex* coll. Jae) (AME), 1♀, 23 July 1964 (# 2000-273), 2♀, 22 July 1963 (# 4332 & 6239); Huánuco, 1♀, Sep–November 1984 (USNM) (# 2000-53); Cuzco, 1♀, Qbda. Quitacalzon,

Table 1. The distribution of *cleonus* group species by country. ● represent known records and ? represent expected records.

Charis sp.	Venezuela	Colombia	Ecuador	Peru	Bolivia	Argentina	Brazil	Paraguay	Guyana	Surinam	French Guiana
ma	●	●	●	●	●		●				
major		?	●	●							
matic	?	●	●	●	?		●				
ariquemes							●				
brasilia						●	●	●			
breves							●				
cacaulandia							●				
caryatis							●				
cleonus	●						?		●	●	●
cuiaba							●				
humaita							●				
ipiranga	●						●				
iquitos		●	●	●			●				
manicore							●				
manu				●	●		?				
maues							●				
negro	●	●					●				
palcazu				●							
rocana							●				
santarem							●				
tapajos							●				
tefe				●			●				
Total recorded	4	4	4	7	2	1	18	1	1	1	1
Total expected	5	5	4	7	3	1	20	1	1	1	1

3°09′ S 71°22′ W, 1050 m, 3 September 1989 (D. Harvey) (USNM) (# 2000-75); Madre de Dios, 1♀, Erika, 12°53′ S 71°14′ W, 550–650 m, 4 September 1989 (D. Harvey) (USNM) (# 2000-61); Parque Nacional Manu, Pakitza, 11°55′48′ S 71°15′18′ W, 400 m (USNM), 1♀, 8 September 1989 (R. Robbins) (# 2000-54), 1♀, 7 October 1991 (M. Casagrande), 1♀, 14 November 1990 (W. Rowe). BRAZIL: Amazonas, 1♂, Benjamin Constant, November 1960 (*ex* coll. Jae) (AME) (# 2000-195); São Paulo de Olivença, 1♂, February 1923 (S. Klages) (CMNH) (# 2000-49), 1♂, 03°27′ S 68°48′ W, December 1962 (Kesselring) (USNM), 1♂, Tonantins, August 1923 (S. Klages) (CMNH), 1♀, Rio Purus, Arima, November 1922 (S. Klages) (CMNH) (# 2000-51); Rondônia, vicinity of Cacaulândia, 10°32′ S 62°48′ W, 160–350 m (J. Kemner) (USNM), 1♂, 8 October 1991 (# 1998-1), 1♂, 30 October 1991, 1♀, Ariquemes, 9°36′ S 63°16′ W, 150 m, 9 April 1990 (E. Furtado) (USNM) (# 2000-62).

Etymology. The specific name *matic* is used to create a euphonious play on words when combined with the generic name *Charis*.

Diagnosis. Male *C. matic* differ externally from *C. major* in its more rounded forewing shape and by having four black forewing fringe elements in the apex instead of three, but can only be distinguished from *C. cleonus* and *C. ma* by examining the genitalia. The male genitalia of *C. cleonus* differ in many respects from those of *C. matic*, particularly in the shape of the pedicel, placing this species in the *cleonus* subgroup. The pedicel of the male genitalia of *C. matic* is considerably longer than that of *C. ma* (1.19–1.5 mm; $n = 29$) and the tip is smaller and flatter with smaller spines (see Fig. 18A). The ratio of pedicel length to 'vogelkop' length ranges from 5.9 to 9.3 in *C. matic* compared to 2.7–5.1 in *C. ma* (see Fig. 18B).

Female *C. matic* does not differ externally from *C. cleonus* and *C. ma*. The female genitalia of *C. matic* possess an ostium bursae that is displaced to the very right edge of the eighth sternite, whereas this is only strongly displaced to the right in *C. ma* and centrally positioned in *C. major*. The last two abdominal sternites are intermediate in width between those of *C. major* and *C. ma*, and the seventh sternite is twice the length of that in either species. The female genitalia of *C. cleonus* are distinguished in that species' account.

Biology. *Charis matic* is a common species, the males of which are frequently observed perching as solitary individuals or in small groups in forest understory sunflecks within 2 m of the ground between 13.00 and 15.30 hours. The species appears to be restricted to wet forest habitats. DeVries *et al.* (1994) reported life history details for *Charis cleonus* from Jatun Sacha and Garzacocha in eastern Ecuador, but the only species in the *cleonus* group known from these localities is *C. matic*. They reported that larvae fed on dead leaves.

Distribution. *Charis matic* is widespread, occurring from central-eastern Colombia, through Ecuador to southern Peru and in to western and southwestern Brazil (see Fig. 16).

***Charis ma* Harvey & Hall, sp.n.** (Figs 2G,H; 8D; 14D; 16)

Male. Does not differ externally from *C. cleonus*. *Genitalia* (Fig. 8D): Differ from *C. matic* in the following respects.

Pedicel approximately half as long, 'vogelkop' slightly more elongate and vertically raised with more elongate acanthae; lower valve process slightly shorter.

Female. Does not differ externally from *C. cleonus*. *Genitalia* (Fig. 14D): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, ductus bursae membranous, ostium bursae positioned two-thirds distance towards right edge of sclerotized eighth abdominal sternite, seventh sternite sclerotized.

Material examined. *Holotype*, ♂, COLOMBIA: Meta, Río Negro, 2400 ft, 10 January 1971 (S. Nicolay) (USNM) (# 2000-63). *Allotype*, ♀, PERU: Loreto, Puerto Almendra, Río Nanay, 03°50′ S 73°23′ W, 120 m, 3 September 1995 (R. Robbins) (USNM) (# 2000-76). *Paratypes*, VENEZUELA: Amazonas, 1♂, Piedra de Cucui, 20 September 1946 (R. Lichy) (AME) (# 2000-184). COLOMBIA: Meta, Río Negro, 2400 ft (S. Nicolay) (USNM), 1♂, 10 January 1971, 1♂, 16 January 1971. ECUADOR: Morona-Santiago, 1♂, Gualaquiza-Zamora Road, Bomboiza, 850 m, 28 July 1993 (J. Hall) (JHKW) (dissected). PERU: Loreto, Castaña, 150 m, 0°48′22′ S 75°14′40′ W (G. Lamas) (USNM), 1♂, 19 October 1993 (# 2000-71), 2♂, 22 October 1993, 2♂, Puerto Almendra, Río Nanay, 03°50′ S 73°23′ W, 120 m, 3 September 1995 (J. Grados) (USNM) (# 2000-65), 1♂, 3 km WNW Iquitos, between Rumacocha and Santa Cruz, 1 April 1981 (J. Miller) (AME) (# 2000-267); San Martín, 2♂, km 18 Tarapoto-Yurimaguas Road, 06°27′ S 76°17′ W, 1250 m, 17 November 1998 (R. Robbins) (USNM) (# 2000-66), 2♂, km 7 Pongo del Cainarache-Barranquita, 06°18′ S 76°14′ W, 250 m, 15 November 1998 (R. Robbins) (USNM) (# 2000-67); Junín, 1♂, Chanchamayo, 10 October 1961 (*ex* coll. Jae) (AME) (# 4331). BOLIVIA: Santa Cruz, 4♂, Río Surutú, 350 m (J. Steinbach) (CMNH) (# 2000-47,48, 398, 399), 3♀, 'Peru' [= Bolivia] (# 2000-55,56, 400). BRAZIL: Amazonas, 1♂, Tonantins, August 1923 (S. Klages) (CMNH) (# 2000-50); Acre, Boca do Tejo (K. Brown) (CJC), 1♀, 12 September 1995, 1♂ 26 September 1991 (# 2000-424).

Etymology. The specific name *ma* is used to create a euphonious play on words when combined with the generic name *Charis*.

Diagnosis. Male *C. ma* differ externally from *C. major* in its more rounded forewing shape and in having four black forewing fringe elements in the apex instead of three, but is externally indistinguishable from *C. cleonus* and *C. matic*. The male genitalia of *C. ma* differ from those of its sister species, *C. matic*, in having a considerably shorter pedicel (0.76–1.14 mm; $n = 12$) with a longer and slightly vertically elongate tip that has longer spines (see Fig. 18A). The ratio of pedicel length to 'vogelkop' length ranges from 2.7 to 5.1 in *C. ma* compared to 5.9–9.3 in *C. matic* (see Fig. 18B). The quite different male genitalia of *C. cleonus* are distinguished from those of *C. ma* in that species' account.

Female *C. ma* does not differ externally from *C. cleonus* and *C. matic*. The female genitalia of *C. ma* possess an ostium bursae that is strongly displaced to the right of the eighth sternite but it is not as strongly displaced as in *C. matic*, and the sclerotized area of the last two abdominal sternites is reduced compared to *C. major* and *C. ma*. The female genitalia of *C. cleonus* are distinguished in that species' account.

Distribution. *Charis ma* is known from southern Venezuela to southern Bolivia and western Brazil (see Fig. 16). Although this range overlaps that of the considerably more common *C. matic*, we have not been able to find specimens of both species from the same locality, and label data indicate that *C. ma* may occur in slightly drier forest habitats.

Charis cleonus **subgroup**

Charis cleonus **(Stoll, 1781)** (Figs 2I,J; 9A; 14E; 17)

Papilio cleonus Stoll, 1781. In: Cramer, 1781: 179, Pl. 380, Figs H,I. Type locality: Surinam. Syntype(s) unknown.

Diagnosis. Typical forewing length: male 12.5 mm, female 11.5 mm. *Charis cleonus* can only be distinguished consistently from *C. matic* and *C. ma* on the basis of genitalia, although the ventral surface of the male is typically somewhat paler with slightly less prominent blue iridescence. The vinculum is shallowly but not deeply notched ventrally, the valvae have a broader, pointed lower process and two additional small upper processes connected to the lower one by a broader and shorter sclerotized ribbon, the aedeagus is broader, its base is not swollen and its tip is rounded, and the pedicel, which joins the aedeagus more posteriorly, is broader in ventral view with a broad and bifurcate tip that is medially grooved dorsally.

The female genitalia of *C. cleonus* differ from those of the aforementioned species in having the last three sternal segments heavily sclerotized and fused together, and a somewhat semicircular and laterally pointed last segment with an approximately medially and more posteriorly positioned ostium bursae that projects somewhat outwards instead of being a simple hole. The female genitalia of the externally similar *C. ipiranga* have only a weakly sclerotized eighth sternite with the ostium bursae positioned at its anterior edge within a small invaginated pouch and a membranous sixth sternite.

Taxonomy. Although no type specimen is known for *C. cleonus* (and none is likely to be ever found), the species was well illustrated by Cramer (1775–1782), and because Surinam, the type locality, only harbours *C. cleonus* of this species group, a neotype designation is unwarranted.

Biology. Brévignon & Gallard (1998) report that *C. cleonus* is a common butterfly in French Guiana, where males perch beneath leaves with their wings outspread in understory sunflecks at the end of the morning and beginning of the afternoon.

Distribution. *Charis cleonus* has traditionally been thought to range throughout the Guianas and Amazon basin. However, the morphological phenotype represented by specimens from the type locality is restricted to a smaller area that extends from eastern Venezuela through Guyana and Surinam to the eastern border of French Guiana (see Fig. 17). Kaye (1921) and Barcant (1970) list *C. cleonus* for Trinidad, but the only *cleonus*-like specimen we have dissected from Trinidad (a female in the collection of M. Cock) proved to be *C. argyrea*, a species not previously reported for the island. This suggests that the two species may have historically been confused by Trinidad workers, and the presence of *C. cleonus* on the island clearly needs confirmation.

Material examined. VENEZUELA: Bolívar, San Francisco Yuruani (1000 m), 2♂, CJC (# 2000-426); Qbda. Jaspe, km 40 El Dorado-Santa Elena Road, 1♂ (AN) (# 2000-179); km 115 El Dorado-Santa Elena Road, 1♀ (AN); Yakoo, nr Santa Elena, 1♀ (AN); km 20–40 Santa Elena-Icabarú Road, 1♂ (AN) (# 2000-178). GUYANA: Mahaica-Berbice, Georgetown, 1♂ (BMNH); Cuyuni-Mazaruni, Roraima, 4♂, 3♀ (BMNH); nr Tukeit, Potaro River, 1♂ (USNM); between Mahdia and Uewang Creeks, Potaro River, 4♂ (USNM); Kaiteur Falls, 9♂, 3♀ (USNM) (♂# 1989-74; ♀ # 2000-59), 2♂ (AME); nr Kangu River, Mt Ayanganna, 1♂ (USNM); Pong River, Mt Ayanganna, 2♂ (USNM); Kuiewa River, Mt Ayanganna, 2♂ (USNM) (# 2000-25); Koatse River, Mt Ayanganna, 1♀ (USNM); Moraballi Creek, Essequibo River, 1♂, 1♀ (BMNH); Bartica, 1♂ (BMNH), 1♂ (AME); Carimang River, 2♂, 3♀ (BMNH); Upper Takutu-Upper Essequibo, Nappi Mtn, Kanuku Mts, 5♂ (USNM) (# 2000-24); Nappi Creek, Kanuku Mts, 1♂ (USNM); Upper Demerera-Berbice, Demerera River, 1♂ (BMNH); Rockstone, 1♂ (USNM) (# 1989-76), 1♀ (AME); km 50 Linden-Timehri Road, 2♂, 1♀ (CJC); Kamuni Creek, Timberhead, 1♂ (CJC); East Berbice-Corentyne, King Frederick Falls, Corentyne River, 2♂ (BMNH); Upper Kutari River, 2♂ (BMNH); confluence of Oronoque and New Rivers, 1♂ (BMNH); Camp Jaguar, New River Triangle, 10♂, 9♀ (AME) (♂# 2000–196); Mabura, 1♀ (USNM); no locality data, 2♂ (BMNH), 1♂, 1♀ (CMNH). SURINAM: Paramaribo, Paramaribo, 2♀ (BMNH), 1♂, 1♀ (SMF); Brokopondo, Berg-en-dal, 6♂, 2♀ (BMNH); Para, Geldersland, Surinam River, 1♂, 1♀ (USNM) (♂# 1989-77); Bersaba 1♂, 1♀ (ZMHU); Marowijne, Albina, 2♀ (BMNH); Onoribo, 1♂, 2♀ (BMNH); no locality data, 7♂, 1♀ (BMNH), 5♂ (ZMHU). FRENCH GUIANA: Saint Laurent du Maroni, Saint Laurent du Maroni, 5♂, 7♀ (BMNH); Saint Jean du Maroni, 3♂, 2♀ (USNM), 1♂ (ZMHU); Riviere Mana, 10♂, 29♀ (CMNH) (♀ # 2000-58); 10 km W of Charvein on D10, 2♂ (USNM); Saint Elie, pk 15.5 on D21, 1♂, 2♀ (USNM) (♂ 1989–75); Cayenne, Saül, 3♂, 5♀ (USNM) (♂ # 2000-26, 297); Cayenne, 3♂, 1♀ (BMNH), 1♂ (ZMHU); Montsinéry, 1♀ (USNM) (# 2000-355), 1♀ (CJC); Galion, 2♂ (CJC); Goudronville, Riviere Kourou, 2♂, 1♀ (BMNH); Pied Saut, Riviere Oyapock, 1♂ (CMNH) (# 2000-27); no locality data, 2♂, 3♀ (BMNH).

Charis rocana **Harvey & Hall, sp.n.** (Figs 2K,L; 9B; 14F; 17)

Male. Differs from *C. negro* in having the inner submarginal silver line in apex of ventral forewing entirely absent. *Genitalia* (Fig. 9B): Differ from *C. matic* in the following ways. Vinculum straighter ventrally with no indentation in ventral view; aedeagus not swollen at base and straighter, vesica contains approximately thirteen pairs of short spinelike cornuti; lower valve process very small and positioned above pedicel; pedicel short and produced into two small posteriorly rounded, smooth lobes.

Female. Differs from *C. negro* in the following ways: inner submarginal silver line in apex of ventral forewing entirely absent, orange-brown scaling proximal to outer submarginal silver line reduced. *Genitalia* (Fig. 14F): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, long posterior section of ductus bursae sclerotized, unsclerotized ostium bursae positioned centrally within invaginated pouch of unsclerotized eighth sternite, seventh sternite unsclerotized.

Material examined. Holotype, ♂, BRAZIL: Amapá, Upper Rio ‘Rocana’ [= Urucaúa], June 1918 (S. Klages) (CMNH) (# 2000-46). *Allotype*, ♀, BRAZIL: sama data as holotype (# 2000-21). *Paratypes*, BRAZIL: same locality data as holotype (S. Klages) (CMNH), 1♂, June 1918, 1♂, July 1918 (# 1989-98).

Etymology. This species is named after its type locality, using the more euphonious, although incorrect, label data spelling of ‘rocana’ instead of ‘urucaúa’.

Diagnosis. *Charis rocana* is a highly derived species and one of the very few in the *cleonus* group that can be identified on the basis of wing pattern alone. Both sexes have no inner silver submarginal line on the ventral forewing. The male genitalia are unique within the group in possessing such an elongate vinculum, such a posteriorly directed upper valve complex, such a straight and long aedeagus, a long series of paired aedeagal cornuti, and a relatively simple, short bilobed pedicel without any acanthae at its tip. Unique apomorphies of the female genitalia include a very long sclerotized posterior portion to the ductus bursae, and an entirely desclerotized ostium bursae and eighth and seventh abdominal sternites.

Distribution. *Charis rocana* is currently only known from a single locality in the northeastern Brazilian state of Amapá, close to the eastern border of French Guiana (see Fig. 17).

Charis negro **Harvey & Hall, sp.n.** (Figs 2M,N; 9C; 14G; 17)

Male. Forewing length 12.5 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal surface*: Forewing ground colour black; two parallel submarginal silver lines, inner one approximately twice thickness of outer one, 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 scaling at margin; fringe white with black scaling at distal tips of veins Cu1 to M1. Hindwing same as forewing except fringe entirely white. *Ventral surface*: Forewing ground colour pale black with faint dark grey-blue iridescence, brown at anal margin; 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 towards base of cell Cu2; postdiscal band of faint black spots extends diagonally outwards from a point halfway between wing base and tornus to vein M3 then extends sharply inwards to vein M1; distal portion of wing same as dorsal surface except inner submarginal silver line restricted to a square in cell R4 + 5 and a faint streak in cell R3 in apex (also occasionally present in upper half of cell M1), outer submarginal silver line twice as broad, and dark orange-brown scaling inbetween silver markings greatly reduced and largely restricted to apex. Hindwing same as forewing except two additional faint black spots visible towards base of cell Sc + R1 above discal cell, postdiscal line of spots a rounded semicircle, no inner submarginal silver present, and submarginal dark orange-brown scaling only faintly visible in tornus. *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 and abdomen black, long brown setae at tip of abdomen. All legs brown, forelegs with some faintly iridescent grey-blue setae. *Genitalia* (Fig. 9C): Uncus rounded and more elongate dorsally, shallowly indented at posterior dorsal margin, tegumen and falces of average size and shape for family, vinculum elongate, narrow, posteriorly bowed in dorsal half and shallowly indented at base of valvae in ventral view; aedeagus long, narrow, arched and rounded at tip, vesica curves to right and contains approximately fifteen narrow spinelike cornuti at tip; pedicel extends from near base of aedeagus as narrow tube to form elongate posterior projection slightly up-turned at tip with fine acanthae along dorsal margin, enveloped by sclerotized tissue ventrally and laterally, and unsclerotized tissue dorsally; valvae consist of a narrow lower process and a slightly longer upwardly directed and pointed upper process joined to the lower one by a short ribbon of sclerotized tissue and dorsally over the aedeagus by a narrow sclerotized transtilla at the valve base.

Female. Differs from the male in the following. Forewing length 11.5 mm. Distal margin of forewing slightly more convex. *Dorsal surface*: Forewing ground colour brown; pattern of dark brown spots as on ventral forewing of male except two additional postdiscal dark brown spots visible towards base of cell R4 + 5 and very faint band of spots visible immediately proximal to postdiscal band, distal orange-brown scaling paler, inner submarginal silver line thinner, fringe scaling brown instead of black with additional brown scaling at distal tips of cells 2A and Cu2. Hindwing ground colour brown; pattern of dark brown spots as on ventral hindwing of male except very faint band of spots visible immediately proximal to postdiscal band, distal orange-brown scaling paler, inner submarginal silver line thinner. *Ventral surface*: Forewing ground colour brown; faint orange-brown scaling surrounds dark brown spots, especially prominent towards wing base, distal orange-brown scaling paler and prominent along entire proximal edge of outer submarginal silver line. Hindwing with same differences as forewing except orange-brown scaling along proximal edge of outer submarginal silver line less prominent. *Head*: Labial palpi and frons and antennal segments paler brown. *Body*: Thorax and abdomen entirely brown. All legs paler brown. *Genitalia* (Fig. 14G): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, posterior portion of ductus bursae sclerotized and coiled almost 360° clockwise in ventral view, opening of ostium bursae large, ostium positioned centrally in sclerotized eighth abdominal sternite with broad middle and narrow lateral margins, seventh sternite sclerotized and 'U'-shaped.

Material examined. Holotype, ♂, VENEZUELA: Amazonas, Mawari-Anejidi, 150 m, 16 May 1950 (R. Lichy) (AME) (# 1996-81). *Allotype*, ♀, VENEZUELA: Amazonas, San Carlos de Río Negro, 1°56′ N 67°03′ W, 6–12 December 1984 (R. Brown) (USNM) (# 1989-78). *Paratypes*, VENEZUELA: Amazonas, Yavita, 128 m (R. Lichy) (AME), 1♀, 28 August 1947 (# 2000-8), 1♀, 5 September 1947, 1♀, 8 September 1947, 1♀, 29 September 1947 (# 2000-9), 1♀, nr Caño Matacha, 440 m, 1 May 1950 (R. Lichy) (AME) (# 2000-345), Mawari-Anejidi, 150 m (R. Lichy) (AME), 1♀, 12 May 1950, 1♀, 16 May 1950 (# 2000-346), 1♂, Cerro de Neblina Base Camp, 0°50′ N 66°9′ W, 140 m, 24 November–1 December 1984 (R. Brown) (USNM). COLOMBIA: Vaupés, 2♂, Río Uaupés, Río 'Caiary' [= Querary], November 1906 (H. Schmidt) (AMNH) (# 1998-5), 1♂, Mitú, Río Uaupés, 25 October 1980 (*ex* coll. P. Smart) (AME) (# 2000-190). BRAZIL: Amazonas, 1♀, Tonantins, August 1923 (S. Klages) (CMNH) (# 2000-12), 1♂, Manacapuru, October 1923 (S. Klages) (CMNH) (# 1989-97).

Etymology. This species is named after the Rio Negro, which extends the length of its known distribution.

Diagnosis. *Charis negro* is putatively the most basal member of the upper Amazon clade, and one of only three species in that clade, including *C. ariquemes* and *C. manu*, that do not have male genitalia with a very posteriorly elongate and asymmetrical pedicel with acanthae on dorsal and ventral surfaces. The male genitalia of *C. negro* are perhaps most similar to those of *C. ariquemes* but differ in having a more strongly bowed aedeagus with a row of longer cornutal spines that curves to the right, a broader and more upwardly curved upper valve process and a longer and broader pedicel with acanthae only on its dorsal instead of ventral surface. The female genitalia have a pronounced stretched ovoid-shaped eighth abdominal sternite and are unique in possessing a sclerotized posterior portion of the ductus bursae that coils almost 360°. The putative female of *C. humaita* also exhibits a markedly coiled ductus bursae, but it only coils about 180°.

Distribution. *Charis negro* appears to be confined to the area between the Rio Solimoes in northwestern Brazil (Amazonas), from Tonantins to Manacaparu, and the Rio Negro, from Manacaparu to the vicinity of Tapurucaura, and on both banks of the upper Rio Negro in southern Venezuela (Amazonas) and eastern Colombia (Vaupés) (see Fig. 17).

***Charis ariquemes* Harvey & Hall, sp.n.** (Figs 2O,P; 9D; 14H; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 9D): Differ from *C. negro* in the following ways: Overall smaller and more compact; vinculum shorter; aedeagus substantially shorter and straighter with more pointed tip, vesica straight with approximately twelve short spinelike cornuti; pedicel shorter and narrower in ventral view, slightly broader distal portion broadest at middle and gradually tapering to more pointed tip in ventral view, and contains fine acanthae on ventral surface only; lower valve process slightly shorter and

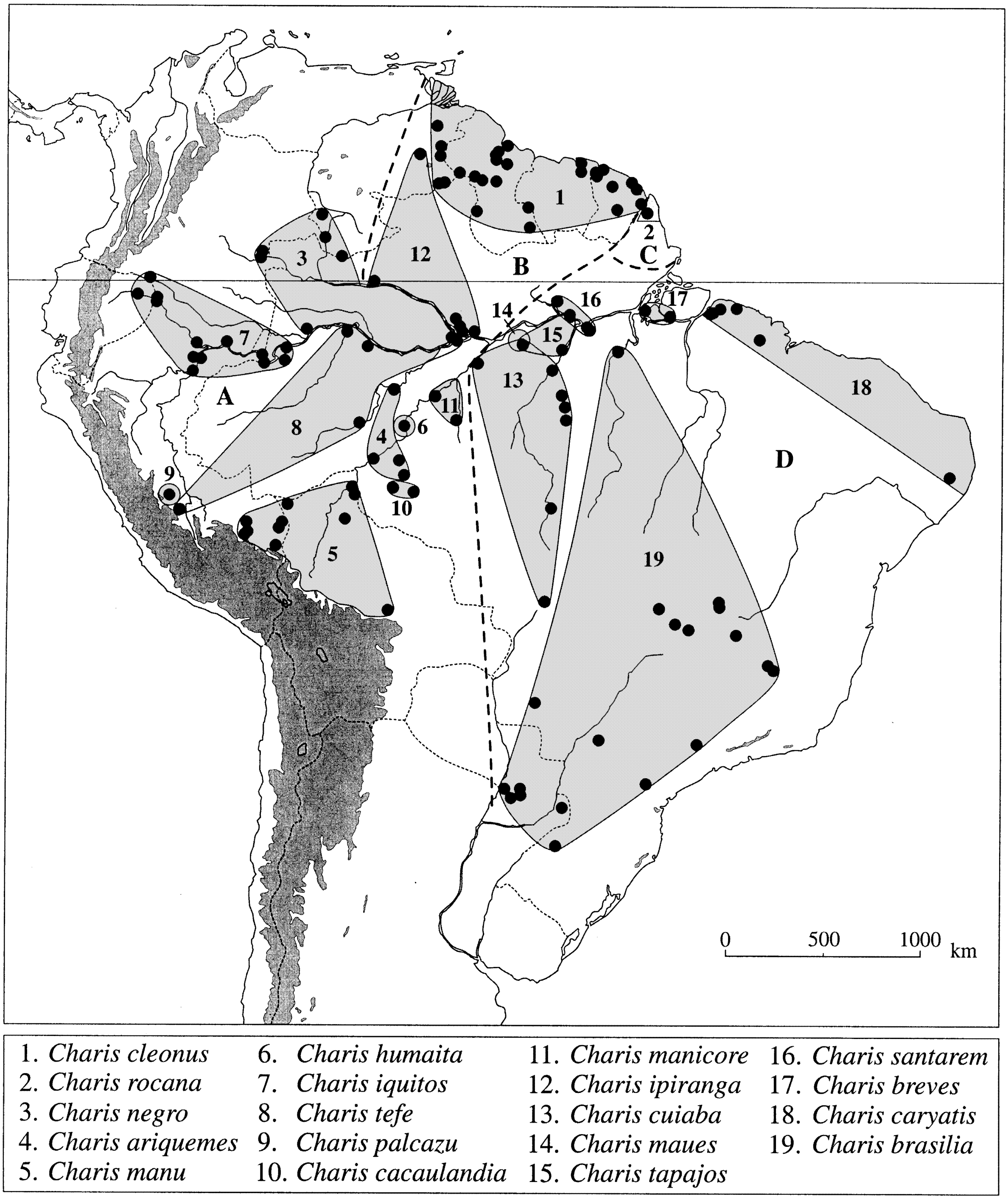

Fig. 17. Map of South America illustrating distributions of *cleonus* subgroup species.

narrower, upper valve process narrower and slightly further from lower process, section between base of these processes and vinculum much broader.

Female. Does not differ externally from *C. negro. Genitalia* (Fig. 14H): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized, ostium bursae positioned centrally at anterior margin of sclerotized eighth sternite and directed slightly to left in ventral view, seventh sternite sclerotized.

Material examined. Holotype, ♂, BRAZIL: Rondônia, Ariquemes, 9°36′ S 63°16′ W, 150 m, 10 April 1990 (E. Furtado) (in accordance with Brazilian law, to be deposited in the Departamento Zoologia, Universidade Federal do Paraná, Brazil (UFPR)) (# 1996-77). *Allotype*, ♀,

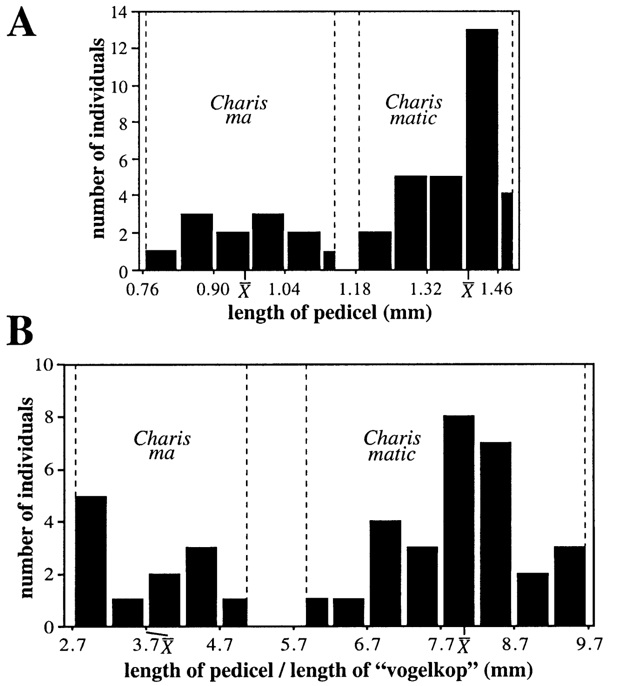

Fig. 18. Histograms illustrating the bimodal distribution of measurements for certain male genital pedicel structures, and aiding the diagnosis of *Charis matic* and *C. ma*. Mean values are shown on the *x* axis for each species. A, Overall length of pedicel from distal tip to base of valvae; B, ratio of pedicel length to 'vogelkop' length.

BRAZIL: same locality data as holotype, 12 April 1990 (E. Furtado) (USNM) (# 2000-32). *Paratypes*. BRAZIL: Amazonas, 3♂, Rio Purus, Arima, November 1922 (S. Klages) (CMNH) (# 1989-91,96); Rondônia, 1♀, Jaciparaná, 22 June 1989 (C. Callaghan) (CJC) (# 2000-431), 1♂, Itapua do Oeste, 23 June 1989 (C. Callaghan) (CJC) (# 2000-430), 1♂, same data as allotype (USNM) (# 2000-45).

Etymology. This species is named after its type locality, Ariquemes.

Diagnosis. The male genitalia of *C. ariquemes* are perhaps most similar to, and are distinguished from, those of *C. negro* in the latter account. The male genitalia are consistently small for the *cleonus* group, and possess a uniquely bulbous tip to the pedicel with acanthae present only on the ventral surface, a character it shares only with *C. manu*. The eighth abdominal sternite of the female genitalia is reduced to a small ovoid anterior portion.

One female in the USNM collected in the vicinity of Ariquemes has quite different genitalia (# 2000-33), with an elongate and strongly curved distal sclerotized portion to the ductus bursae somewhat approximating that of *C. negro*. Because the genitalia of this specimen do not match any known species, the female of neighbouring *C. humaita* is unknown, and the specimen in question was collected on a different day to any of the other specimens from that locality (suggesting that it may have been collected in a different location), we suggest that this female specimen may represent *C. humaita*. This hypothesis requires confirmation through the collection of females in the vicinity of Humaitá or males of *C. humaita* near Ariquemes.

Distribution. *Charis ariquemes* is currently known to occupy a range extending from the middle Rio Purus (Amazonas) to the Rio Madeira and its tributary the Rio Jamari (Rondônia), in southwestern Amazonian Brazil (see Fig. 17).

***Charis manu* Harvey & Hall, sp.n.** (Figs 2Q,R; 7; 10A; 14I; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 10A): Differ from *C. negro* in the following ways. Aedeagus shorter and straighter with more pointed tip, vesica with no cornuti; pedicel shorter, consisting of posteriorly tapering triangle with sparse very fine acanthae on ventral surface only; lower valve process very elongate, upwardly curving, and slightly asymmetrical in ventral view with tips turned outwards, ventrally notched at base, upper valve process slightly shorter and gradually narrowing to abruptly up-turned tip, section between base of these processes and vinculum broader.

Female. Does not differ externally from *C. negro*. *Genitalia* (Fig. 14I): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized and ending in blind sac, ostium bursae positioned approximately two-thirds distance towards right side at anterior margin of sclerotized and ribbed, ovoid eighth sternite, seventh and shorter sixth sternites sclerotized.

Material examined. *Holotype*, ♂, PERU: Madre de Dios, 10 km N Puerto Maldonado, 12°36′ S 69°11′ W, 200 m, 26–31 December 1993 (C. Tello) (USNM) (# 1996-78). *Allotype*, ♀, PERU: Madre de Dios, same locality data as holotype, 11–15 January 1994 (C. Tello) (USNM) (# 2000-347). *Paratypes*, PERU: Madre de Dios, 1♀, 5 km ENE Shintuya, Cerro Pantiacola, 460 m, 21 July 1980 (J. Douglass) (AME) (# 2000–348), 3♂, 1♀, Erika, 12°53′ S 71°14′ W, 550–650 m, 4 September 1989 (D. Harvey & R. Robbins) (USNM) (♂ # 1989-80) Parque Nacional Manu, Pakitza, 11°55′48′ S 71°15′18′ W, 400 m (USNM), 1♂, 9 April 1991 (D. Harvey), 2♀, 19 April 1991 (D. Harvey), 5♂, 20 April 1991 (D. Harvey & N. Clarke), 1♂, 1♀, 21 April 1991 (D. Harvey), 1♂, 3♀, 22 April 1991 (D. Harvey), 1♂, 26 April 1991 (D. Harvey), 1♀, 27 April 1991 (N. Clarke), 1♀, 28 April 1991 (D. Harvey), 4♂, 2♀, 29 April 1991 (D. Harvey), 1♀, 2 May 1991 (N. Clarke), 1♂, 3 May 1991 (D. Harvey), 1♀, 4 May 1991 (N. Clarke), 1♂, 11 May 1991 (N. Clarke), 1♀, 12 May 1991 (N. Clarke), 2♂, 8 September 1989 (D. Harvey), 1♀, 9 September 1989 (R. Robbins), 2♀, 10 September 1989 (D. Harvey), 1♀, 12 September 1989 (R. Robbins), 2♀, 18 September 1989 (D. Harvey), 3♂, 19 September 1989 (D. Harvey), 2♂, 4♀, 21 September 1989 (D. Harvey), 1♂, 24 September 1989 (R. Robbins), 2♀, 26 September 1991 (O. Mielke), 1♂, 27 September 1991 (O. Mielke), 2♂, 2♀, 28 September 1991 (O. Mielke, M. Casagrande & R. Robbins), 2♂, 2♀, 29 September 1991 (O. Mielke & R. Robbins), 1♀, 1 October 1991 (G. Lamas), 2♂, 2 October 1991 (O. Mielke & R. Robbins), 1♂, 1♀, 3 October 1991 (M. Casagrande), 2♂, 1♀, 4 October 1991

(M. Casagrande & R. Robbins), 1♂, 5 October 1990 (R. Robbins), 1♂, 5 October 1991 (M. Casagrande), 3♂, 2♀, 6 October 1990 (R. Robbins), 2♂, 7 October 1987 (M. Pogue), 1♀, 8 October 1990 (R. Robbins), 1♂, 9 October 1991 (M. Casagrande), 1♂, 19 October 1990 (G. Lamas), 2♂, 19 October 1991 (O. Mielke), 1♀, 21 October 1990 (W. Rowe), 1♀, 23 October 1990 (W. Rowe), 1♀, 25 October 1991 (O. Mielke), 1♀, 27 October 1990, 1♂, 29 October 1990 (J. MacDonald), 1♂, 30 October 1990 (J. MacDonald), 1♀, 31 October 1990 (W. Rowe), 2♀, 2 November 1990 (W. Rowe), 1♂, 1♀, 3 November 1990 (W. Rowe), 1♂, 4 November 1990 (J. MacDonald), 1♀, 10 November 1990 (W. Rowe), 2♀, 12 November 1990 (W. Rowe), 1♀, 14 November 1990 (W. Rowe), Puerto Maldonado, 12°36′ S 69°11′ W, 250 m (C. Tello) (USNM), 1♂, 4 November 1993, 1♀, 3 November 1993, same locality data as holotype (C. Tello) (USNM), 1♀, 26–30 September 1993 (# 2000-5), 1♀, 11–15 October 1993, 1♂, 21–25 October 1993, 1♀, 26–31 October 1993, 1♀, 1–5 November 1993, 1♂, 6–10 November 1993, 1♀, 11–15 November 1993, 1♂, 1♀, 16–20 November 1993, 1♀, 21–25 November 1993, 2♂, 1♀, 26–30 November 1993, 1♀, 29 November 1993, 1♂, 1–5 December 1993, 3♂, 21–25 December 1993, 1♀, 26–31 December 1993, 1♀, 1–4 January 1994, 0–2 km W Puerto Maldonado, 250 m (AME), 1♂, 16 August 1981 (L. Miller), 1♀, 7 August 1981 (L. Miller), 30 km SW Puerto Maldonado, 300 m (USNM), 4♂, 1♀, 19 October 1983 (S. Nicolay) (♂ # 1989-71; ♀ # 2000-7), 1♀, 21–25 November 1979 (J. Heppner), 2♂, 1♀, 26–30 November 1979 (J. Heppner), 8♂, 9♀, 50 km WSW Puerto Maldonado, 12°45′ S 69°35′ W, 250♂, Sep–November 1992 (C. Tello) (USNM) (♂ # 1996–79 2000–295), 2♀, Reserva Tambopata, 12°50′ S 69°17′ W, 300 m, 25 October 1991 (O. Mielke) (USNM), 1♂, Boca Rio La Torre, 26 July 1980 (C. Callaghan) (CJC); Puno, Río Huacamayo & Carabaya, La Union (G. Ockenden) (BMNH), 2♂, 3100 ft, June 1904 (# 1999-122-123), 1♂ 2000 ft, December 1904, 1♂, 1♀, Yahuarmayo, 1200 ft, Feb–March 1912 (H. & C. Watkins) (BMNH) (♂ # 1999-126). BOLIVIA: Pando, 1♂, S. Cobija, El Porvenir, 1 June 1997 (C. Callaghan) (CJC) (# 2000-437); Beni, Guayará-Merim (ZSM), 1♂, 15 May 1954, 1♂, 9 May 1954, 1♀, 17 May 1954, 1♂, Villa Bella, 10 October 1909 (Haseman) (CMNH) (# 2000-20), 1♂, Río Benecito, 19–25 July 1960 (*ex* coll. M. Simon) (AME) (# 1996-80); Santa Cruz, Río Yapacani, 600 m (J. Steinbach) (CMNH), 1♂, March 1915 (# 1989-95), 1♀, August 1913 (# 2000-6).

Etymology. This species is named after the Parque Nacional Manu, where the majority of specimens have been collected.

Diagnosis. The male genitalia of *C. manu* are highly autapomorphic and possess very long and asymmetrical lower valve processes (readily seen protruding from the tip of the abdomen under a microscope or field lens), short slightly asymmetrical upper valve processes that are markedly up-turned at the very tips, and a short triangular tip to the pedicel with acanthae only ventrally. The female genitalia have the ostium bursae displaced to the right and a sclerotized sixth abdominal sternite, found elsewhere in the upper Amazon clade only in *C. iquitos* and *C. tefe*, respectively.

Biology. Several females were observed ovipositing eggs on the underside of dead and decomposing leaves on the forest floor during April 1991 at Pakitza, Parque Manu, Madre de Dios, Peru (Harvey, unpublished data). Additional females were induced to oviposit in captivity by confining them with leaf litter. The resulting larvae were fed decaying leaves and survived through several instars, but failed to reach pupation.

Distribution. *Charis manu* ranges throughout the tributaries of the upper Rio Madeira drainage in southern Peru (Madre de Dios, Puno) and northern Bolivia (Pando, Beni, Santa Cruz) (see Fig. 17).

Charis humaita **Harvey & Hall, sp.n.** (Figs 3A,B; 10B; 14J; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 10B): Differ from *C. negro* in the following ways. Vesica straight with approximately six downwardly pointing long spinelike cornuti; distal portion of pedicel substantially more elongate, bent upwards at middle at about 80° and diagonally to right in ventral view, contains very fine acanthae on both slightly uneven dorsal and ventral surfaces; lower valve process points slightly upwards, upper valve process slightly shorter, more bulbous at base and narrower towards tip.

Female. Unknown with certainty, but see the diagnosis of *C. ariquemes*. For future reference, a putative example of the female genitalia of *C. humaita* is figured (Fig. 14J), based on a specimen from Ariquemes.

Material examined. *Holotype*, ♂, BRAZIL: Amazonas, Rio Madeira, Humaitá, Jul–September 1906 (W. Hoffmanns) (BMNH) (# 1999-127).

Etymology. This species is named after its type locality, Humaitá.

Diagnosis. In having male genitalia with a very posteriorly elongate and asymmetrical pedicel with acanthae on dorsal and ventral surfaces, *C. humaita* can be placed in a group with *C. iquitos*, *C. tefe* and *C. palcazu*. The pedicel of *C. humaita* is the longest of these species and is the only one to be markedly directed to the right instead of the left, the upper valve complex is short and more distantly separated from the lower valve processes, and the aedeagal cornuti are fewer in number, longer and form a straighter line than those of *C. iquitos*. The genitalia of a putative *C. humaita* female have a very broad posterior sclerotized portion to the ductus bursae that is coiled approximately 180°.

Distribution. *Charis humaita* is currently only known from the unique holotype from Humaitá on the upper-central Rio Madeira in southern Amazonian Brazil (Amazonas) (see Fig. 17). Ferrari & Lopes (1992a,b) suggest that the marmoset species in the genus *Callithrix* that is endemic to the Humaitá region is restricted to the east bank of the Rio Madeira with the Rio Jiparaná as its southern range boundary. Because these primates exhibit a similar pattern of distributions along the Rio Madeira and Rio Tapajós as *Charis cleonus* group species (see also the *Distribution* section of *C. maues*), *C. humaita* may occupy a similar range.

Charis iquitos **Harvey & Hall, sp.n.** (Figs 3C,D; 6C,D; 10C; 14K; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 10C): Differ from *C. negro* in the following ways. Aedeagus straighter, vesica with numerous short spinelike cornuti; distal portion of pedicel substantially longer, broadest at middle in lateral and ventral views, curves slightly to left in ventral view, contains very fine acanthae on both dorsal and ventral surfaces; lower valve process shorter and broader, upper valve process slightly narrower and down-turned at tip, section between base of these processes and vinculum much broader.

Female. Does not differ externally from *C. negro*. *Genitalia* (Fig. 14K): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized, ostium bursae positioned centrally at anterior margin of ovoid eighth sternite and directed to left in ventral view, eighth sternite heavily sclerotized with two broad, slightly asymmetrical indentations, seventh sternite long and sclerotized.

Material examined. *Holotype*, ♂, PERU: Río Nanay, Puerto Almendra, 03°50′S 73°23′W, 120 m, 3 September 1995 (J. Grados) (USNM) (# 1996-64). *Allotype*, ♀, PERU: Río Sucusari, Explornapo-ACEER, 03°14′S 72°55′W, 140 m, 5 September 1995 (R. Robbins) (USNM). *Paratypes*, COLOMBIA: Putumayo, 1♂, 'Upper Putumayo', 3 January 1932 (MNHN) (# 2000-2); Amazonas, Leticia, 1♂, November 1975 (AME) (# 1996-68), 2♂, 1♀, 14 December 1980 (C. Callaghan) (CJC). ECUADOR: Napo, 1♀, 'Upper Río Napo' (Bassler) (AMNH). PERU: Loreto, Río Aguas Negras, 0°31′38′S 75°15′41′W, 150 m (USNM), 4♂, 2♀, 1 March 1994 (G. Lamas & R. Robbins) (♂ # 1996-65; ♀ # 2000-11), 1♂, 1♀, 3 March 1994 (R. Robbins), 1♀, 4 March 1994 (R. Robbins), 1♂, Arcadia, 0°59′37′S 75°18′55′W, 150 m, 6 November 1993 (R. Robbins) (USNM), Castaña, 0°48′22′S 75°14′40′W, 150 m (R. Robbins) (USNM), 3♂, 21 October 1993, 2♂, 24 October 1993, 1♂, 29 October 1993, Río Sucusari, Explornapo-ACEER, 03°14′S 72°55′W, 140 m (USNM), 6♂, 5 September 1995 (R. Robbins & A. Caldas), 1♂, 2♀, 7 September 1995 (R. Robbins & A. Caldas) (♀ # 2000-350), 1♂, 9 September 1995 (A. Caldas), 2♂, 12 September 1995 (D. Harvey & A. Caldas) (# 1996-66), 3♂, 1♀, 13 September 1995 (A. Caldas), 4♂, 2♀, 16 September 1995 (D. Harvey & A. Caldas), 1♂, 1♀, 17 September 1995 (D. Harvey & J. Grados), 1♂, 19 September 1995 (D Harvey), 1♂, 23 September 1993 (D. Harvey), 2♂, 6♀, Río Nanay, Puerto Almendra, 03°50′S 73°23′W, 120 m, 3 September 1995 (R. Robbins, J. Grados & D. Harvey) (USNM) (♂ # 2000-296; ♀ # 2000-349), 1♀, Nauta (A. Moss) (BMNH), Iquitos, 1♂, December 1932 (MNHN), 1♂ 1894 (Stuart) (BMNH), 1♂, 2♀ (LeMoult) (AME) (♂ # 1996-67; ♀ # 6243), 2♂, Pebas 1880 (M. de Mathan) (BMNH) (# 1999-124). BRAZIL: Amazonas, 1♂, Benjamin Constant, November 1930 (Jae) (AME) (# 1996-69), São Paulo de Olivença, 2♂, 1♀, January 1933 (S. Waehner) (BMNH), 1♂, Jun–July 1935 (A. Moss) (BMNH), 1♀, August 1907 (M. de Mathan) (BMNH), 1♀,February 1923 (S. Klages) (CMNH) (# 1996-72), 2♀, São João, 1913 (BMNH) (# 2000-82).

Etymology. This species is named after Iquitos, the town at the centre of its distribution.

Diagnosis. In having male genitalia with a very posteriorly elongate and left curving pedicel with acanthae on dorsal and ventral surfaces, *C. iquitos* can be placed in a group with *C. tefe* and *C. palcazu*. The shapes of the pedicel and valvae of *C. iquitos* are most like those of *C. tefe* but the upper valve processes are slightly shorter and more inwardly curved in dorsal view, the lower valve processes are slightly shorter, and its aedeagus possesses a curving band of small cornuti. The female genitalia of the two species are rather dissimilar, those of *C. iquitos* possessing a well sclerotized ovoid eighth abdominal sternite with two deep indentations, the right one containing the slightly displaced ostium bursae which is directed towards the left. The seventh sternite is broader and not 'U'-shaped, and the sixth sternite is not sclerotized.

Biology. Females were observed ovipositing on leaf litter on the forest floor at the ACEER facility, Loreto, Peru, during September 1995 (Harvey, unpublished data).

Distribution. *Charis iquitos* ranges from the southern border of Colombia (Putumayo) through far eastern Ecuador (Napo) to northern Peru (Loreto) and western Amazonian Brazil (Amazonas) (see Fig. 17).

Charis tefe **Harvey & Hall, sp.n.** (Figs 3E,F; 10D; 14L; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 10D): Differ from *C. negro* in the following ways. Aedeagus straighter, vesica with no cornuti; distal portion of pedicel substantially longer, curves to left towards tip in ventral view, contains very fine acanthae on both dorsal and ventral surfaces; upper valve process slightly narrower and less up-turned, section between base of these processes and vinculum much broader.

Female. Does not differ externally from *C. negro*. *Genitalia* (Fig. 14L): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized, ostium bursae positioned centrally at anterior margin of sclerotized eighth sternite with posterior 'cone'-shaped blind sac at opening (intraspecifically variable in size), eighth sternite posteriorly bulbous in elongate medial section, posterior section shaped like a figure of eight, heavily ribbed, with two shallow indentations, 'U'-shaped seventh and narrow sixth sternites sclerotized.

Material examined. *Holotype*, ♂, BRAZIL: Amazonas, Fonte Boa, July 1906 (S. Klages) (BMNH) (# 1999-125). *Allotype*, ♀, BRAZIL: Amazonas, Manacapuru, September 1923 (S. Klages) (CMNH) (# 2000-31). *Paratypes*, PERU: Junín, 1♂, Río 'Tono' [= Toro], 1200 ft (Watkins) (MNHN) (# 2000-4), 1♀, La Merced, 2500 ft, August 1903 (Watkins & Tomlinson) (BMNH) (# 2000-83). BRAZIL: Amazonas, Fonte Boa (S. Klages) (BMNH), 1♂, July 1906 (# 2000-36), 1♂, November 1906, 1♂, Juruti, April 1905 (M. de Mathan) (BMNH) (# 1999-128), Tefé, 1♀, January 1905 (M. de Mathan) (BMNH), 1♂, June 1906 (W. Hoffmanns) (BMNH), 2♂, September 1907 (M. de Mathan) (BMNH), 2♂, October 1907

(M. de Mathan) (BMNH), 1♂, 1♀ (H. Bates) (BMNH), 1♂ (A. Moss) (BMNH), 6♂, October 1930 (coll. LeMoult) (AME) (# 1996-73; 6242), 1♀, 4 December 1919 (Parish) (CMNH) (# 2000-30), 1♂, 5 December 1919 (Parish) (CMNH), 1♂, 1♀, 16 December 1919 (Parish) (CMNH) (♂ # 1989-92; ♀ # 2000-352), 1♂, 26 January 1920 (Parish) (CMNH), Manacapuru (S. Klages) (CMNH), 1♂, March 1925, 1♂, 1♀, March 1926 (♀ # 2000-351), 2♂, April 1925 (# 2000-40), 1♂, April 1926, 10♂, 6♀, September 1923 (♂ # 1989-93 and 94 2000-37,39), 2♂, October 1923 (# 2000-41,42), 1♂, October 1925 (# 2000-38), 1♂, Rio Purus, 'Hyatanahan' [Huitanaã], February 1922 (S. Klages) (CMNH) (# 1996-71).

Etymology. This species is named after the small town of Tefe, the classic collecting locality of H. W. Bates (as Ega) at the centre of its distribution.

Diagnosis. The male genitalia of *C. tefe* are perhaps most similar to, and are distinguished from, those of *C. iquitos* in the latter account. The female genitalia have an unusual 'figure of eight'-shaped posterior portion to the last abdominal sternite with indentations at the broadest points, a variably sized 'cone'-shaped blind sac at the posterior entrance of the ostium bursae and a sclerotized sixth sternite, a character shared only with *C. manu* among the upper Amazon clade species.

Distribution. *Charis tefe* has a relatively broad range that extends from central Peru (Junín) to the Manaus area in central Brazil (Amazonas), encompassing the Rio Juruá and at least the upper Rio Purus (see Fig. 17). It seems likely that those historical specimens labelled Manacaparu, on the north bank of the Rio Solimoes, actually originated on the south bank, because *C. negro* is known to occupy the north bank.

Charis palcazu **Harvey & Hall, sp.n.** (Figs 3G,H; 11A; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 11A): Differ from *C. negro* in the following ways. Aedeagus straighter, dorsally swollen near middle, dorsoventrally bifurcate at tip, vesica with no cornuti; distal portion of pedicel substantially longer, broadest at middle in ventral view, curves very slightly to left at tip in ventral view, contains very fine acanthae on both dorsal and ventral surfaces; lower valve process longer, angular at tip and directed upwards in lower half, upper valve process very elongate and sharply up-turned towards tip, section between base of these processes and vinculum much broader.

Female. Unknown.

Material examined. *Holotype*, ♂, PERU: Pasco, Río Chuchurras, Río Palcazu, 320 m (W. Hoffmanns) (BMNH) (# 1999-120). *Paratypes*, PERU: Pasco, 4♂, same data as holotype (BMNH) (# 1999-121).

Etymology. This species is named after its type locality, Río Palcazu.

Diagnosis. The male genitalia of *palcazu* differ from those of the similar *C. tefe* and *C. iquitos* by possessing a broad and bifurcate aedeagal tip, no aedeagal cornuti, a pedicel that bends only very weakly to the left, a considerably longer upper valve process that is up-turned at its tip and not inwardly curved in dorsal view, and a longer lower valve process that is directed upwards to almost touch the upper process.

Distribution. *Charis palcazu* is currently only known from the upper Río Ucayali drainage in central Peru (Pasco) (see Fig. 17).

Charis cacaulandia **Harvey & Hall, sp.n.** (Figs 3I,J; 11B; 15A; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 11B): Differ from *C. negro* in the following ways. Aedeagus slightly straighter, vesica with no cornuti; pedicel narrower in ventral view, distal portion slightly longer and bifurcate at tip, contains very fine acanthae on dorsal surface; upper valve process narrows more gradually towards tip and slightly downwardly pointed, serrate along distal two-thirds of dorsal margin.

Female. Does not differ externally from *C. iquitos*. *Genitalia* (Fig. 15A): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized with small section ending in a blind sac, ostium bursae positioned centrally at anterior margin of eighth sternite and directed slightly to left in ventral view, eighth sternite weakly and unevenly sclerotized, heavily ribbed, and completely desclerotized medially, seventh sternite sclerotized.

Material examined. *Holotype*, ♂, BRAZIL: Rondônia, vicinity of Cacaulândia, 10°32′ S 62°48′ W, 160–350 m, 12 October 1991 (J. Kemner) (to be deposited in the UFPR) (# 2000-28). *Allotype*, ♀, BRAZIL: Rondônia, same locality data as holotype, 9 October 1991 (J. Kemner) (USNM). *Paratypes*, BRAZIL: Rondônia, same locality data as holotype (J. Kemner) (USNM), 1♂, 1♀, 8 October 1991, 1♀, 9 October 1991 (# 2000-357), 1♂, 13 October 1991 (# 1996–76), 1♀, 15 October 1991 (# 2000–356), 1♂, 19 October 1991 (# 2000–299), 1♂, 1♀, 20 October 1991 (♀ # 2000-14), 1♂, 23 October 1991, 1♂, 1♀, 24 October 1991, 1♂, 1♀, 25 October 1991 (♀ # 2000-13), 1♂, 4 November 1989 (T. Emmel) (FSCA), 1♀, 21 March 1991 (T. Emmel, L. Groce & J. Nation) (FSCA), 1♂, Jaru, 250 m, 10 August 1976 (C. Callaghan) (CJC) (# 2000-429).

Etymology. This species is named after its type locality, Cacaulândia.

Diagnosis. *Charis cacaulandia* is putatively the most basal member of the lower Amazon clade, and it is the only species with the inner silver submarginal line on the ventral forewing reduced to an apical fleck whose male genitalia have a serrate dorsal margin to the upper valve process. The male genitalia are most similar to those of the externally readily distinguishable *C. cuiaba*, but have a shorter pedicel with a broader and more pronoucedly bifurcate tip, valvae that extend only posterior to the vinculum and a shorter, broader and straighter upper valve process. The female genitalia are perhaps most similar to those of the neighbouring *C. ariquemes*, but the eighth abdominal sternite is largely membranous with only scattered punctate sclerotization and heavy transverse ribbing.

Distribution. *Charis cacaulandia* is currently only known from a small area extending between the towns of Cacaulândia and Jaru in southwestern Amazonian Brazil (Rondônia) (see Fig. 17).

Charis manicore **Harvey & Hall, sp.n.** (Figs 3K,L; 11C; 15B; 17)

Male. Does not differ externally from *C. negro*. *Genitalia* (Fig. 11C): Differ from *C. negro* in the following ways. Aedeagus substantially shorter and straighter, vesica with no cornuti; pedicel joins aedeagus at a point one-quarter distance from base to tip, narrower in ventral view, distal portion slightly longer and bifurcate at tip, contains very fine acanthae on dorsal surface; valvae, especially base of upper process, extend substantially anterior to vinculum, lower valve process narrower and slightly longer, upper valve process separated further from lower process and substantially longer, narrower and slightly down-turned at tip.

Female. Does not differ externally from *C. negro*. *Genitalia* (Fig. 15B): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, elongate posterior portion of ductus bursae sclerotized, ostium bursae positioned centrally at anterior margin of eighth sternite, eighth sternite well sclerotized along anterior margin either side of ostium with remainder weakly sclerotized, seventh sternite very long and sclerotized.

Material examined. *Holotype*, ♂, BRAZIL: Amazonas, Rio Aripuanã, Beneficiente, March 1955 (USNM) (# 1989-79). *Allotype*, ♀, BRAZIL: Amazonas, Rio Madeira, Manicoré, 18 August 1976 (C. Callaghan) (CJC) (# 2000-439). *Paratypes*, BRAZIL: Amazonas, same locality data as allotype, 1♂, 14 August 1976 (C. Callaghan) (AME) (# 1996-75), 1♂, 1♀, 16 August 1976 (C. Callaghan) (CJC), 2♂, 17 August 1976 (C. Callaghan) (CJC), 1♂, 18 August 1976 (C. Callaghan) (CJC) (♂ # 2000-428), 1♂, Jun–July 1921 (A. Fassl) (MNHN) (# 2000-291).

Etymology. This species is named after the largest town in its known area of distribution, Manicoré.

Diagnosis. The male genitalia of *C. manicore* are not particularly similar to those of any other species, particularly those with the inner silver submarginal line on the ventral forewing reduced to an apical fleck. The pedicel is markedly bifurcate, the valvae extend considerably anterior to the vinculum, both valve processes are parallel and the upper valve process is very long, straight and slightly down-turned at its tip. The female genitalia are equally distinctive, with a long and straight sclerotized posterior portion to the ductus bursae, a largely membranous eighth sternite with sclerotization extending in narrow bands either side of the anteriorly positioned ostium bursae, and a long seventh sternite.

Distribution. *Charis manicore* is known only from a small area encompassing the lower central Rio Madeira and one of its tributaries, the Rio Aripuanã in central Amazonian Brazil (Amazonas) (see Fig. 17).

Charis ipiranga **Harvey & Hall, sp.n.** (Figs 3M,N; 11D; 15C; 17)

Male. Differs externally from *C. cleonus* in the following respects: inner submarginal silver line on both ventral wings thinner (sometimes absent on hindwing) and on forewing tapers towards tornus; blue iridescence on ventral surface more prominent. *Genitalia* (Fig. 11D): Differ from *negro* in the following ways. Aedeagus pronouncedly bowed and slightly broader at middle, tip more pointed and curved slightly upwards, vesica with no cornuti; pedicel shorter and broader in lateral view, narrower and more gradually tapering in ventral view, distal portion produced into a small slightly bifurcate tip; valvae extend anterior to vinculum, lower valve process slightly narrower at base, upper valve process separated further from lower process and slightly longer and considerably narrower.

Female. Differs externally from *C. cleonus* in the following respects: inner submarginal silver line on both ventral wings thinner (often absent on hindwing) and on forewing tapers towards tornus. *Genitalia* (Fig. 15C): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae lightly sclerotized with small section ending in a blind sac, ostium bursae positioned centrally at anterior margin of eighth sternite within an invaginated pouch, eighth sternite weakly and unevenly sclerotized and heavily ribbed with two very shallow indentations, seventh sternite sclerotized.

Material examined. *Holotype*, ♂, BRAZIL: Amazonas, 26 km from Manaus on AM-010, Reserva Ducke, 2°55′S 59°59′W, 14 December 1993 (J. Sullivan & W. Hutchings) (to be deposited in the UFPR) (# 2000-293). *Allotype*, ♀, BRAZIL: Amazonas, same locality data as holotype, 13 December 1993 (J. Sullivan & W. Hutchings) (USNM) (# 2000-353). *Paratypes*, VENEZUELA: 2♂, Bolívar, Auyán Tepui, Río Carrao, 1500 ft, March 1993 (S. Fratello) (AME) (# 2000-187, 358). BRAZIL: Amazonas, 2♂, Tapurucuara, Rio Negro, 30 November 1962 (C. Lindemann) (ZSM) (# 2001-15), 72 km from Manaus on BR-174, Fazenda Dimona, 2°19′S 60°05′W (W. Hutchings & J. Sullivan) (JBS), 2♂, 8 December 1993 (# 1998-4; 1999-141), 1♂, 2♀, 9 December 1993, 2♂, 10 December 1993, same locality data as holotype (J. Sullivan & W. Hutchings) (JBS), 1♂, 2♀, 13 December 1993 (♂# 1999-142), Manaus, Vivenda Verde (W. Hutchings & J. Sullivan) (JBS), 7♂, 5♀, 5 December 1993 (♂ # 1999-143 and # 2000-19), 2♂, 6 December 1993, 1♂, 1♀, km 2.5 Manaus-Manacapuru Road, 25 November 1973 (C. Callaghan) (AME) (♂ # 1996-74 and # 2000-10), 1♂, km 3.8 Manaus-Manacapuru Road, 12 February 1972 (W. Benson) (# 2000-438), 2♂, Ipiranga (*ex* coll. LeMoult) (AME) (# 1996-70,82).

Etymology. This species is named after Ipiranga, the historical locality from which, to our knowledge, it was first collected.

Diagnosis. *Charis ipiranga* is very similar to but can be externally distinguished from *C. matic* and *C. ma* and the neighbouring *C. cleonus*. The ventral blue iridescence is brighter, particularly compared to *C. cleonus*, and the ventral submarginal silver lines are typically thinner and positioned closer together. The inner hindwing line is sometimes absent. The male genitalia are rather distinctive, with a strongly arched aedeagus, widely separated upper and lower valve processes, and a relatively small, broadly curving pedicel that is only weakly bifurcate at its tip. The female genitalia have two shallow indentations in the eighth abdominal sternite that are somewhat similar to those in *C. tefe*.

Distribution. *Charis ipiranga* is known to range from eastern Venezuela (Bolívar) to the north bank of the middle Rio Negro south to the Manaus area in central Amazonian Brazil (Amazonas) (see Fig. 17). Although the historical locality of Ipiranga is given by Brown (1979) as being at the mouth of the Rio Madeira on the south bank of the Rio Amazonas, it seems more likely that it is actually situated on the north bank (K. Brown, personal communication).

Charis cuiaba **Harvey & Hall, sp.n.** (Figs 3O,P; 12A; 15D; 17)

Male. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 12A): Differ from *C. negro* in the following ways. Aedeagus slightly straighter, tip more pointed, vesica with no cornuti; pedicel slightly narrower in ventral view, distal portion longer and bifurcate at tip, contains very fine acanthae on dorsal surface; valvae extend anterior to vinculum, upper valve process substantially more elongate, narrow, serrate along medial portion of dorsal margin and up-turned at tip.

Female. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 15D): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized with small bifid section ending in a blind sac, ostium bursae positioned centrally at anterior margin of eighth sternite, eighth sternite sclerotized only in small ovoid anterior section, remainder largely unsclerotized scattered with weak punctate sclerotization, medially completely unsclerotized, seventh and sixth sternites sclerotized.

Material examined. *Holotype*, ♂, BRAZIL: Mato Grosso, 90 km E Cuiabá, São Vicente, 600 m, 28 May 1969 (S. Nicolay) (USNM) (# 1998-13). *Allotype*, ♀, BRAZIL: Pará, km 1118 Cuiabá-Santarém Highway, 18 July 1978 (S. Nicolay) (USNM) (# 2000-23). *Paratypes*, BRAZIL: Amazonas, Maués, 1♂, November 1998 (*ex* coll. M. Simon) (AME) (# 2000-188), 1♀, June 1997 (*ex* coll. M. Simon) (AME) (# 2000-202); Pará, 1♂, Rio Tapajós, Itaituba, December 1961 (USNM) (# 2000–436), km 1347 Cuiabá-Santarém highway, 21 July 1978, 1♀ (S. Nicolay) (USNM) (# 2000-15), 1♀ (C. Callaghan) (CJC), 1♂, km 1288 Cuiabá-Santarém highway, Rio Ari, 19 July 1978 (C. Callaghan) (AME) (# 2000-191), 2♂, Rio Tapajós, Jun–July 1920 (A. Fassl) (MNHN) (# 2000-16), 1♂, km 500 Cuiabá-Santarém Highway, Sinop, 13 July 1978 (C. Callaghan) (CJC) (# 2000-435).

Etymology. This species is named after its type locality, Cuiabá.

Diagnosis. The male genitalia of *C. cuiaba* are most similar to those of the externally different *C. cacaulandia*, and are distinguished in the latter account. The female genitalia are readily separated from those of all other species by the vestigial sclerotization of the eighth abdominal sternite around the ostium bursae and the bifurcate tip to the posterior sclerotized blind sac of the ductus bursae. A single male in the SMF from Borba on the lower Rio Madeira possesses male genitalia with a triangular aedeagal tip that is atypical of the species and the specimen is therefore not included in the type series.

Distribution. *Charis cuiaba* occurs along the length of the upper Rio Tapajós from the vicinity of Cuiabá (Mato Grosso) to the Maués region and Borba on the lower Rio Madeira in central-eastern Brazil (Amazonas, Pará) (see *Distribution* section for *C. maues*) (see Fig. 17).

Charis maues **Harvey & Hall, sp.n.** (Figs 3Q,R; 12B; 17)

Male. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 12B): Differ from *C. negro* in the following ways. Vinculum not significantly bowed in dorsal half; aedeagus slightly straighter with uneven triangular projection at tip pointing right, down and slightly anteriorly, vesica with no cornuti; distal portion of pedicel tapers more abruptly in lateral view, longer and bifurcate at tip, contains very fine acanthae on dorsal surface; valvae extend slightly anterior to vinculum, lower valve process slightly shorter and downturned, upper valve process longer, narrower, serrate along medial portion of dorsal margin, and outwardly turned at tip, large downwardly pointed, triangular process inside upper valve processes.

Female. Unknown.

Material examined. *Holotype*, ♂, BRAZIL: Amazonas, Maués, June 1997 (*ex* coll. M. Simon) (to be deposited in the UFPR) (# 2000-199). *Paratypes*, BRAZIL: Amazonas, Maués (*ex* coll. M. Simon) (AME), 1♂, June 1997 (# 2000-200), 4♂, March 1999 (# 2001-19,23,24,27).

Etymology. This species is named after its type locality, Maués.

Diagnosis. The possession of an additional triangular process inside the upper valve processes of the male genitalia clearly places *C. maues* as the sister species of the neighbouring *C. tapajos*. Its male genitalia differ by having a slightly downwardly instead of upwardly directed upper valve process, which is turned outwards at its tip, with a downwardly directed inner triangular process that is smooth along its dorsal margin, a slightly shorter lower valve process, a slightly shorter distal portion to the pedicel, and a prominent triangular process at the tip of the aedeagus.

Distribution. *Charis maues* is currently only known from the vicinity of Maués on the southern bank of the central-eastern Brazilian Amazon (Amazonas) (see Fig. 17). Specimens of three species, *C. maues*, *C. cuiaba* and *C. tapajos*, bear labels stating they were collected at Maués, but these were collected by a commercial dealer who is known to have travelled and collected widely in this region (M. Simon, personal communication). These specimens also bear a variety of dates. This region is topographically and biogeographically highly complex, and it seems likely that these three species were collected in nearby but different localities. The species of the marmoset genus *Callithrix* exhibit a similar pattern of distributions along the Rio Madeira and Rio Tapajós as *cleonus* group species, and so the suggestion by Mittermeier *et al.* (1992) that the range of *Callithrix maues* is bounded by the Rio Maués and the Rio Abacaxis, to the west of the town of Maués, may apply to *maues*. *Charis tapajos* probably occurs to the east of the lower Rio Maués, with *C. cuiaba* extending as far north as the upper Rio Maués or Rio Abacaxis.

Charis tapajos **Harvey & Hall, sp.n.** (Figs 4A,B; 12C; 15E; 17)

Male. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 12C): Differ from *C. negro* in the following ways. Aedeagus slightly straighter with pointed tip, vesica with no cornuti; distal portion of pedicel broader in lateral view, longer and bifurcate at tip, contains very fine acanthae on dorsal surface; valvae extend slightly anterior to vinculum, lower valve process longer and narrower, especially towards base, upper valve process longer, narrower, serrate along basal portion of dorsal margin, and up-turned at tip, large triangular process with serrate dorsal margin inside upper valve processes.

Female. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 15E): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized with small section ending in a blind sac, ostium bursae positioned slightly to right of centre at anterior margin of eighth sternite and directed slightly to left in ventral view, eighth sternite ovoid, unevenly sclerotized and heavily ribbed, seventh and sixth sternites sclerotized.

Material examined. *Holotype*, ♂, BRAZIL: Pará, Rio Tapajós, Aveiro (MNHN) (# 2000-22). *Allotype*, ♀, BRAZIL: Pará, Óbidos, Oct–November 1904 (M. de Mathan) (BMNH) (# 2000-80). *Paratypes*, BRAZIL: Amazonas, Maués (*ex* coll. M. Simon) (AME), 1♂, 1♀, November 1998 (♂ # 2000-198 and # 2000-201), 1♂, June 1997 (# 2000-189), 5♂, March 1999 (# 2001-20-22,25,26), 1♀ (A. Moss) (BMNH) (# 2000-79), Pará, same locality data as allotype, 1♂, Oct–November 1904 (M. de Mathan) (BMNH), 2♂, August 1928 (Wucherpfennig) (MNHN) (# 2000-3), 3♂, Rio Tapajós, Itaituba to Óbidos, Jan–April 1906 (W. Hoffmanns) (BMNH) (# 1999-131, 132), 2♂, no locality data (coll. Neumogen) (USNM) (# 2000-43,44).

Etymology. This species is named after the Rio Tapajós, along whose lower course the species predominantly occurs.

Diagnosis. The possession of an additional triangular process inside the upper valve process of the male genitalia places *C. tapajos* as the sister species of *C. maues*. Its male genitalia are distinguished in the latter account. Like those of the closely related *C. cuiaba* and *C. santarem*, the female genitalia of *C. tapajos* have the last three sternites sclerotized, but the eighth sternite is ovoid with weak scattered sclerotization and the sclerotized posterior blind sac of the ductus bursae is short and curves abruptly to the left.

Distribution. *Charis tapajos* is confined to the lower Rio Tapajós in eastern Amazonian Brazil (Pará) (see *Distribution* section for *C. maues*) (see Fig. 17). We suggest that historically labelled Óbidos specimens may have originated from the south bank of the Rio Amazonas.

Charis santarem **Harvey & Hall, sp.n.** (Figs 4C,D; 12D; 15F; 17)

Male. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 12D): Differ from *C. negro* in the following ways. Aedeagus pointed at tip, vesica with a very small weakly sclerotized triangular cornutus; distal portion of pedicel slightly longer and bifurcate at tip, contains very fine acanthae on dorsal surface; valvae extend anterior to vinculum, lower valve process shorter and triangular, upper valve process longer, narrower, and downwardly curved, base of upper process developed into a large raised, ventrally recurved and medially grooved sclerotized structure with large posteriorly directed spines along both inner margins, spines becoming smaller anteriorly.

Female. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 15F): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized with small section ending in a blind sac, ostium bursae positioned slightly to left of centre at anteriorly extended anterior margin of eighth sternite and directed slightly to left in ventral view, opening of ostium large, eighth sternite narrow, deeply indented, and unevenly sclerotized with heavily ribbed posterior portion, 'U'-shaped seventh sternite sclerotized, sixth sternite sclerotized medially and posteriorly.

Material examined. *Holotype*, ♂, BRAZIL: Pará, Santarém, October 1884 (BMNH) (# 1999-130). *Allotype*, ♀, Pará, same locality data as holotype, October 1884 (BMNH) (# 2000-159). *Paratypes*, BRAZIL: Pará, 1♂, Rio Trombetas, Rio Cuminá, 20 January 1973 (C. Callaghan) (CJC) (# 2000-433), 1♂, Óbidos, August 1928 (Wucherpfennig) (MNHN) (# 2000-290); same locality data as holotype, 4♂ (H. Smith) (BMNH), 1♂ 1947 (H. Smith) (BMNH), 1♀ (A. Wallace) (BMNH), 2♂, October 1884 (BMNH), 1♂, November 1884 (BMNH), 5♂, Mar–April 1920 (A. Fassl) (MNHN) (# 2000-292), 1♂, December 1920 (A. Fassl) (MNHN), 1♂, May 1919 (S. Klages) (CMNH) (# 1989-99), 1♂, July 1919 (S. Klages) (CMNH) (# 1998-19), 1♂: Santarém, Diamantina, 23 November 1973 (C. Callaghan) (CJC) (# 2000-434), 1♂, 1♀, Rio Tapajós (H. Bates) (BMNH) (♀ # 2000-81).

Etymology. This species is named after its type locality, Santarém.

Diagnosis. The possession of a pouch of spines at the anterior dorsal margin of the upper male genital valve processes places *C. santarem* in a monophyletic group with *C. breves*, *C. caryatis* and *C. brasilia*. The pouch in *C. santarem* is more broadly rounded and strongly grooved in a head-on view with larger and more externally positioned spines, the upper valve process is slightly longer and downwardly curved and the ventral tip of the pedicel is smooth without any nodules. The female genitalia have a deeply grooved eighth abdominal sternite set within a weakly sclerotized pouch, and a strongly 'U'-shaped seventh sternite. *Charis santarem* is the only known female in this derived group of species to have a sclerotized sixth sternite (the female of *C. breves* is unknown).

Distribution. *Charis santarem* is currently only known from the vicinities of Santarém and Óbidos on the lower Rio Amazonas in eastern Amazonian Brazil (Pará) (see Fig. 17). Modern locality data clearly indicate that this species occurs on both banks of the very broad lower Rio Amazonas, suggesting either that the island-studded lower river course has not been a barrier to dispersal (as Ayres & Clutton-Brock, 1992, have suggested for primates), or that historical fluctuations in river course direction have played an important part in the current distribution of *C. santarem*.

Charis breves **Harvey & Hall, sp.n.** (Figs 4E,F; 13A; 17)

Male. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 13A): Differ from *C. negro* in the following ways. Aedeagus straighter and pointed at tip, vesica with no cornuti; distal portion of pedicel slightly longer and trifucate at tip, contains very fine acanthae on dorsal surface; valvae extend anterior to vinculum, lower valve process substantially shorter and triangular, upper valve process longer, narrower, downwardly curved and serrate along dorsal margin, base of upper process developed into a large anteriorly directed hollow sclerotized structure containing small posteriorly directed spines lining inner edges and opening, spines largest posteriorly.

Female. Unknown.

Type material. Holotype, ♂, BRAZIL: Pará, Rio do Pará, Breves, 1 March 1896 (E. Austen) (BMNH) (# 1999-134). *Paratypes*, BRAZIL: Pará, 1♂, Rio Amazonas, Gurupa, 23 January 1896 (E. Austen) (BMNH) (# 1999-133).

Etymology. This species is named after its type locality, Breves.

Diagnosis. The male genitalia of *C. breves* are most similar to those of the neighbouring *C. caryatis*, but the upper valve process is arched with a serrate dorsal margin, the pouch of spines is considerably narrower and forms a different shape, and the ventral tip of the pedicel is narrower and possesses a single prominent triangular projection instead of several small nodules.

Distribution. *Charis breves* is restricted to a small area at the mouth of the lower Rio Amazonas along the western edge of the Ilha de Marajó (no specimens are known from the eastern portion of the island) in eastern Amazonian Brazil (Pará) (see Fig. 17).

Charis caryatis **Hewitson, 1866** (Figs 4G,H; 13B; 15G; 17)

Charis caryatis Hewitson, 1866: 114, Pl. 57, Fig. 6. Type locality: Pará, eastern Brazil. Lectotype ♂ BMNH (designated).

Diagnosis. Typical forewing length: male 12.5 mm, female 11.5 mm. Male *C. caryatis* belongs to a terminal clade of lower Amazonian species, including *C. santarem*, *C. breves* and *C. brasilia*, from which it can not be distinguished externally. The possession of several ventral nodules towards the tip of the genital pedicel and a small lateral spine at the right tip of the aedeagus indicate that it is most closely related to *C. brasilia*. *Charis caryatis* differs from *C. brasilia* as outlined in that species' account. The female genitalia of *C. caryatis* have a large membranous eighth abdominal sternite with a simple round ostium bursae at its anterior margin.

Taxonomy. In order to definitively confine the *C. caryatis* genital phenotype to a single specimen, we designate the only labelled syntype (and possibly the only syntype since no other specimens from the type locality bear a Hewitson label) of *C. caryatis* in the BMNH as a lectotype. It bears the following label data: 'Hewitson Coll./79-69./ Charis/ caryatis. 1/Para'.

Distribution. *Charis caryatis* has traditionally been thought to range throughout the lower Amazon southwards to southeastern Brazil and Paraguay. However, the morphological phenotype represented by the type of *C. caryatis* is restricted to a smaller area that extends from the Belém region at the mouth of the Rio Amazonas in Pará State, from where most specimens are recorded, southeast along the coast through Maranhão to Pernambuco State (see Fig. 17).

Material examined. BRAZIL: Pará, Pará, 35♂, 17♀ (BMNH) (♂ # 2000-77), 1♂ (MNHN), 2♂ (AME) (# 1998-17); Benevides, 21♂, 13♀ (CMNH) (♂ # 1989-100, 1998-18 and # 2000-34,35); Igarapé-Açu, 1♂ (BMNH) (# 2000-78); Bragança, 1♂ (BMNH); Maranhão, Montes Aureos, 1♂, 1♀ (BMNH); no specific locality, 1♂ (BMNH); Pernambuco, no specific locality, 1♂ (BMNH) (# 1999-135).

Charis brasilia **Harvey & Hall, sp.n.** (Figs 4I,J; 13C; 15H; 17)

Male. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 13C): Differ from *C. negro* in the following ways. Tip of aedeagus pointed with small spine on right side, vesica with no cornuti; distal portion of pedicel slightly longer and bifurcate at tip with several small ventral nodules near tip, contains very fine acanthae on dorsal surface; valvae extend anterior to vinculum, lower valve process substantially shorter and triangular, upper valve process longer, narrower and finely pointed at tip, base of upper process developed into a large raised, hollow, ventrally recurved sclerotized structure containing small posteriorly directed spines lining inner edges and opening (varies slightly in shape intraspecifically but always positioned vertically).

Female. Does not differ externally from *C. caryatis*. *Genitalia* (Fig. 15H): Corpus bursae elongate, signa small and squat spinelike sclerotized invaginations, small posterior portion of ductus bursae sclerotized, ostium bursae positioned approximately centrally at anteriorly extended anterior margin of eighth sternite and directed to left in ventral view, opening of ostium large and round, posterior portion of eighth sternite ribbed with only scattered weak sclerotization, medial portion invaginated to form a pouch with ostium set in heavily sclerotized anterior portion, 'U'-shaped seventh sternite sclerotized.

Material examined. Holotype, ♂, BRAZIL: Distrito Federal, Planaltina, 1000 m, 6–25 October 1985 (S. Miller) (to be deposited in the UFPR) (# 1989-70). *Allotype*, ♀, BRAZIL: Distrito Federal, Parque do Gama, 950 m, 14 May 1969 (S. Nicolay) (USNM) (# 2000-29). *Paratypes*, BRAZIL: Pará, 3♂, *c*. 60 km S Altamira, Rio Xingu camp, 52°22′ W 3°39′ S, 8–12 October 1986 (P. Spangler & O. Flint) (USNM) (# 1998-11; 2000-1); Mato Grosso do Sul, 1♂, 'Nivac' [= Nioaque] (E. Jones) (BMNH) (# 1999-137); Distrito Federal, same locality data as allotype, 2♂, 14 May 1969 (S. Nicolay) (USNM) (♂ # 1998-15), 1♂, 17 May 1969 (S. Nicolay) (USNM), Sobradinho (K. Brown) (USNM), 1♂, 22 February 1966 (# 2000-298), 1♀, 24 February 1966 (# 2000–354), 2♂, 1♀, Sobradinho (AME), 1♂, same locality data as holotype, 6–25 October 1985 (S. Miller) (USNM) (# 1998-14), Goiás, 2♂, 1♀, Goiânia, 30 April 1973 (C. Callaghan) (CJC), 3♂, 40 km W Goiás, 29 April 1973 (C. Callaghan) (AME) (# 4362 & 6237), 3♂, Vianópolis, March 1930 (A. Seitz) (SMF); Minas Gerais, 1♂, 8 km from Belo Horizonte-Brazilia Highway on Road to Curvelo, Cabaceira Corrego Leitão, 14 April 1973 (C. Callaghan) (AME), 4♂, km 500 Belo Horizonte-Brazilia Highway, 15–16 April 1973 (C. Callaghan) (AME) (# 1998-16), 1♂, 1♀, km 510 Belo Horizonte-Brazilia Highway, 15 April 1973 (C. Callaghan) (CJC); São Paulo, 1♀, 10–20 km W Teodoro Sampãio, 22°31′ S 52°12′ W, 300 m, 17 March 1991 (R. Robbins) (USNM) (# 2000-60), 1♂, 2♀, São Paulo, 2300 ft (E. Jones) (BMNH) (♂ # 1999-138), 2♂, Loreto, September 1926 (E. May) (BMNH) (# 1999-129); Paraná, 2♂, Castro, 950 m (E. Jones) (BMNH) (# 1999-136). PARAGUAY: Central, 1♀, Patiño Cué, Feb (S. Montfort) (BMNH); Paraguarí, 1♂, Sapucay (W. Foster) (USNM) (# 1998-12), Guairá, 4♂, Villarica, Feb (MNHN) (# 2000-17); Caaguazú, 1♂, San José (R. Perrens) (BMNH) (# 1999-140); unknown province, 6♂, 2♀, Molinas, 26 October 1925 (F. Schade) (MNHN) (♂ # 2000-18), 2♂, 2♀, Molinasque, 9 November 1925 (F. Schade) (MNHN), Santa Barbara (MNHN), 1♂, November 1928; 1♂, 12 October 1926 (F. Schade), 2♂, southern Paraguay (R. Perrens) (BMNH) (# 1999-139), 1♀, Paraguay, 25 November 1924 (F. Schade) (BMNH).

Etymology. This species is named for the capital city of Brazil, Brasilia, which lies at the centre of its range.

Diagnosis. By possessing male genitalia with several ventral nodules towards the ventral tip of the pedicel, a small lateral spine at the right tip of the aedeagus, and a deeply invaginated pouch lined with fine spines at the anterior margin of the upper valve processes, *C. brasilia* can be placed as the sister species of *C. caryatis*. The male genitalia differ by having a vertically instead of anteriorly directed pouch of spines that is more similar to that of *C. santarem* (the pouch is more deeply invaginated and the spines finer than in that species), a more rounded lower valve process, and a deeper ventral indentation at the tip of the aedeagus with a larger spine. The female genitalia are very distinctive, with the eighth abdominal sternite medially folded inwards and the large aperture of the ostium bursae positioned on a well sclerotized anterior fold, and the seventh sternite 'U'-shaped.

Biology. Label data indicate that males were caught in cerrado and woodland habitats, on a hilltop, and in a malaise trap.

Distribution. *Charis brasilia* has the broadest range of any species in the *cleonus* group. It is widespread throughout eastern Paraguay (Central, Paraguarí, Guairá, Caaguazú) and southern Brazil (Paraná, Mato Grosso do Sul, São Paulo, Minas Gerais, Goiás, Distrito Federal), and is known to extend as far north as the central Rio Xingu in Pará State at the edge of the Amazon basin (see Fig. 17). Despite being a relatively well collected region, the coastal wet forest of southeastern Brazil is not known to harbour any *cleonus* group species, suggesting that *C. brasilia* is probably a southern Amazonian species in origin and not a southeastern Brazilian one. The following additional localities are listed by Brown & Mielke (1967) (as *C. caryatis*): BRAZIL: Distrito Federal, Chapada de Contagem; Minas Gerais, km 222 and 485 Belo Horizonte-Brazilia Highway, Paraopeba; and by Hayward (1973); ARGENTINA: Misiones, no specific locality. Biezanko *et al*. (1979) report '*Charis caryatis*' from Guarani in the southeastern Brazilian state of Rio Grande do Sul, and this record probably represents *C. brasilia*, but needs confirmation.

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Appendix 1. Characters used in the phylogenetic analysis.

Wing pattern

1. *Inner silver submarginal line on VFW*: (0) separated from outer silver line; (1) merged with outer silver line. See Figs 2–4. CI = 1; RI = 1.
2. *Inner silver submarginal line on VFW*: (0) complete; (1) reduced to a small apical fleck. See Figs 2–4. CI = 0.5; RI = 0.88.

   The taxon *rocana* completely lacks an inner submarginal silver line and is coded with a '?'.
3. *Inner silver submarginal line on VHW*: (0) present; (1) absent. See Figs 2–4. CI = 0.5; RI = 0.8.
4. *Forewing fringe*: (0) brown with white elements in cells Cu2, M3, and R4 + 5; (1) brown with solid white from anal margin to vein Cu1 and 4 white flecks in subsequent 4 cells; (2) brown with solid white from anal margin to vein M3 and 3 white flecks in subsequent 3 cells. See Figs 2–4. CI = 0.67; RI = 0.86.

Male genitalia

5. *Ventral portion of vinculum in ventral view*: (0) straight or with shallow posterior indentation (e.g. Fig. 8A); (1) with deeply notched indentation (e.g. Fig. 8C). CI = 1; RI = 1.
6. *Ventral swelling at anterior base of aedeagus*: (0) present (e.g. Fig. 8C); (1) absent (e.g. Fig. 9B). CI = 1; RI = 1.
7. *Pedicel joins aedeagus*: (0) above anterior base (e.g. Fig. 8A); (1) at very base (e.g. Fig. 8D). CI = 1; RI = 1.
8. *Lateral spine near right tip of aedeagus*: (0) absent; (1) present (Fig. 13C). CI = 1; RI = 1.
9. *Ventral margin of aedeagal tip*: (0) straight; (1) indented (e.g. Fig. 13C). CI = 1; RI = 1.
10. *Aedeagus contains*: (0) single elongate cornutus (Fig. 8A); (1) cluster of several small spines (e.g. Fig. 9D); (2) a parallel row of short paired spines (Fig. 10B); (3) no cornuti. CI = 0.6; RI = 0.33.
11. *Distance from junction of pedicel base and distal portion to tip*: (0) less than two-thirds length of pedicel base (e.g. Fig. 9C); (1) at least two-thirds length of pedicel base (e.g. Fig. 10C). CI = 1; RI = 1.
12. *A raised 'vogelkop' at tip of pedicel*: (0) present (e.g. Fig. 8C); (1) absent (e.g. Fig. 9C). CI = 1; RI = 1.
13. *Spines on tip of pedicel*: (0) coarse (e.g. Fig. 8C); (1) fine (e.g. Fig. 10C). CI = 1; RI = 1.

    The taxon *rocana* lacks spines and is coded with a '?'.
14. *Dorsal spines on tip of pedicel*: (0) present (e.g. Fig. 8C); (1) absent. CI = 1; RI = 1.

    The taxon *rocana* lacks spines and is coded with a '?'.
15. *Ventral spines on tip of pedicel*: (0) absent; (1) present (e.g. Fig. 10C). CI = 1; RI = 1.

    The taxon *rocana* lacks spines and is coded with a '?'.
16. *Distal portion of pedicel*: (0) symmetrical (e.g. Fig. 10A); (1) asymmetrical (e.g. Fig. 10C). CI = 1; RI = 1.
17. *If distal portion of pedicel asymmetrical (16 : 1), it bends to*: (1) left (e.g. Fig. 10C); (2) right (Fig. 10B). CI = 1; RI = 1.
18. *If distal portion of pedicel asymmetrical and bent to left (17 : 1), bend is*: (1) very slight (Fig. 11A); (2) pronounced (e.g. Fig. 10C). CI = 1; RI = 1.
19. *Tip of pedicel*: (0) rounded (e.g. Fig. 11A); (1) bifurcate (e.g. Fig. 11C). CI = 0.5; RI = 0.9.
20. *Ventral medial tip of pedicel*: (0) smooth (e.g. Fig. 9C); (1) with one or more small projections (e.g. Fig. 13C). CI = 1; RI = 1.
21. *If ventral medial tip of pedicel with one or more smallprojections (20 : 1), it has*: (1) a single horn (Fig. 13A); (2) several nodules (e.g. Fig. 13C). CI = 1; RI = 1.
22. *Valvae extend*: (0) exclusively posterior to vinculum (e.g. Fig. 11A); (1) anterior as well as posterior to vinculum (e.g. Fig. 11D). CI = 1; RI = 1.
23. *Base of upper valve process*: (0) posterior to base of lower valve process (e.g. Fig. 11A); (1) anterior to base of lower valve process (e.g. Fig. 11C). CI = 0.5; RI = 0.83.
24. *Upper valve process*: (0) a small rounded protrusion (e.g. Fig. 9A); (1) an elongate pointed projection (e.g. Fig. 9C). CI = 1; RI = 1.
25. *Dorsal surface of upper valve processes*: (0) approximately smooth (e.g. Fig. 11C); (1) significantly serrate (e.g. Fig. 11B). CI = 0.33; RI = 0.5.
26. *Anterior portion of upper valve processes*: (0) smooth (e.g. Fig. 1C); (1) developed into a raised area of long spines (e.g. Fig. 12D). CI = 1; RI = 1.
27. *If anterior portion of upper valve processes developed into a raised area of long spines (26 : 1), these spines*: (1) coarse (Fig. 12D); (2) fine (e.g. Fig. 13B). CI = 1; RI = 1.

28. *If anterior portion of upper valve processes developed into a raised area of long spines (26 : 1), these spines*: (1) largely external (Fig. 12D); (2) largely contained within a medial invaginated pouch (e.g. Fig. 13B). CI = 1; RI = 1.
29. *A continuous sclerotized transtilla joining upper valve processes over aedeagus*: (0) present and broad (e.g. Fig. 9A); (1) reduced to narrow band or absent (e.g. Fig. 12C). CI = 1; RI = 1.
30. *A broadly triangular sclerotized process inside and slightly ventral to each upper valve process*: (0) absent; (1) present (e.g. Fig. 12C). CI = 1; RI = 1.
31. *Lower valve process*: (0) at least half length of upper process (e.g. Fig. 12C); (1) reduced to a small triangle less than half length of upper process (e.g. Fig. 12D). CI = 0.33; RI = 0.6.
32. *Upper and lower valve portions separated by*: (0) a narrow, elongate sclerotized rod (e.g. Fig. 9B); (1) a broad, short sclerotized region (e.g. Fig. 9D). CI = 0.5; RI = 0.75.

Female genitalia

33. *Heavy sclerotization on abdominal sternite 6*: (0) absent; (1) present (e.g. Fig. 14E). CI = 0.2; RI = 0.2.
34. *Eighth abdominal sternite predominantly*: (0) a smooth, strongly sclerotized plate (e.g. Fig. 14K); (1) a punctate, weakly sclerotized plate (e.g. Fig. 15G). CI = 1; RI = 1.
35. *Position of ostium bursae*: (0) left of centre (e.g. Fig. 14A); (1) right of centre (e.g. Fig. 14I); (2) central (e.g. Fig. 14H). CI = 0.67; RI = 0.5.
36. *Sclerotization at posterior end of ductus bursae*: (0) absent; (1) present (e.g. Fig. 14J). CI = 1; RI = 1.

Appendix 2. Data matrix for the phylogenetic analysis.

					5					10					15					20					25					30					35	
Charis argyrea	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	0	0	0	0	0	0	0	0
Charis major	0	0	0	2	1	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Charis matic	0	0	0	1	1	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Charis ma	0	0	0	1	1	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Charis cleonus	0	0	0	1	0	1	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0
Charis rocana	0	?	1	1	0	1	0	0	0	2	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1
Charis negro	0	1	1	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	2	1
Charis ariquemes	0	1	1	1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	2	1
Charis manu	0	1	1	1	0	1	0	0	0	3	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	1
Charis humaita	0	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	?	?	?	?
Charis iquitos	0	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	1	2	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	2	1
Charis tefe	0	1	1	1	0	1	0	0	0	3	1	1	1	0	1	1	1	2	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	2	1
Charis palcazu	0	1	1	1	0	1	0	0	0	3	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	?	?	?	?
Charis cacaulandia	0	1	1	1	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	1	0	0	1	0	1	2	1
Charis manicore	0	1	1	1	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	2	1
Charis ipiranga	0	0	0	1	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	2	1
Charis cuiaba	1	0	1	2	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	1	1	1	2	1
Charis maues	1	0	1	2	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	1	0	1	?	?	?	?
Charis tapajos	1	0	1	2	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	1	1	1	1	1	2	1
Charis santarem	1	0	1	2	0	1	0	0	0	3	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	1	0	1	1	1	1	2	1
Charis breves	1	0	1	2	0	1	0	0	1	3	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	1	0	1	1	?	?	?	?
Charis caryatis	1	0	1	2	0	1	0	1	1	3	0	1	1	0	0	0	0	0	1	1	2	1	1	1	0	1	2	2	1	0	1	1	0	1	2	1
Charis brasilia	1	0	1	2	0	1	0	1	1	3	0	1	1	0	0	0	0	0	1	1	2	1	1	1	0	1	2	2	1	0	1	1	0	1	2	1